Population ecology and conservation of hazel dormice

Submitted by Eleanor Ruth Scopes to the University of Exeter as a thesis for the
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Cover art by Emily Strong

Abstract

The current biodiversity crisis will continue to accelerate as anthropogenic pressures, especially climate change, increase. Single species conservation can aid the recovery of wider biodiversity by promoting the preservation of particular habitats, and landscape-scale changes to connectivity. Understanding species' population ecology and their response to environmental variation is vital for effective conservation.

In this thesis, I investigate the population ecology and habitat requirements of hazel dormice *Muscardinus avellanarius* in Britain, a flagship species for early successional woodland. I have used methods at different scales to assess patterns in dormouse status and translate my findings into conservation actions.

First, I conduct a literature review to investigate how hibernation, an obligate component of dormouse life history in Britain, interacts with threats and conservation actions. I find that hibernation biology conveys some protection against threats such as predation but also exposes hibernators to additional pressures. Hibernator responses to climate change are diverse but can enhance population decline. Some conservation actions have successfully targeted hibernation biology to promote species recovery.

Next, I investigate the habitat factors associated with the presence of hazel dormice in understudied hedge and scrub habitats. Dormice were more frequently present in hedges with a high abundance of honeysuckle and hazel, multiple intersections with other hedges and without an earthen bank, and in scrub without a bracken-dominated mid-story and where the local population of dormice is large. Dormice would benefit from landscape-scale hedge and scrub creation to promote connectivity.

I then update the dormouse population trend for Britain, using data from a citizen science monitoring scheme, the National Dormouse Monitoring Programme (NDMP). I show there has been a decline of 78% (95% confidence interval = 72–84%) over 27 years 1994–2020 and provide evidence that dormouse could be up-listed to Endangered on the next Red List assessment for British mammals. I also discuss the broader implications of Red Listing for chronically declining species.

I also use the NDMP to investigate the habitat and climate factors driving local colonisation and extinction in nest boxes. I account for the effects of preferential sampling, revealing how this changes our understanding of both the decline in dormouse occupancy and abundance, and the environmental drivers of occupancy changes. I find the area of woodland within 1km of the NDMP site, and the late winter (February, March) temperature range impact local extinction probability, with implications for habitat management and climate change.

I then consider population ecology on a finer scale, using an integrated population model to estimate recruitment and monthly survival for two dormouse populations, one in Lithuania and the other in Britain. I calculate the contribution of each vital rate to realised population growth, showing that juvenile recruitment has the biggest effects on growth at both sites, though the stage class with the biggest contribution differs. I investigate the correlations between climate variables and vital rates, demonstrating that climate variation has more impact on rates in Britain, at the edge of the dormouse range.

Finally, I discuss my findings in relation of hazel dormouse conservation, and broader context of citizen science and population ecology. This work identifies connectivity

and climate are important influences on dormouse status and suggests conservation actions to promote dormouse recovery in Britain. This highlights the importance of investigating multiple aspects of species' population ecology to gain an integrated understanding of variation in status and future management opportunities.

Contents

List of Figures

List of Tables

List of Tables

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Author's Declaration

Chapters 2, 3 and **4** have been published in journals as co-authored papers. **Chapters 5** and **6** have been written for publication as co-authored papers. **Chapters 2, 3, 4, 5** and **6** were developed with the aid of Robbie McDonald, Jon Bennie, Alice Broome and Kat Walsh.

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Chapter 1: Introduction

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Conservation in a biodiversity crisis

We are currently facing a biodiversity crisis amounting to a sixth mass extinction (Ceballos et al., 2020; Cowie et al., 2022), resulting not just from species loss but also declines in populations and ranges (Pacifici et al., 2020). With anthropogenic pressures set to persist or accelerate in the near future (Ceballos et al., 2020), this crisis is only likely to deteriorate further. In particular, the effects of climate change will intensify, with an estimated 15-37% of species becoming highly likely to go extinct under mid-range climate scenarios (Thomas et al., 2004). This highlights the vital need for conservation science, policy and action to reduce threats and halt or reverse population losses.

Conservation science has contributed to multiple successes. Several bird and mammal extinctions have been prevented since 1993, primarily through legislation, reintroductions and ex-situ conservation (Bolam et al., 2021). In some cases threats can be entirely removed, for example the eradication of invasive species which has greatly improved the conservation status of local native species (Simberloff et al., 2011). Our understanding of global threat status across taxa stems primarily from the International Union for Conservation of Nature (IUCN) Red List. This is a globally recognised method to quantify extinction risk, which has motivated substantial scientific effort to complete threat assessments (Betts et al., 2020). The Red List has also raised public awareness of the biodiversity crisis, increased access to funding and encouraged conservation actions (Betts et al., 2020). With regards to conservation successes, it is important that the narratives of these recovering species are celebrated and down-listing on the Red List brought into public awareness to motivate future conservation actions for other species (Roman et al., 2015).

Conservation successes tend to result from specific actions to remove targeted threats from individual species (Cowie et al., 2022). It has been argued that this form of single species conservation cannot address the biodiversity crisis, as we cannot have specialised actions for each of the many threatened species globally (Cowie et al., 2022). However, single species conservation can have broader benefits for their ecosystems. Individual species can act as 'keystones' by having disproportionately large effects on ecosystem function and structure, for example ecosystem engineers such as beavers *Castor fiber* which create wetland habitats (Dee et al., 2019). Species interactions, including predation and mutualism, can mean cascading species losses when one goes extinct (Gaston, 2010). Charismatic threatened species can also act as 'flagship' species to create momentum and raise funds for vital biodiversity conservation, providing they are carefully selected (McGowan et al., 2020). Furthermore, conserving most species, and greater abundances of all species, is more likely to preserve ecosystem functioning and services (Baker et al., 2019). Thus, single species conservation can still have its place in broader conservation policy and programmes.

Conservation on a local scale, where species may be regionally but not globally threatened, has been similarly criticised. Such actions can cause inefficient allocation of resources as richer countries invest more in their species, and it may be futile to preserve peripheral populations along range edges (Hunter and Hutchinson, 1994), especially the trailing edges of range shifts due to climate change. However, species can have local cultural value and so provide ecosystem services that need to be conserved at that level (Miller et al., 2006). National Red Lists are associated with positive conservation action (Gärdenfors et al., 2001), which may be inefficient overall but is likely to be more rapidly implemented as most conservation organisations function at this level (Hunter and Hutchinson, 1994). There are also benefits to preserving locally rare but globally common species, including the maintenance of genetic diversity and ecological roles, and preventing species from becoming globally threatened in the first place (Hunter and Hutchinson, 1994).

Population ecology and species monitoring

Population ecology is fundamental to conservation science as it explains how populations are regulated, intrinsically by demographic processes and extrinsically by environmental factors and biotic interactions (Sibly and Hone, 2002). Understanding these processes can indicate threats to population persistence through, for example, a mechanistic understanding of the causes of high individual mortality rates (Sibly and Hone, 2002). For example, higher rainfall in the breeding season of meerkats *Suricata suricatta* increases the body mass and fecundity of multiple age classes, which has implications for population extinction risk under climate change (Paniw et al., 2019). Population ecology theory underpins the small population and declining population paradigms which are experienced by threatened species (Caughley, 1994). The latter concerns understanding how external processes drive populations to decline, whilst the former describes how small populations face additional threats, such as inbreeding depression and demographic stochasticity, which can accelerate extinction risk (Caughley, 1994). These paradigms underlie the criteria of the IUCN Red List (Mace et al., 2008) as well as conservation science more broadly. Population ecology can also lead to practical applications, such as determining management programmes to halt declines by projecting the expected outcomes (Schaub and Abadi, 2011), or highlighting the most resilient populations to prioritise for action (Donaldson et al., 2019).

Comparing multiple species' population ecology can reveal patterns in species responses to change, which can aid generalising conservation and management strategies to species that have yet to be studied. Across birds, the population growth rate of long-lived species which mature late and have small clutch sizes tends to be most sensitive to adult survival (Sæther and Bakke, 2000). Conservation of birds with similar life histories may then focus on reducing threats to adults. However, species with similar life histories do not always respond to change in the same way. For example, hibernation is a life history strategy for enduring adverse environmental conditions, often from seasonal changes in climate and food availability (Geiser, 2013). Some evidence suggests that hibernators are responding to climate change in different ways, such as emerging from hibernation earlier or later, even within the same species (Wells et al., 2022; Findlay-Robinson et al., 2023). The possibility of detrimental responses suggests multiple hibernator species could be threatened by climate change, despite evidence that hibernation broadly reduces extinction risk in mammals (Liow et al., 2008, 2009). Studies of population ecology are therefore important for understanding when generalisation is and is not possible, which has implications for conservation.

For population ecological analyses, there is a need for species monitoring data including occupancy or abundance, and individual-level data on survival and reproduction. Species-level data are more accessible through observational surveys, whilst individual data frequently require capture-mark-recapture (CMR) methods to identify and observe individuals (Romairone et al., 2018). However, the additional effort of CMR techniques is rewarded with information-rich data. Though more data are universally welcomed in science, long term and spatially extensive data are of particular value in population ecology (Reinke et al., 2019). Individual population dynamics vary spatially due to local environmental differences, which must be accounted for when considering overall trends (White, 2018), and are of key importance in metapopulation studies of overall persistence (Donaldson et al., 2019). Long term data is needed to detect declines due to inter-annual variability, with, on average, 15.9 years of data required to detect a decline in vertebrate species (White, 2018). Short time periods for assessing population trends, coupled with observation error and variation from ecological processes can also lead to both incorrect determination of declines, and perhaps more troublingly, incorrect determination of stability when a population is in fact declining (Connors et al., 2014).

The need for long term data is particularly exacerbated by the biodiversity crisis and anthropogenic threats. Most population monitoring started in the 20th or 21st Century, but at this point, populations had already been greatly reduced by accelerating pressures in the 19th Century (Mihoub et al., 2017). This means the baseline against which the population decline is measured can affect our understanding of declines; for example, baselines set in 1850 revealed significantly greater declines in North American mammals than those set in 1970, which suggested some populations had increased (Collins et al., 2020). Although recent increases in abundances are positive for conservation, long term data is required to understand species abundance and range when minimal anthropogenic pressures occurred. However, of long term monitoring schemes ($>$10 years of data) studied only 15% had data for $>$100 years and over half did not have continuous data (Bonebrake et al., 2010). Conservation science is therefore reliant on making the most of monitoring data which started when anthropogenic threats were already in place. Though we cannot create long term data from the past, this emphasises the need to support and maintain current monitoring schemes for future robust analysis.

Monitoring programmes and citizen science

Monitoring programmes provide data on species abundance and distribution, and occasionally, individual life histories. They can also lead to direct conservation action beyond solely identifying trends (Danielsen et al., 2005). There are estimated to be 3,300 - 15,000 monitoring programmes globally, many with annual data collection, which collect data on a broad range of taxa, though with a bias towards birds and mammals (Moussy et al., 2022). The duration and maintenance of schemes differs with national income, such that high income countries have longer running schemes that are more likely to be funded by the government than NGOs (Moussy et al., 2022). Of the 1,168 schemes in the analysis, 37% were partly or wholly completed by volunteers, and these schemes tended to have greater sample sizes and cover more species than those completed by professionals alone (Moussy et al., 2022). This highlights the value of volunteers to species monitoring and so conservation science.

The term “citizen science” can be used broadly to cover volunteer contributions to species monitoring programmes, as it can be defined as ”the practice of engaging the public with a scientific project” (McKinley et al., 2017). Citizen scientists can directly collect data, and/or can aid in processing the vast amounts of data collected through automated recording devices such as camera traps (Hsing et al., 2018). Citizen science has direct benefits for conservation science, with the estimated 1.3 million volunteers involved in projects globally contributing an estimated $2.5 billion annually (Theobald et al., 2015). Citizen science also tends to be broader in both geographic and temporal scale than professional programmes (Theobald et al., 2015; McKinley et al., 2017). More indirectly, citizen science can also have benefits for conservation by increasing public scientific knowledge and encouraging public action (McKinley et al., 2017). The contributions of citizen science are only likely to increase as new technologies for effective biodiversity monitoring, such as acoustic recording, become cheaper and easier to use (Stephenson, 2020), providing data can be made readily available (Joppa et al., 2016).

Issues with monitoring and citizen science data

Despite the value of monitoring programmes to conservation science, the data produced can have issues for robust analysis. Some of these issues result from the nature of observing species, for example, imperfect detection, where species or individuals are present but are missed, which leads to bias in abundance and trend estimates (Dail and Madsen, 2011). However, some biases are introduced to monitoring data through the programme design and execution. Sites for monitoring programmes may be selected due to focal species presence or high abundance. Starting a programme with sites of high abundance can lead to declines being detected even when the population is stable (Fournier et al., 2019). Similar detection of false declines occurs when only occupied sites are initially surveyed, as these sites can only be abandoned and the colonisation of unoccupied sites is missed (McClure and Rolek, 2023). These issues are more likely to occur in citizen science data where volunteers choose their sites, as they are more likely to select sites where they have a high chance of observing the focal species, such as protected areas (Johnston et al., 2023). Biases in trend calculations can lead to incorrectly classifying species or populations in threat assessments or conservation priorities, leading to unsuitable and inefficient conservation actions (d'Eon-Eggertson et al., 2015).

Citizen science can also introduce additional biases into monitoring data. There are more likely to be spatial biases in citizen science data as volunteers select sites that are more easily accessible (Johnston et al., 2023), rather than the randomly chosen sites in formal surveys. Some programmes use untrained volunteers which can introduce variation in volunteer skills and experience, leading to heterogeneity in both false negative and false positive detection rates that is difficult to compensate for in analysis (Johnston et al., 2023). Citizen science data can also be completely unstructured through the use of opportunistic sightings rather than prescribed surveys. Unstructured datasets contain significant noisy variation that makes them difficult to analyse, especially when key metadata information, such as effort, is missing (Bayraktarov et al., 2019). This means that unstructured datasets can sometimes contain little additional information on trends (Horns et al., 2018) or even produce misleading trends (Kamp et al., 2016), even if they fill spatial gaps in other formal studies. There is a trend towards data quantity over data quality which encourages the creation of unstructured datasets despite these issues (Bayraktarov et al., 2019). Focusing instead on structured surveys with trained volunteers, which can form robust analyses (Kéry et al., 2010; Barlow et al., 2015), can leverage the benefits of citizen science whilst minimising these issues (Theobald et al., 2015).

Advances in population modelling

Advances in population modelling can also compensate for some biases in monitoring data, giving robust estimates of population and demographic parameters. There are multiple ways to model data with imperfect detection, most frequently by explicitly modelling the detection process (MacKenzie et al., 2003; Dail and Madsen, 2011; Reddell et al., 2021). This requires repeated surveys within a period when biological changes in the population size or occupancy of a site do not occur. For example, multiple electrofishing passes on the same day to count the individual fish in a stream (Kanno et al., 2015). These multiple surveys provide information on detection, as each survey provides a different number of individuals, which is used in the model to asses detection probability and estimate the ‘true’ abundance at a site. This form of data collection highlights the importance of structured citizen science surveys to aid modelling processes (Kéry et al., 2010). Population models give insight into species population ecology, for example dynamic occupancy models reveal the underlying dynamics of site colonisation and extinction, rather than only focusing on overall changes in range (Fandos et al., 2021), and are better at estimating populations trends than species distribution models (Briscoe et al., 2021). A Bayesian framework can also incorporate information from other sources, such as previous studies or expert opinion, into the analysis of sparse or low quality data. Rodhouse et al. (2019) bridged a temporal gap in the monitoring of two bat species using empirically informed priors which gave the model additional information on how site occupancy related to environmental variables such as forest cover. This allowed the model to create continuous estimates of occupancy for the whole survey period, detecting a decline in the occupancy of one species, and increased the precision of estimated parameters.

Combining datasets in integrated population models (IPMs) is also a key advance in population modelling that has several benefits. IPMs can jointly analyse datasets which share one or more parameters, for example survival parameters are shared across population count models (e.g. Leslie matrix) and CMR models (e.g. Cormack-Jolly-Seber model, Schaub and Abadi 2011). Using IPMs increases the precision of estimated parameters and can allow the estimation of additional demographic parameters, such as fecundity when only count and CMR data is available (Schaub and

Abadi, 2011). Integrating multiple datasets makes the most of sparse data which can be difficult to collect for endangered species (Robinson et al., 2018b), and IPMs are able to handle missing data and uneven temporal coverage effectively (Tavecchia et al., 2009; Schaub and Abadi, 2011). There are many applications for IPMs, but key ones include integrating opportunistic data and planned surveys to account for sampling biases whilst leveraging large opportunistic datasets (Fletcher et al., 2019), and including telemetry data to identify causes of mortality and estimate their contribution to population declines to identify threats (Rhodes et al., 2011). The increased use of IPMs has had positive impacts on conservation science, including enhancing management schemes (Zipkin and Saunders, 2018).

Monitoring as conservation action?

This section has highlighted the importance of monitoring programmes for conservation science, even with limitations and biases. However, monitoring data usually needs to be analysed to contribute to conservation, unless it is integrated within a management programme. Of 388 reviewed citizen science projects, only 12% provided data to peer-reviewed journals despite a third providing good quality data (Theobald et al., 2015). Meanwhile, only 5% of global threat data are robust (suitable spatial resolution, up to date, repeated and assessed for accuracy) and freely available (Joppa et al., 2016). This highlights the need for monitoring programmes to be designed with data management, accessibility and publication in mind, perhaps by making data publication as valuable as article publication (Chavan and Ingwersen, 2009).

Even when monitoring data is available and robustly analysed, it contributes most to conservation when it leads to action to prevent continued declines. There have been multiple regional and local extinctions of species, such as the Vancouver Island marmot *Marmota vancouverensis*, that have occurred whilst the populations were monitored (Lindenmayer et al., 2013). Monitoring programmes alone can also be used by policy makers to delay action, by using conservation funding without initiating management (Nichols and Williams, 2006). This highlights the need to integrate management plans and monitoring programmes, and designing them to be as useful as possible by engaging and communicating with local people and ensuring good data management (Robinson et al., 2018a).

UK conservation and monitoring

The biodiversity crisis is felt particularly strongly in the UK, which globally is one of the most nature-depleted countries (Burns et al., 2023). This is the legacy of numerous anthropogenic threats including intensive agricultural practices (Robinson and Sutherland, 2002), invasive species (Manchester and Bullock, 2000) and predator control (Sainsbury et al., 2019). Although there has been progress both indirectly from changes in land management, such as afforestation strategies for timber production which have gradually become more biodiversity-friendly (Raum, 2020), and directly from conservation actions, including reintroduction programmes (Mitchell-Jones and White, 2009; Burnside et al., 2012) and protective legislation (e.g. Wildlife and Countryside Act 1981), UK species and populations continue to decline. The latest State of Nature report suggests that 16% of assessed species are threatened with extinction, with the abundance of terrestrial freshwater species declining by 19% on average since 1970 (Burns et al., 2023). UK biodiversity continues to decline due to the deteriorated state of our remaining and newly created habitats. For example, the area of UK woodland is increasing whilst woodland wildlife, such as specialist birds (Burns et al., 2020), are decreasing, perhaps because only 7% of woodland is currently in ecologically good condition (Burns et al., 2023).

This detailed, if disheartening, understanding of UK biodiversity loss stems in part from extensive species monitoring. There are multiple structured programmes that cover a variety of taxa including bats (National Bat Monitoring Programme, Barlow et al. 2015), birds (e.g. Common Bird Census, Fewster et al. 2000) and butterflies (e.g. United Kingdom Butterfly Monitoring Scheme, Middlebrook et al. 2022). These programmes conduct repeated standardised surveys of the same sites each year, with multiple surveys within a year, collecting data which is more easily and robustly analysed. There are also numerous ad hoc recording societies and citizen science programmes, such as 'Project Splatter' for recording roadkill data (Bíl et al., 2020), which collect opportunistic data. The State of Nature report uses data from at least seven structured monitoring programmes and over 25 recording societies (Burns et al., 2023). A large portion of UK biodiversity data is therefore collected by volunteer citizen scientists.

Hazel dormice

Hazel dormice *Muscardinus avellanarius* are largely nocturnal, arboreal rodents with a global distribution mostly in Central and Eastern Europe (Hutterer et al., 2021). Compared to other rodents, they have a relatively slow life-history, with only one to two litters per season and a maximum lifespan of six years (Juškaitis, 2014). This is partly because hazel dormice hibernate throughout most of their range (Juškaitis, 2014), restricting the time available for breeding, with hibernation broadly associated with longer life spans and slower reproductive rates in mammals (Turbill et al., 2011). Hazel dormice have small home ranges of only around 0.5 - 1ha (Juškaitis, 1997;

Bright and Morris, 1991; Goodwin et al., 2018a), with some territoriality between individuals (Bright and Morris, 1991). Despite these small home ranges, dormice have relatively low densities from 0.12 to 13.6 individuals per hectare, with considerable variation throughout their range (Juškaitis, 2014). Dormice appear to be selective, though opportunistic, foragers (Bright and Morris, 1993; Goodwin et al., 2020). They lack a caecum, so likely cannot digest cellulose, effectively limiting their ability to exploit food sources such as leaves (Juškaitis, 2014). They therefore rely on a wide variety of fruit, seeds, nectar and insects, which varies with food availability throughout the season and within their home range (Bright and Morris, 1993; Goodwin et al., 2020).

Partly due to their dietary requirements, hazel dormice have been considered habitat specialists of broadleaved woodland with sufficient understorey structure to support their arboreal movements (Bright and Morris, 1996). Several plant species have been associated with increased hazel dormouse abundance and breeding, due to their provision of flowers, seeds and fruits or as host plants for insects, including hazel *Corylus avellana*, honeysuckle *Lonicera periclymenum*, bramble *Rubus fruticosus*, birch *Betula spp.* and willow *Salix spp.*, (Bright and Morris, 1993, 1996; Goodwin et al., 2018b). However, species diversity is likely important to maintain sufficient food resources through the active season (Bright and Morris, 1996; Greaves et al., 2006; Goodwin et al., 2018b). Shading is also thought to be an issue in high canopy woodland, as this both reduces flowering and fruiting, and limits the connectivity of under-storey shrubs (Bright and Morris, 1990). Dormice are therefore often associated with early-successional woodland and woodland edges, where there is more shrub growth (Bright and Morris, 1996; Ramakers et al., 2014; Dietz et al., 2018). This type of woodland can also be maintained through woodland management such as coppicing, which has commonly been suggested as a conservation action for dormice (Bright and Morris, 1990), although evidence is equivocal whether such management benefits populations (Juškaitis, 2008; Sozio et al., 2016).

However, there is increasing evidence that dormice utilise a broader range of habitats, altering our understanding on potential conservation actions. Dormice have been found more than expected in conifer woodland and low-diversity woodland throughout their range (Juškaitis, 2007; Trout et al., 2012; Juškaitis, 2014), though populations in low quality habitat may be at low densities. Compared to other dormouse species, recent research suggests hazel dormice are quite generalist in terms of their woodland habitat requirements (Fedyń et al., 2021). There is also evidence of dormice utilising non-woodland habitats, especially hedges (Phillips et al., 2022). Hedges provide connectivity between populations (Dietz et al., 2018) but also residential habitat which can support local populations (Ehlers, 2012; Schulz and Büchner, 2018). There appear to be some consistencies with dormouse habitat requirements between hedges and woodland, in particular the preference for complex physical structure and native species (Dondina et al., 2016). Dormice have occasionally been found in more unusual habitats, including heathland and reed beds, suggesting that they are not as specialised as had been thought (Juškaitis, 2014).

Habitat connectivity is important for dormice as they have low dispersal ability (Bright and Morris, 1996), with a natal dispersal distance typically less than 500m, though up to 1.2km (Juškaitis, 1997). Limited dispersal ability, coupled with barriers such as roads and open areas, means there is minimal gene flow at a landscape scale within dormouse populations (Naim et al., 2012), suggesting they are vulnerable to habitat fragmentation and inbreeding from isolation. However, some barriers, particularly roads, appear not to be as impermeable to dormice as previously thought. There is evidence of both individual movement (Chanin and Gubert, 2012; Kelm et al., 2015) and genetic intermixing (Friebe et al., 2018) across roads as wide as motorways. This suggests dormice are able to cross small distances on the ground, though possibly not frequently (Bright, 1998), indicating that habitat connectivity could be increased using ’stepping stones’ rather than only habitat corridors.

Hazel dormice are also sensitive to climate, and have been considered an indicator species for environmental change (Bright and Morris, 1996). During the active season, typically May to September throughout their range although longer in milder climates (Juškaitis, 2014), dormice prefer warmer sunnier weather which encourages flowering and fruiting (Bright and Morris, 1996; Goodwin et al., 2018b). During wet and cold weather, dormice reduce their activity and enter torpor, a state of reduced metabolic rate, to save energy (Bright et al., 1996b; Juškaitis, 2005). Dormice appear to avoid foraging in wet weather, possibly because their fur is easily waterlogged (Bright et al., 1996b). Climate is also important during hibernation, with dormice preferring consistent cold winters (Goodwin et al., 2018b) to increase the efficiency of hibernation (Humphries et al., 2002). Furthermore, as hazel dormice hibernate on the ground (Gubert et al., 2021), they may be vulnerable to heat loss and drowning in waterlogged soils, with some models suggesting dormice prefer dry soils (Greaves et al., 2006). Research on dormouse hibernation has mostly focused on mechanisms (Juškaitis, 2014) and the characteristics of hibernation locations (Gubert et al., 2023) and nests (Gubert et al., 2021). There has been a little discussion of how hibernation ecology might affect dormouse population changes, for example how warmer winters might threaten dormice due to higher metabolic rates depleting fat stores faster (Bright and Morris, 1996). However, considering the importance of hibernation to dormouse life history, there is minimal understanding of how hibernation may affect dormouse conservation more broadly. This is particularly important in the face of climate change, where alterations to the average temperature and the frequency of severe weather could have large impacts on dormouse populations.

Population status and conservation

Globally, hazel dormice are not threatened and are listed as Least Concern by the IUCN (Hutterer et al., 2021). However, this obscures localised trends; dormice are declining in the north-west of its range (Ramakers et al., 2014), and are listed as Endangered in Latvia, Estonia and Belarus, with possible extinction in Estonia (Juškaitis, 2018). Although the global range of hazel dormice is broad, there are concerns that this range is becoming increasingly fragmented, which could further threaten populations (Amori and Gippoliti, 2003).

In the UK, hazel dormice are distributed across southern England, with a remnant population in Cumbria, and patchily across Wales (Figure 1.1, Bright and Morris 1996). Dormice are not native to Ireland, but a population of introduced dormice were confirmed to exist in County Kildare in 2010 (Glass et al., 2015). However, there have been known range and population declines in Britain throughout the 19th and 20th centuries, with an estimated loss of half its range in the last 100 years (Bright and Morris, 1996). A recent estimate of the trend suggests a decline of 72% (95% confidence intervals: 62–79%) from 1993 to 2014 (Goodwin et al., 2017). On the basis of this analysis, dormice were listed as Vulnerable, a threatened category, on the Red List of British mammals (Mathews et al., 2020).

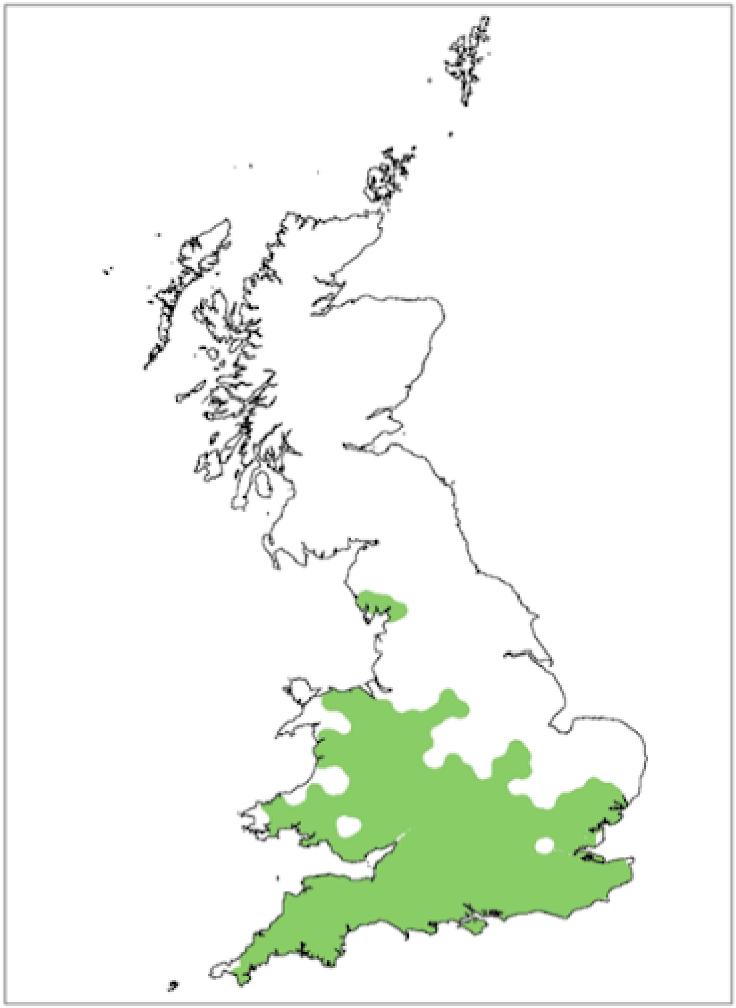

Figure 1.1. The current range of hazel dormice in Great Britain. *Figure adapted from Mathews et al. (2018)*

The population decline in Britain is likely the result of habitat loss and fragmentation, and sensitivity to climate variation as this is the edge of its range (Bright and Morris, 1996). Despite recent increases in cover, woodland is still distributed patchily in the landscape (Reid et al., 2021), and the woodland that does remain is in poor ecological condition (Burns et al., 2023). There has also been a decline in the types of woodland management that might be beneficial to dormice, such as coppicing (Buckley, 2020), leading to most of British woodlands developing into high canopy forests with a loss of under-storey structure. Habitat quality increases the survival and population density of dormice (Mortelliti et al., 2014), suggesting British dormice population may have reduced population growth rates. There have also been declines in the total length of hedgerows due to agricultural intensification (Reid et al., 2021). Habitat connectivity is important for dormice, and is key to driving patch colonisation and extinction rates (Iannarilli et al., 2017). The fragmented British landscape suggests that patches that experience local population extinctions will have a low probability of recolonising in the future (Bright and Morris, 1996). Finally, climate change is expected to increase air temperature, and change rainfall patterns such that more rain occurs in winter, less in summer and the frequency of extreme rainfalls increase (Watts et al., 2015). This threatens dormice in their active period, as decreased rain in summer or variation in spring may affect food supplies and reduce foraging opportunities, and during the winter as hibernation is less efficient in warm temperatures.

To combat the decline of dormice in Britain, several conservation actions are in place. Dormice are legally protected under UK law (Conservation of Habitats and Species Regulations 2017, Wildlife and Countryside Act 1981, as amended), preventing disturbance to individuals or their resting places. Legislation also means dormice are embedded in local and national Biodiversity Action Plans, and surveys for dormice are required before development projects occur (Morris, 2003). There is also an extensive monitoring programme called the National Dormouse Monitoring Programme (NDMP), established in 1988 and run by the People's Trust for Endangered Species (PTES). Over the course of the programme, the number of participating sites has increased, with 250-300 sites in operation since 2010 (Goodwin et al., 2017). Each site consists of nest boxes, usually a grid of 50, which the dormice readily use.

From May to October, volunteers with dormouse licences, and therefore extensively trained, check the boxes and weigh, sex and age any dormice they find (PTES, 2019a). This programme provides extensive data on dormice at the population level, but there are also a few sites which individually mark dormice with PIT-tags (Combe et al., 2023). There has also been a reintroduction programme, starting in 1993, aiming to restore dormice to parts of England where natural recolonisation would be unlikely (Mitchell-Jones and White, 2009). There have been 24 reintroduction projects thus far, and though many have short-term success with survival over two winters, only half have maintained populations for longer than ten years (Cartledge et al., 2021). Most of these conservation efforts, however, have occurred alongside continued population decline, suggesting further action is needed to conserve this flagship species of British mammals and woodland ecosystems (Morris, 2003).

Thesis aims and outlines

In this thesis, I investigate the population ecology of hazel dormice with the aim of understanding how and why dormice are declining in Britain, and to suggest recommendations for future conservation actions that may benefit the species.

Specifically, I aim to:

I. Understand how hibernation biology alters the impact of current threats to mammals globally, and how conservation actions can target hibernation biology

II. Investigate the habitat associations of dormouse presence in understudied hedge and scrub habitats

III. Update and review the population decline of British dormice in relation to IUCN threat categories

IV. Evaluate the habitat and climate drivers of local dormouse colonisation and extinction at nest box sites

V. Estimate demographic parameters for British dormice, in comparison to a Lithuanian population, using an monthly integrated population model and identify the parameters with the greatest contribution to population growth rates

To achieve these aims I use a combination of techniques including a literature review, observational fieldwork and several models of population and individual-level data. This thesis consists of five chapters for each of the objectives above, followed by a general discussion synthesising my results. In each chapter, I have aimed to detail practical recommendations for hazel dormouse conservation in Britain.

In **Chapter 2** I have produced a literature review of how mammalian hibernation biology interacts with existing threats to the benefit or detriment of species, and how conservation actions are helped or hindered by hibernation. This chapter explores the mixed benefits and costs of hibernation, including multiple divergent responses to climate change related threats which makes it difficult to predict the outcomes for unstudied species.

In **Chapter 3** I used innovative detection techniques to investigate the habitat influences on the presence of dormice in hedge and scrub habitat in southwest England. This chapter shows that dormice are extensively detected in both habitats, though more so scrub, and reveals that habitat factors can influence dormouse presence, suggesting future routes for conservation action relating to habitat connectivity.

In **Chapter 4** I updated the population decline of British dormice using the latest data from the NDMP, to investigate whether dormice could be considered Endangered in the next Red List assessment. This chapter also highlights the issues around how to prioritise conservation for species in chronic decline which is not well-accommodated by the IUCN Red List assessment.

In **Chapter 5** I used a Bayesian dynamic site occupancy model to evaluate the local colonisation and extinction rates of NDMP sites whilst accounting for preferential sampling biases. This chapter investigates how habitat and climate influence these rates and so the overall occupancy of the monitoring scheme. I also investigate how accounting for the preferential sampling bias changes our understanding of abundance changes at NDMP sites.

In **Chapter 6** I produced a Bayesian integrated population model of population counts and capture-mark-recapture data to estimate monthly active season survival rates, and yearly hibernation survival and productivity rates of adults and two juvenile age classes. This chapter highlights how these rates drive population growth and are influenced by climate, revealing targets for future conservation action.

Finally, in **Chapter 7** I synthesise the results of my thesis into a general discussion. I have addressed how my work contributes to our understanding of dormouse population ecology and how my work reveals conservation recommendations. I also detail the broader implications of my thesis for species in chronic decline and hibernators, and the application of population ecology to conservation science.

Chapter 2: Conservation implications of hibernation in mammals

Chapter 2: Conservation implications of hibernation in mammals

This chapter has been published as:

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Abstract

1. Hibernation is a life history strategy for conservation of energy during adverse conditions, primarily of temperature or resource availability. While energy conservation is beneficial in itself, it is less clear whether hibernation confers wider conservation benefits, or mitigates or exacerbates a wide range of threats.

2. We briefly review how hibernation manifests in mammalian biology, primarily through energy budgets, activity levels and resource requirements, but then ask how these interact with existing pressures to affect conservation risk. We also explore conservation actions that could alleviate the negative relations between some pressures and hibernation biology, and review the available evidence for these measures.

3. Hibernation can convey some protection from disease and predation, though there are notable exceptions, for example white nose syndrome. There is well-established evidence that hibernators are prone to hazards of disturbance during hibernation, necessitating careful mitigation. Hibernators exhibit diverse responses to the pressures related to climate change, including temperature variability, and phenological and range mismatches. Yet for each aspect, there

are examples of species and populations responding negatively, such as with reduced survival, which suggests that hibernation could exacerbate the negative consequences of climate change.

4. Though there are times when hibernators do not respond as expected, we find several positive conservation actions, such as modern grilles and regulations reducing the disturbance of cave-hibernating bat species. Understanding and working with hibernation biology can, therefore, successfully mitigate the additional risks it confers.

Introduction

The current sixth mass extinction is driven by anthropogenic threats, including climate change and habitat destruction (Dirzo et al., 2014). These threats vary in their severity and timing, with chronic threats, such as increasing temperature variance, sometimes also manifest in acute events, such as extreme weather. Traits that allow an individual to maintain its fitness during such periods of threat might render populations less prone to local extinction, increasing the species' resilience to climatic and resource disturbances. A key characteristic for maintaining fitness in the face of climate change is likely to be thermal physiology. The expected outcomes of climate change for ectotherms and endotherms have been explored (Buckley et al., 2012). However, there has been less focus on heterothermy, the ability to temporarily vary body temperature, presenting the opportunity to explore how these species might respond to anthropogenic pressures.

Temporal heterothermy (hereafter, heterothermy) can describe changes in body temperature relating to hypo- or hyperthermia, however here we focus on the facultative reduction of metabolic rate and body temperature for periods of variable duration using torpor (McKechnie and Mzilikazi, 2011). Whilst in torpor, an individual's energy requirements are markedly reduced (Geiser, 2013), decreasing the costs of thermoregulation, and conserving energy during periods when resources are limited and reproduction is less feasible (Geiser, 2013; Blanco et al., 2018). Heterothermy is apparent in taxonomically diverse mammals and birds (Ruf and Geiser, 2015; Lovegrove, 2016), and is also globally distributed, including in the tropics (McKechnie and Mzilikazi, 2011; Nowack et al., 2020), though most research has focused on Holarctic mammals. Due to the broad phylogenetic distribution of heterothermy in endothermic species, particularly in all early branching clades within monotremes, marsupials and placental mammals (Lovegrove, 2016), heterothermy is considered a conserved ancestral trait in these groups (Grigg et al., 2004; Lovegrove, 2016), and may have been a precursor condition to the evolution of endothermy (Grigg et al., 2004).

Temporal heterothermy can be broadly categorised into hibernation (multiday torpor) and daily torpor, which can be distinguished by the length and depth of torpor. Hibernation lasts several weeks or months, during which the torpor bouts are longer than 24 hours, and mean metabolic rate is lower than in daily torpor (Ruf and Geiser, 2015). A third category has been proposed consisting of bouts of torpor interspersed with activity, which lasts several days (Nowack et al., 2020), but is broadly consistent with hibernation (Geiser, 2020), as torpor bouts tend to be >24 hours. Due to this similarity, for the purposes of this review where hibernation is our main focus, we maintain the dichotomy between hibernation (>24 hours of torpor) and daily torpor. Hibernation is found in many mammal clades, but only one bird species, the common poorwill (*Phalaenoptilus nuttallii*), hibernates (Ruf and Geiser, 2015; Lovegrove, 2016).

Although both types of heterothermy appear ancestral, hibernation has been suggested as a trait that allowed basal mammals and birds to survive the last mass extinction (Lovegrove, 2016). Unlike those exhibiting daily torpor, hibernating individuals could lower their metabolic requirements for several months, enduring both the immediate impacts of the asteroid collision in refugia, likely underground, and the longer-term ecological collapse and global cooling where resources were limited (Lovegrove, 2016). There is some evidence from phylogenetic analyses (Liow et al., 2008, 2009) that hibernation decreases extinction risk, though the analyses combine 'sleeping' traits, including heterothermic traits and dormancy, with 'hiding' traits, such as using caves. Species with these 'sleep or hide' traits appear to have a lower species' extinction risk in the fossil record (Liow et al., 2008). Moreover, among contemporary mammals, having 'sleep or hide' traits increases the likelihood of being categorised as Least Concern on the IUCN Red List (Liow et al., 2009). However, when hibernation is considered in isolation from the other 'sleep or hide' behaviours, and is compared with Red List categorisation, whilst controlling for phylogeny, this effect was non-significant (Liow et al., 2009), suggesting that hibernation alone may not contribute to reduced threat of extinction. It is therefore unclear if hibernation confers advantages that could increase the likelihood of persistence under current threats, and how specific pressures may affect hibernators beyond broad correlations with threatened status. In this article, we consider whether an understanding of hibernation can clarify possible relationships between biological consequences of hibernation and current pressures.

We devised a conceptual framework (Figure 2.1) to structure our literature search (Appendix 1). We summarised this in narrative form covering hibernation and its biological consequences, and the key pressures interacting with hibernators. For each biological consequence to pressure relation, we categorise whether the evidence indicates negative, positive or mixed effects for hibernators (Figure 2.1). We also indicate how certain we are of this effect using a four box model approach that combines levels of evidence and agreement (Quine et al., 2011). We hypothesised that negative relations between pressures and hibernation biology could be alleviated through targeted conservation action, asked what evidence is available to support this, and identified key knowledge gaps.

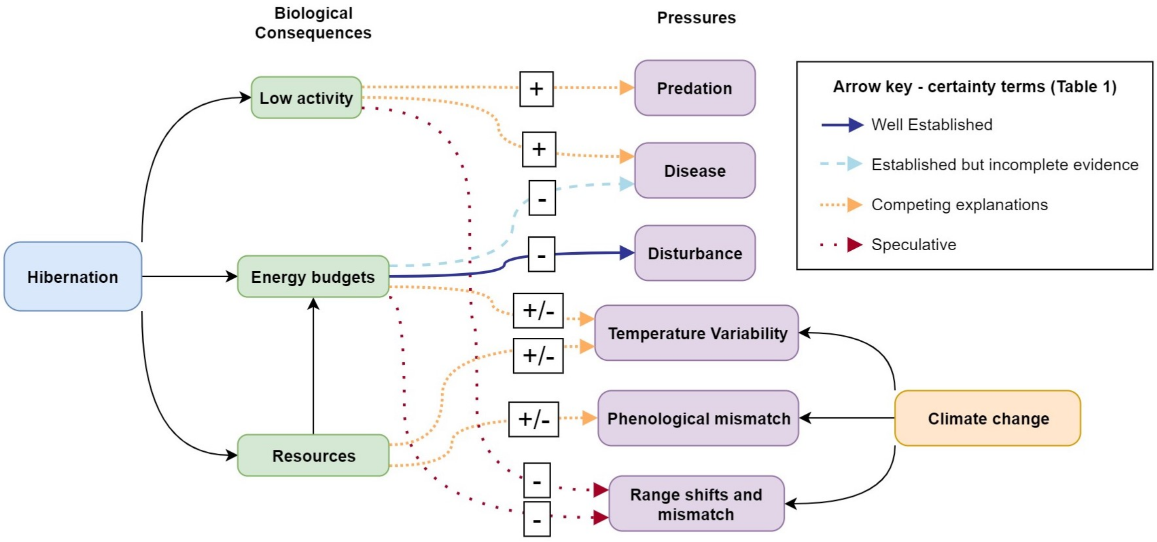

Figure 2.1. The biological consequences of hibernation (green) and their relations (arrow) to existing pressures (purple). *The symbols on the arrows indicate the overall effect the relation has on hibernators (positive +, negative - or mixed +/-). Arrow colour indicates certainty from analysis of the literature of the relations effect, based on the four box model approach combining low/high agreement and limited/substantial evidence (adapted from Quine et al. 2011). The certainty categories are shown in the diagram key; well established (dark blue), established by incomplete evidence (light blue), competing explanations (orange) and speculative (red). Climate change is included as the cause of several separate pressures.*

Chapter 2

Hibernation Biology

Hibernation physiology has three characteristics that interact with pressures; activity levels, energy budgets and resource requirements (Figure 2.1). It is important to understand how these features arise before considering how they impact conservation. Hibernation causes periods of low activity, as species are inevitably immobile for extended periods within their hibernation locations (hibernacula; Ruf and Geiser 2015). In some cases, immobility may influence survival by affecting exposure to hazards, either positively, for example, as hibernators have reduced exposure to severe weather (Turbill et al., 2011) or negatively, as when found they can be easily predated (Cichocki et al., 2021). Survival during hibernation is usually relatively high, with small mammals on average five times more likely to die during each month of the active season than during each month of hibernation, hence annual survival is also 15% higher in hibernators than similar sized non-hibernators (Turbill et al., 2011). However, a minority of species exhibit high hibernation mortality, for example 75% of woodland jumping mice (*Napaeozapus insignis*) that enter hibernation do not emerge in spring (Merritt, 2010). Hibernation is associated with a slower life history, including longer lifespans and generation times (Turbill et al., 2011), possibly due to high hibernation survival due to low activity.

Extended periods of immobility with low metabolic rate also save energy; individuals in hibernation require less than 15% of the energy used by active individuals (Geiser, 2013), nevertheless there are significant physiological costs. There are numerous costs including dehydration, which may impair circulation, the inability to sleep, which may cause neurological damage (Humphries et al., 2003b). Hibernation also increases oxidative stress, while simultaneously reducing physiological functions involved in repair, such protein synthesis (Humphries et al., 2003b), which may contribute to the shortening of telomeres, a marker of cellular aging, observed in torpor (Nowack et al., 2019). Further costs due to reductions in immune function and digestion (Bouma et al., 2010) are explored in more detail below. These costs mean that maximum energy conservation, through maximum hibernation, is unlikely to be ideal, with the greatest benefits resulting from optimising hibernation, through changes to torpor length or depth (Boyles et al., 2020). During prolonged torpor, costs are reduced through periodic increases in body temperature to >28℃ (Ruf and Geiser, 2015), termed arousal, allowing temporary resumption of normal physiological function. Most species achieve this by periodically increasing their metabolic rate through active thermogenesis (Humphries et al., 2003b). Some, primarily tropical, species (e.g. Malagasy fat-tailed dwarf lemur *Cheirogaleus medius*) hibernate at high ambient temperatures, and so can achieve re-warming passively (Dausmann et al., 2008; Lovegrove et al., 2014), though some temperate species can also passively re-warm through their hibernacula, such as tree-roosting bats (Stawski et al., 2014). A few others (e.g. black bears *Ursus americanus*) can maintain high body temperatures, alongside low metabolic activity (Geiser, 2020), due to their larger body size and associated thermal inertia. Hibernation with passive re-warming may be closer to the ancestral form, whilst actively regulated arousals might be a more recent adaptation (Nowack et al., 2020).

However, there are still energetic costs associated with the periods when body temperature is high, especially if thermogenesis is required to reach this state (Humphries et al., 2003b; Dausmann et al., 2008). Active arousals can cause physiological damage, such as telomere shortening caused by the release of reactive oxygen species as metabolic rate increases (Nowack et al., 2019). Thus, while arousal periods are necessary to prevent physiological damage, they are the most costly part of hibernation, and an individual must balance its energy budget, offsetting the frequency and length of arousals against its stored energy (Figure 2.1; Humphries et al. 2002, 2003b) or the energy gathered from foraging during arousals, albeit subject to availability (Mas et al., 2022). Temperate hibernators often store energy in fat reserves, though some species cache food (Humphries et al., 2003b), and these resources are gathered primarily in the pre-hibernation period, which is usually timed to match predictable seasonal increases in food availability (Merritt, 2010). Several tropical hibernators also store energy in this manner, though some enter hibernation without pre-fattening (Nowack et al., 2020), or forage during arousals (Turbill, 2008). Changes to resource availability or the number/length of arousals will therefore have a direct impact on the survival of an individual and the condition in which it enters the breeding season.

Predation

Low individual risk of predation is thought to be a key factor associated with reduced mortality during hibernation (Figure 2.1; Turbill et al. 2011), and may explain why several species hibernate even when conditions are favourable (Stawski et al., 2014). Hibernation facilitates predator avoidance as low activity reduces an individual's exposure, and makes them difficult to detect as they are motionless, with reduced body temperature and odour (Turbill et al., 2011). Hibernacula can also provide protection (Geiser, 2019), as many species hibernate in caves (Furey and Racey, 2016), burrows (Armitage, 2013) or trees (Stawski et al., 2014), though some species, such as the hazel dormouse (*Muscardinus avellanarius*), build unprotected nests on the ground (Gubert et al., 2021). Hibernators may need to select hibernacula, or locations within hibernacula, that dynamically balance risks, for example, during hibernation bats move into cooler temperatures, where hibernation is more efficient but more physiologically costly, at cave entrances as they near starvation, exposing themselves to greater predation risk (Ryan et al., 2019). Hibernation may mitigate growing threats from introduced predators by reducing exposure, with daily torpor and hibernation decreasing extinction risk for native Australian mammals (Hanna and Cardillo, 2014).

Conversely, hibernation may increase mortality, particularly in terms of numbers of individuals killed during predation events (Haarsma and Kaal, 2016). Hibernators can be targeted as they are entering/leaving hibernacula (Estók et al., 2010), including by human hunters who might prefer hibernating individuals because of their high fat content (Gardner and Davies, 2014). Individuals may be especially vulnerable if they have high fidelity to hibernacula (Furey and Racey, 2016). Low activity can also hinder hibernators, as they cannot easily escape predators whilst in, or emerging from, torpor (Humphries et al., 2003b; Stawski et al., 2014; Ruf and Geiser, 2015). Therefore, predators can be associated with locally high mortality rates (Haarsma and Kaal, 2016), and can innovate to exploit the high rewards of hibernacula, such as great tits (*Parus major*) learning to hunt systematically for hibernating bats (Estók et al., 2010). Invasive non-native predators can also exploit hibernating species, which naively select vulnerable hibernacula (Cichocki et al., 2021). In New Zealand, during seed mast years with abundant mice (*Mus musculus*), invasive stoats (*Mustela erminea*) breed more prolifically, which reduces the over-winter survival of native long-tailed bats (*Chalinolobus tuberculatus*; Pryde et al. 2005). Climate change might also exacerbate the threat of predation to hibernators. In this New Zealand example, warming temperatures are likely to increase the frequency of masting events (Pryde et al., 2005) and, hence, mouse and stoat outbreaks. Globally, climate change may increase predation opportunities through earlier snowmelt exposing previously secure hibernacula (Armitage, 2013), and shorter hibernation periods causing individuals to be more active (Wells et al., 2022).

Conservation actions could work with high hibernation survival. In general, seasonal variation in survival rates can influence population growth (Hagen et al., 2009), suggesting that hibernation may affect the sensitivity of populations to the timing of both positive conservation and negative perturbation events, although this has yet to be tested (Table 2.1). For example, hibernating prey species are most likely to benefit from predator control which aims to reduce populations during the active season.

Disease

As with predation, low activity may reduce exposure to infection (Stawski et al., 2014). This is beneficial as the majority of the immune system is downregulated during hibernation (Bouma et al., 2010), albeit with temporary elevation during arousals (Fritze et al., 2019). Only some immune functions, such as the inflammatory response, can be activated when challenged (Fritze et al., 2019), although more functionality is maintained in key areas, such as the gut (Bouma et al., 2010). During hibernation, the gut microbiome reduces in diversity, due to the lack of substrate and lower body temperature (Carey and Assadi-Porter, 2017), in turn, changing the composition of microbe-derived metabolites and local immune and intestinal barrier function (Carey and Assadi-Porter, 2017).

Hibernation physiology can also reduce disease risk (Figure 2.1). Parasite load decreases during host hibernation due to low parasite survival in the cooled host (Fietz et al., 2014), and some parasites exhibit adaptations to overwinter outside the hibernating host, as eggs or cysts in the environment or inside a non-hibernating intermediate host (Callait and Gauthier, 2000). Although some parasites can tolerate unfavourable conditions inside the host during hibernation (Callait and Gauthier, 2000), they experience reduced development (Fietz et al., 2014).

Similarly, pathogens can experience reduced growth rates in a hibernating host (Stawski et al., 2014). This slows the course of disease, allowing the host, and consequently the tolerant pathogen, to survive until the active season. Hibernation may therefore contribute to the maintenance of disease reservoirs, including of zoonoses (Singer et al., 2009; Fietz et al., 2014; Tang et al., 2022). This is detrimental to hibernator populations, and can be associated with wildlife management challenges as species sometimes hibernate in buildings (Furey and Racey, 2016), whilst other hibernating species are used as occasional human food sources (Tang et al., 2022), both potentially exposing humans to infection. The timing of disease control interventions for zoonoses can be affected by hibernation; for example, rabies vaccination for raccoon dogs (*Nyctereutes procyonoides*) is most effective just after hibernation emergence and before juvenile dispersal, when vaccine bait is most readily consumed (Singer et al., 2009).

Some pathogens proliferate at low temperatures, causing disease when hibernating hosts have minimal immune defences. White nose syndrome (WNS), caused by the fungus *Pseudogymnoascus destructans*, has devastated populations of several North American bat species, and may ultimately contribute to local extinctions (Turner et al., 2022). The interaction between infection and hibernation may also be the fundamental cause of WNS high mortality rates; WNS, among other pathogens (Arnold and Lichtenstein, 1993), appears to increase the frequency of arousals during hibernation (Stawski et al., 2014; Forney et al., 2022), such that bats are more likely to exhaust their energy reserves and starve (Figure 2.1). Increased temperature during arousal periods inhibits fungal growth (Forney et al., 2022), suggesting the increase in arousal frequency could be a host response to fungal infection. Some bat populations have increased in their southern range, despite WNS and decreases in the north, perhaps due to the longer availability of insects increasing their hibernation resources (Boyles et al., 2024). Population stabilisation and increase of tricolored bats (*Perimyotis subflavus*) in the presence of WNS has been associated with greater use of colder microclimates within their hibernacula (Loeb and Winters, 2022). This is likely a response to starvation, potentially linked to WNS, though it may increase survival. Building on this observation, researchers experimentally cooled subterranean hibernaculum sites to investigate whether this is a viable conservation action for WNS (Turner et al., 2022). Though a few bats moved into these cooled areas (Turner et al., 2022), it is unclear whether survival was increased or if the researchers were observing the known starvation response. There are also concerns about unintended consequences to cave environments when manipulating internal temperature (Meierhofer et al., 2022), particularly increasing temporal variability in temperature and humidity which can decrease hibernating bat fitness (Boyles et al., 2023). Though caution must be applied, individual-based models suggest successful cave manipulations could focus on reducing this temporal variability and increasing spatial gradients (Boyles et al., 2023).

Despite reduced movement and exposure to new infections, hibernation may facilitate disease and parasite transmission among aggregations of hibernating individuals. Several species hibernate socially to reduce the costs of rewarming (Ryan et al., 2019) and increase survival during harsher conditions (Boyles and Brack, 2009), or due to limited hibernacula such as caves (Furey and Racey, 2016) There is some limited evidence of disease and parasite spread in social hibernators; for example, ectoparasites may reduce the fitness of communally-hibernating yellow-bellied marmots (*Marmota flaviventris*) at the burrow-scale (Van Vuren, 2010), and there is the potential for *Yersinia pestis* spread between socially-hibernating Himalayan marmots (*Marmota himalayana*) via fleas which can remain active during hibernation (Tang et al., 2022). However, pathogen transmission among hibernating animals has not been generally linked to whether a species hibernates colonially (Hoyt et al., 2018), nor has ectoparasite load been linked to group size (Arnold and Lichtenstein, 1993). The disturbance caused by a WNS-infected individual arousing causes its neighbours to also re-warm, which may widen and accelerate the energetic impact and risk of starvation across the group (Turner et al., 2015). Where social hibernation is obligatory for successful hibernation, the remaining individuals may be unable to survive if the group becomes too small (Langwig et al., 2015), amounting to an Allee effect. In practice, this effect, coupled with high transmission rates, likely makes selectively removing infected individuals an ineffective intervention for WNS control in some socially hibernating bat species (Langwig et al., 2015).

Disturbance

Disturbance, particularly from human activities, can negatively affect hibernator energy budgets (Figure 2.1). Individual-based models suggest disturbance causes more frequent arousals (Boyles and Brack, 2009). Disturbed brown bears (*Ursus arctos*) may abandon their hibernacula, which can reduce subsequent reproductive output (González-Bernardo et al., 2020). The number of disturbance events exhibits a threshold point when continuing disturbances rapidly diminish hibernation survival

(Boyles and Brack, 2009), indicating an evolved ability to initially withstand some level of disturbances, perhaps by altering torpor patterns to reduce energy loss (Abarzúa et al., 2023). Some species choose hibernacula isolated (Pigeon et al., 2014) and/or hidden from potential human contact (González-Bernardo et al., 2020). Species using caves as hibernacula may have limited ability to avoid human activity, as they are restricted by the availability of suitable sites. In caves, tourism activity can cause disturbance and climatic changes, both from the presence of humans and the physical modifications that permit access, causing mortality (Furey and Racey, 2016) and population decline (Grol et al., 2011) in hibernating bats. Some bat species shift their position within the cave system to avoid disturbance, whilst others in the same system do not (Grol et al., 2011). Research activities can also disturb hibernating species, and have been associated with population declines (Olson et al., 2011), though the long-term benefits of research can outweigh this potential cost.

Due to the negative effects of disturbance, and risks of disease transmission, access by people to hibernacula is often restricted (Table 2.1). In caves, grilles and walls have been used since the 1950s, but early attempts were poorly designed and nearly always reduced bat populations (Furey and Racey, 2016). Grilles can reduce cave accessibility for bats ((Mitchell-Jones et al., 2007), and also influence cave microclimates. Walls and closely-spaced grilles reduce airflow, increasing internal temperature and decreasing the efficiency of torpor (Richter et al., 1993). More modern designs can increase bat numbers (Richter et al., 1993; Berthinussen et al., 2020), but they are still not recommended for some species (Mitchell-Jones et al., 2007), and seem to have mixed effects for others (Berthinussen et al., 2020). Alternatively, enforcing access regulations, for example by only allowing tourist access to caves outside of the hibernation season, can also increase bat numbers (Olson et al., 2011). Other hibernacula, such as trees, are more difficult to safeguard physically, though they could be considered in the designation of protected areas (Pigeon et al., 2014).

Management for conservation and commercial purposes, such as forestry, can also cause disturbance during hibernation (Pigeon et al., 2014; González-Bernardo et al., 2020). Such disturbance may be regulated or prohibited under some conservation legislation and it is often recommended that such activities are restricted during key seasons, primarily the breeding season. However, hibernation can also be considered a key season (Pigeon et al., 2014), meaning the opportunities for management can end up being very limited, deterring practitioners from implementing otherwise positive management. For example, woodland management may help improve habitat quality for the declining hazel dormouse (Goodwin et al., 2017), but legislation limits management to short periods between seasons (Forestry Commission, 2019) Additional constraints from other conservation legislation can narrow this period even further. However, there are no studies exploring whether changing the timing of management activities actually benefits hibernator populations overall (Table 2.1; Berthinussen et al. 2020), as the risk may only be to a few individuals.

Temperature variability

During hibernation, body temperature decreases to close to ambient. Thus, hibernator body temperature becomes sensitive to environmental changes, and they can have more in common with aspects of ectotherm physiology (Geiser, 2013). Hibernating in warm temperatures increases an individual's metabolic rate and arousal frequency, and while it can reduce the costs of arousals, this leads to an overall increase in energy usage (Humphries et al., 2002). Unlike ectotherms, when experiencing cold temperatures, hibernating individuals maintain their body temperature above a species-specific minimum by thermogenesis (Geiser, 2013), sharply increasing energetic demands (Humphries et al., 2002). Therefore, each species has a small range of ideal ambient temperatures for hibernation, above their specific minimum but below a temperature that would require more energy than they have stored. The ideal ambient temperature for hibernation is likely to increase with greater temperature variability (Boyles and McKechnie, 2010). This is because there are greater energetic costs associated with hibernating at ambient temperatures below the minimum possible body temperature, when thermogenesis occurs, than hibernating at a warmer ambient temperature where metabolic rate increases passively (Boyles and McKechnie, 2010). With increased ambient temperature variability, a warmer location is less likely to drop below the critical thermogenesis point. However, it is still more energetically costly than hibernating in a cooler stable temperature, due to the passive increase in metabolic rate at warmer temperatures. Though hibernators are always trading off cooler temperatures against more variable ones, as few hibernacula are stable in relative terms, increasing temperatures and variability due to climate change could have negative consequences by increasing the energy requirements of hibernation.

Most individuals select hibernacula, or microclimates within a hibernaculum, that remain close to their specific ideal temperature (Geiser, 2019). This ideal temperature will change over the hibernation season, and so individuals of some species may move between microclimates (Ryan et al., 2019), or change hibernation locations during arousal (Sendor and Simon, 2003), though moving can itself be metabolically expensive (Wells et al., 2022). Individuals will also select microclimates based on their energy state, with larger individuals with greater energy stores selecting warmer microclimates (Ryan et al., 2019), reflecting the balance between the efficiency of cooler temperatures and the physiological costs. Conversely, some tropical hibernating species appear not to favour stable hibernation climates and select poorly insulated, variable hibernacula for the benefit of passive rewarming (Dausmann et al., 2008; Lovegrove et al., 2014), so may be vulnerable to heat stress. The balance between energy reserves and hibernation temperature may differ between environments, species and individuals, as well as the specific temperature change under climate change, as globally winter temperatures are warming at a different rates to summer temperatures (IPCC, 2021).

The effects of increasing temperatures on hibernators remain unclear (Figure 2.1). A recent review found mixed effects of climate change on body condition and survival, and positive effects on reproduction, though many papers reviewed reported no effects (Wells et al., 2022). Models suggest that increasing temperatures will reduce the impacts of WNS for some bats, but not for all species tested nor in all geographic areas (McClure et al., 2022). Further uncertainty results from warming winter temperatures having differing effects on adults and juveniles, which can differ among species. Warmer winters decrease the survival of hibernating adult Uinta ground squirrels (*Urocitellus armatus*), but increases juvenile survival, possibly because their smaller body size increases the relative costs of keeping warm in colder temperatures (Falvo et al., 2019). Meanwhile, adult and juvenile long-tailed bats both show reduced survival in warmer winters, though juvenile survival is more affected as they have less time to gather resources pre-hibernation (Pryde et al., 2005). This intra-specific class-related variation highlights the difficulty in predicting overall population responses to temperature variation, as well as generalising predictions amongst hibernating species (Findlay-Robinson et al., 2023).

Climate change-induced increases in temperature can have differing effects depending on season. For example, increased summer temperatures and drought severity decrease the survival of yellow-bellied marmots the following winter, due to reduced resource availability (Cordes et al., 2020), though this is mitigated during in milder shorter winters which require less energy reserves (Paniw et al., 2020). The effect of winter temperatures may also be mediated by other changes in climate; European Hamsters (*Cricetus cricetus*) are emerging from hibernation with lower body weights due to increased rainfall, possibly due to increasing heat loss via wet fur, and this has been implicated in their population decline (Tissier et al., 2016).

Warming winter temperatures may increase access to resources, for example, hibernating Australian long-eared bats (*Nyctophilus spp.*) exploit warm humid nights to forage, but these conditions are predicted to become less common under climate change (Turbill, 2008). Eventually warming temperatures could mean individuals forgo hibernation completely; several bat species in coastal Mediterranean wetlands arouse from hibernation to forage when temperatures are $>$11℃, which is expected to be the average winter temperature in 60-80 years (Mas et al., 2022). Between site variation in the duration of hibernation, torpor bouts and arousals (McKechnie and Mzilikazi, 2011; Sheriff et al., 2015), likely driven by local climate, suggests that there is an opportunity to adapt to climate change. There is also between-individual variation in the facultative use of hibernation as, in some species, individuals that have high energy reserves when they enter hibernation, reduce the amount of time spent in torpor (Ruf and Geiser, 2015), and implement torpor at higher temperatures (Humphries et al., 2003a). The influence of resource availability suggests that supplementary feeding could be a beneficial conservation action (Humphries et al., 2003a) however, the effects are hard to predict; female European hamsters given supplementary food did not change their hibernation patterns, whilst males shortened their hibernation duration (Siutz et al., 2018).

Where hibernation is facultative, it could be a useful strategy for dealing with changing climate and future variation in resource access. However, if hibernation is obligatory, it may end up as an ecological trap, forcing species into a pattern they cannot maintain. Therefore, it is difficult to predict the exact response of hibernators to temperature variability (Figure 2.1; Wells et al. 2022), however, evidence available thus far suggests a potential for detrimental consequences for some species and populations.

Phenological mismatch

Warming temperatures have advanced biological springs and delayed winters (Penuelas et al., 2009). As hibernators rely on access to seasonal, often short-lived, food sources before and/or after hibernation, they are vulnerable to phenological mismatch (Blanco et al., 2018). Species that use photoperiod or physiological cues to enter hibernation (Geiser, 2020) are perhaps more likely to experience such mismatch. Meanwhile, species that use climate cues (Merritt, 2010; Kauhala and Kowalczyk, 2011) are more likely to track phenological shifts. For example, brown bears emerge earlier during warm springs but are more sensitive to conditions just prior to emergence (González-Bernardo et al., 2020). Some hibernators, such as Arctic ground squirrels (*Urocitellus parryii*), show sex differences in the cues used for emergence, which may vary to different extents under climate change, effecting reproductive competition (Findlay-Robinson et al., 2023).

Warmer springs have allowed many species to emerge from hibernation earlier (Wells et al., 2022), giving more time for breeding and foraging, enabling greater population growth (Adamík and Král, 2008). Longer growing seasons appear to have positive effects for hibernator body condition and reproduction, though mixed effects on survival (Wells et al., 2022). In the central USA, yellow-bellied marmots breed earlier, reach greater weights pre-hibernation, and have increased survival (Ozgul et al., 2010), despite emerging earlier in response to warm temperatures while snow cover is still present (Inouye et al., 2000). There may be a limit to the extent of this benefit, however, as longer summers reduce marmot pup survival (Cordes et al., 2020), potentially as a consequence of reduced summer resources (Cordes et al., 2020), as the same flowering plant production is spread over a longer season (CaraDonna et al., 2014), limiting supplies at key times. The phenological response may also be mediated by resource availability, for example edible dormice (*Glis glis*) emerge from hibernation earlier in response to warming temperatures only if there was low food availability the previous years (Fietz et al., 2020). As described above, shorter hibernation periods may increase vulnerability to predation and disease, and can cause greater human-wildlife conflict; climate change could prolong the den-entry period for brown bears, which is when there is greatest risk of bears injuring humans (Evans et al., 2016). Earlier snow melt can also reduce survival, due to the loss of the insulating layer of snow (Rézouki et al., 2016). For example, there is 70% reduction in juvenile hoary marmot (*Marmota caligata*) survival between years with the highest and lowest snow cover depth and duration (Patil et al., 2013). Overall, shorter winters appear to have mixed effects across survival, reproduction and body condition (Figure 2.1; Wells et al. 2022).

Conversely, the length of hibernation may also increase under climate change, for example at high altitudes warmer temperatures tend to delay spring, due to reduced winter dormancy (Yu et al., 2010) and late snows (Inouye et al., 2000) which hinder new plant growth. Delayed emergence of adults from hibernation can postpone the start of breeding, and reduce the survival of juveniles the following winter (Findlay-Robinson et al., 2023). Prolonged hibernation is also associated with decreased survival (Paniw et al., 2020) and reproductive output (Hufnagl et al., 2011). In Canada, climate change has increased the frequency of late-season snowstorms, delaying hibernation emergence and reducing individual fitness and population growth rate in Columbian ground squirrels (*Urocitellus columbianus*; Lane et al. 2012). However, species can respond to delayed emergence, for example by investing in fewer larger offspring which are more likely to survive winter (Findlay-Robinson et al., 2023). The diverse responses to different phenological shifts within and between studied species indicate some difficulties in generalising (Findlay-Robinson et al., 2023).

Range shifts and mismatch

Many species, including hibernators (Humphries et al., 2002), are expected to shift their range to higher altitudes and latitudes under climate change. This may also be associated with changes in range size. Several bat species have expanded their range to higher latitudes (Festa et al., 2023), whilst several other species, including alpine chipmunks (*Tamais alpinus*), have locally contracted theirs to higher elevations (Moritz et al., 2008). Non-hibernators may be able to invade areas where they previously could not survive the harsh winters, potentially increasing competition and predation of hibernators (Geiser, 2013). Hibernation might allow a species to persist under unfavourable conditions whilst they establish themselves in the new range, which may not yet be entirely suitable (Estrada et al., 2018). For example, a life history involving temperature dependent hibernation has been implicated in the expanding range of invasive raccoon dogs in Europe (Kauhala and Kowalczyk, 2011). Successful establishment may assist a species in filling all their available climatically suitable range, producing a larger, more widespread population, decreasing extinction risk (Estrada et al., 2018).

Conservation programmes could expand or create hibernacula along the expanding distributional edge (Berthinussen et al., 2020), or even within current ranges. Existing cave hibernacula have been enlarged, for example new chambers added (Furey and Racey, 2016), or additional roosts provided (Mitchell-Jones et al., 2007). Although artificial caves have been created, 25 years of provision in the UK reveals that occupancy is very low (Furey and Racey, 2016). Though there is less research on other species, other taxa also seem to use artificial nest boxes for hibernation (Gazzard and Baker, 2022), suggesting designs for other species could be possible.

Evidence thus far suggests hibernation is not a trait associated with species whose ranges fill the climatically suitable area available to them under climate change (Estrada et al., 2018). This may be because non-volant hibernators may have reduced mobility, limiting their capacity for dispersal. Hibernators spend half, if not more, of their lives inactive, reducing the time they have to conduct longer-range movements compared to non-hibernators. Inactivity, for example via hibernation, and dispersal may be contrasting strategies to deal with seasonal food shortages; similar patterns are observed within species, where individuals opt for reduced activity or active foraging strategies (Gutman et al., 2007). As hibernation is more common among small mammals (Liow et al., 2008), shortened dispersal time may considerably limit dispersal capability, though clearly less so for volant species. Although there has been little research into this potential relationship, the slow range expansion of non-native edible dormice in the UK (Morris, 2008) could be due to this effect. Therefore, hibernation may prevent species from fully realising their potential niches under climate change, resulting in smaller ranges and populations that are at greater risk of extinction. In this case, hibernators may benefit from translocations or reintroductions; some programmes for hibernating species have occurred, and though successful in establishing a new population, further expansion from the initial site has been minimal (Mitchell-Jones and White, 2009).

Conclusion

Hibernation and conservation pressures

Suggestions that hibernation has helped species cope with environmental change (Liow et al., 2008, 2009) imply that hibernators would respond relatively well to current climate change and other anthropogenic pressures. However, evidence for actual or potential responses to climate change are very mixed (Figure 2.1). Generally, hibernation does seem to confer some protection from the pressures of predation and disease. However, when exceptions occur, such as with WNS, there can be severe consequences for individuals and species. There are well-established negative consequences of excessive disturbance. Hibernator responses to climate change related pressures are diverse, influenced by interactions between environment, and species range and ecology, at a variety of spatial and temporal scales. However, within each climate change related pressure, there are clear examples of hibernators responding negatively, such as decreases in survival. This indicates that hibernation has the potential to exacerbate the negative consequences of climate change.

Nonetheless more research will be required to understand the exact outcomes. For phenotypic responses, greater understanding of why differences occur within and between species (Figure 2.1) could aid in predicting the consequences for understudied species, and direct conservation efforts towards species with mismatches. The effect of hibernation on range mismatch is speculative (Figure 2.1), but it is important to understand whether hibernators need to be the focus of more translocations projects, and to incorporate the possible impacts of subsequent dispersal into the design of such programmes. Overall, there is a lack of research on tropical hibernators (Wells et al., 2022), who's distinctive hibernation strategies (Lovegrove et al., 2014) make it difficult to predict their responses to threats.

Conservation action for hibernators

We found evidence of conservation actions with the potential to mitigate some of the negative consequences of hibernation (Table 2.1). For example, modern grille designs and access regulations restrict cave entry during bat hibernation, reducing disturbance. There are, however, unexpected negative consequences for many actions, where species have not responded as expected; for example, the artificial hibernacula conservationists have created mostly remain unused, even if expanding existing hibernacula can be beneficial. Despite apparent theory that increasing resource availability should aid hibernating species, supplementary feeding has, at best mixed, outcomes. Clarifying some of the relations between hibernation and pressures highlighted above may indicate future opportunities for conservation action.

There are also theorised conservation actions that have yet to be tested (Table 2.1). Disturbance during hibernation has clear negative effects on hibernators (Figure 2.1).

It is, however, unclear how habitat management during hibernation effects the overall population of species that hibernate singularly or in pairs, when only a few individuals might be impacted, and when the species also relies on such action. There needs to be greater understanding of the costs and benefits of management during hibernation at the population level to aid conservation decision making. There might also be an opportunity to optimise conservation actions for hibernators, by timing them to exploit seasonal changes in survival and so population growth.

Table 2.1. A summary of plausible management actions that could alleviate negative effects of hibernation-pressure interactions. *For each action we summarise: the hibernation biology and pressure it relates to; whether the response is from the habitat, animal or legislature; whether evidence for the action was found in the literature; the result of the study if evidence was found; whether the effect on the hibernator was positive, negative, mixed or unclear; and the reference if applicable.*

Hypothesised action	**Hibernation biology**	**Pressure**	**Response**	**Evidence**	**Result**	**Effect**	**References**
Timing conservation action to match seasonal variation in survival rates	Low activity	Predation	Animal	No		Unclear	
Protection of hibernacula when designating protected areas	Energy Balance	Disturbance	Legislative	No		Unclear	
Changing timing of management activities e.g. forestry	Energy Balance	Disturbance	Animal	No		Unclear	
Supplementary feeding to aid preparation for hibernation	Resources	Phenological mismatch	Animal	No		Unclear	
Supplementary feeding to increase survival from WNS infections	Energy Balance / Resources	Disease	Animal	Yes	Electrolyte supplementation during arousals did not reduce mortality or weight loss in WNS infected bats	Negative	(McGuire et al., 2019)

Removal of WNS infected individuals to reduce transmission	Energy Balance	Disease	Animal	Yes	High infection rates and Allee effects suggest it will be ineffective	Negative	(Langwig et al., 2015)
Timing of disease control interventions	Low activity	Disease	Animal	Yes	Vaccination of raccoon dogs most effective after emergence as readily eat bait	Positive	(Singer et al., 2009)
Manipulation of hibernaculum microclimates to aid energy balance	Energy Balance	Disease	Animal	Yes	Cooling subterranean hibernaculum sites led to slightly increased counts of several bat species. Uncertain if affected survival	Mixed	(Turner et al., 2022)
Manipulation of hibernaculum microclimates to aid energy balance	Energy Balance	Disease	Animal	Yes	Reducing temporal variability in temperature and humidity and increasing spatial gradients increased modelled cave-hibernating bat fitness	Positive	(Boyles et al., 2023)

WNS treatments whilst hibernating cause disturbance	Energy Balance	Disturbance	Model	Yes	Disturbance reduces treatment success and adds variation when predicting outcomes	Negative	(Grider et al., 2022)
Gates and walls to prevent human access to hibernation caves	Energy Balance	Disturbance	Animal	Yes	Early attempts reduced bat populations	Negative	(Furey and Racey, 2016)
					Gates reduce access to bats	Negative	(Mitchell-Jones et al., 2007)
					Walls and gates can reduce airflow increasing internal temperature	Negative	(Richter et al., 1993)
					Some bat species react poorly to grilles for example abandoning caves and decreased flight speed	Negative	(Mitchell-Jones et al., 2007)
					Modern designs can increase numbers of bats	Positive	”(Richter et al., 1993; Berthinussen et al., 2020)”

					Modern designs have mixed effects for some bat species	Mixed	(Berthinussen et al., 2020)
Enforcing access regulations to prevent tourist access during hibernation	Energy Balance	Disturbance	Animal	Yes	Increase in bat numbers	Positive	(Olson et al., 2011)
Protection of hibernating individuals from management related disturbance	Energy Balance	Disturbance	Legislative	Yes	Conservation legislation preventing disturbance of protected species e.g. European Habitats Directive (1992) though results unclear	Unclear	
Supplementary feeding during times of increased temperature	Energy Balance / Resources	Temperature Variability	Animal	Yes	Male hamsters shortened hibernation duration; females did not	Mixed	(Siutz et al., 2018)
Maintaining ideal temperatures in hibernacula via man-made interventions	Energy Balance	Temperature Variability	Habitat	Yes	Detrimental increases in temperature variability	Negative	(Berthinussen et al., 2020)
					Detrimental changes to other aspects of cave environment e.g. humidity	Negative	(Meierhofer et al., 2022)

					Cooling subterranean hibernaculum sites led to slightly increased counts of several bat species. Uncertain if affected survival	Mixed	(Turner et al., 2022)
Reintroductions and translocations to aid range filling	Low activity	Range shifts and mismatch	Animal	Yes	Successful establishment of hazel dormouse populations though limited spread	Mixed	(Mitchell-Jones and White, 2009)
Create new hibernacula to aid range filling	Energy Balance	Range shifts and mismatch	Animal	Yes	Poor use of man-made bat hibernation caves	Negative	(Mitchell-Jones et al., 2007)
					Review of 25 years of provisioning in UK shows low occupancy and abundance	Negative	(Furey and Racey, 2016)
					Hazel dormice avoid nest boxes for hibernation	Negative	(Bright and Morris, 1996)
	Energy Balance	Range shifts and mismatch	Animal	Yes	Hedgehogs use artificial nest boxes for hibernation in gardens	Positive	(Gazzard and Baker, 2022)

Expand existing hibernacula to increase capacity to aid range filling	Energy Balance	Range shifts and mismatch	Animal	Yes	Addition of chambers to existing caves used by bats	Positive	(Furey and Racey, 2016)
					Added new hibernation roosts for bats in an existing hibernaculum leading to increased numbers	Positive	(Mitchell-Jones et al., 2007)

Chapter 3: Variation in hazel dormouse (*Muscardinus avellanarius*) presence in hedge and scrub habitats

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This chapter has been accepted as:

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Abstract

1. Habitat restoration at a landscape scale is key to reversing the loss of biodiversity arising from habitat destruction. In landscapes that are intensively used by people, such as for agriculture, valuable restoration efforts might be applied not just to 'prime' habitats that are known to have strong associations with target species, but also to 'sub-prime' habitats that might nevertheless provide sufficient resources to support populations.

2. Hazel dormouse (*Muscardinus avellanarius*) populations are in chronic decline in the UK. The species is typically associated with broadleaf woodland but restoration of this habitat at scale in agricultural landscapes is difficult. Other habitats used by dormice might therefore provide opportunities for restoration. We investigated the use by hazel dormice of hedgerow and scrub habitats in southwest England. From June-November 2022, using footprint-recording tunnels, we surveyed 38 hedges and 21 scrub patches in the vicinity of 18 sites known to contain established dormouse populations.

3. We found that dormice were frequently present in scrub (9.3 detections per 100 tunnel checks, 95% confidence interval 6.6–12.0) and less frequently in hedges (4.5 detections, 95% CI 3.2–5.8).
4. In scrub patches, dormice were present more frequently as the abundance of dormice in the closest population increased, and less frequently where bracken (*Pteridium aquilinum*) was dominant.
5. In hedges, dormice were detected more frequently where there was abundant hazel (*Corylus avellana*) and honeysuckle (*Lonicera periclymenum*), as frequency of intersections with other hedges increased, and where an earthen bank was not present.
6. Understanding hazel dormouse association with a wide range of habitats, particularly scrub, offers more opportunities for habitat restoration as part of species conservation strategies.

Introduction

One of the main drivers of current and rapid biodiversity loss is habitat destruction (Dirzo et al., 2014), especially for habitats that are difficult to restore, such as forests. Although habitat loss can result from both natural and anthropogenic causes, the latter is more likely to result in permanent losses due to conversion to other land uses, such as agriculture (Foley et al., 2005). Habitat destruction also fragments the remaining habitat patches. In forested landscapes, anthropogenic habitat fragmentation causes further degradation of the residual woodlands (Wade et al., 2003), as well as loss of total area (Hansen et al., 2020), which together can accelerate the decline of forest-reliant species. Forest fragmentation is a particular issue in temperate areas, where over half of forests had been fragmented by human activities by 1993 (Wade et al., 2003)

Habitat fragmentation has additional effects beyond habitat loss. At the population level, habitat fragments are smaller, decreasing resident population sizes, and more isolated, decreasing population mixing (Haddad et al., 2015). These effects of fragmentation can be exacerbated by the surrounding habitat matrix, as more hostile matrices, with greater contrast between habitats, limit dispersal (Prugh et al., 2008) and reduce population persistence within fragments (Dunford and Freemark, 2005). These small, isolated populations in fragmented landscapes are at greater risk of extinction (Haddad et al., 2015), due to stochastic events (Caughley, 1994) and reduced genetic diversity (Almeida-Rocha et al., 2020), especially if the species has limited dispersal capability.

Conservation actions are therefore required to alleviate the negative effects of habitat loss and fragmentation. For species with strong associations with particular habitats, actions tend to focus on linking remaining fragments of ‘prime’ habitat by creating corridors (Baum et al., 2004) and/or increasing patch size through creating new prime habitat. However, there is often a lack of knowledge about how other habitats, which might not be considered prime as they support small or transitory populations, might contribute to sustaining populations. For example, pine martens (*Martes martes*) are typically associated with forest, but benefit from additional resources from matrix habitats, such as grassland where their food species are frequently found (Caryl et al., 2012). Non-classical, or ’sub-prime’ habitats might also provide dispersal routes or supplementary residential habitat if they contain sufficient resources. Though there may be less certainty about how target species use such habitats, they might have equal or greater value than prime habitats by helping to sustain and enhance local metapopulations, and understanding their benefits could increase the opportunities for conservation. A diverse set of actions, targeting multiple habitats, means strategies might be more readily tailored to the restrictions and opportunities of each landscape context.

Hazel dormice (*Muscardinus avellanarius*) are small arboreal rodents, populations of which are threatened by habitat loss and fragmentation (Hutterer et al., 2021). In Great Britain, hazel dormice are in chronic decline (Scopes et al., 2023), are currently listed as Vulnerable on the Great Britain Red List (Mathews et al., 2020), and are in ’Unfavourable Conservation Status’ (JNCC, 2019). Both these latter assessments reference insufficient habitat to support long-term population persistence (JNCC, 2019; Morris, 2021). There is a statutory obligation to return dormice to ’Favourable Conservation Status’, which, as currently defined, would require doubling the population in the next 10 years, and again the following 10 years (Scopes et al., 2023). Increasing dormouse populations will require a focus on restoring viable habitat to alleviate the threat of fragmentation. The recent Environment Act (2021) allows the creation of ’Species Conservation Strategies’ which could focus on species conservation at a landscape scale, rather than relying primarily on more localised protection, including of individual animals and their nests. This presents an opportunity to investigate the multitude of actions that could be applied to restore dormouse habitat at this scale.

Conventionally, hazel dormice are thought to use and prefer broadleaf woodland (Bright and Morris, 1996; Fedyń et al., 2021), though there is increasing evidence, including from conservation practitioners, that they use a wider variety of habitats (Phillips et al., 2022). The established view has led to an abundance of research into approaches to woodland management for dormouse conservation, focused on maintaining mid-successional stages. There is a general consensus that woodland creation and active management are key approaches, however, there can also be practical restrictions such as the financial costs of removing land from agriculture and working effectively at scale with inherently small-scale practices such as coppicing (Phillips et al., 2022). There has also been some work on the importance of increasing landscape connectivity (Iannarilli et al., 2017; Dietz et al., 2018), mainly through creating and managing hedgerows.

Hedgerows and scrub have not been extensively studied as dormouse habitats in their own right, though hedge density has frequently been linked to dormouse presence and abundance in fragmented woodland patches (Capizzi et al., 2002; Dietz et al., 2018), and local surveys have frequently found hazel dormice and their nests in these habitats (Ehlers, 2012; Bright and MacPherson, 2002; Phillips et al., 2022). Some studies have also identified habitat factors (such as species diversity and structural complexity) that are associated with more frequent detection of dormouse nests (Dondina et al., 2016). Conservation practitioners frequently indicate that hedges and scrub are important habitats for dormice, and though there is little discussion of the management of scrub beyond its creation, for hedges they suggest that, alongside hedge creation, changing trimming practices to encourage wider hedges with fewer gaps and increasing species diversity would benefit dormice (Phillips et al., 2022). Surveys in England have also found evidence of dormice using primarily large species-rich hedges (Bright and Morris, 1996; Bright and MacPherson, 2002), as well as some that are more intensively managed (Chanin and Woods, 2003).

Given these expert opinions, additional evidence is required to understand how hazel dormice use these habitats. In this study, we surveyed hedges and scrub in the vicinity of known hazel dormouse populations to estimate and compare occurrence within these sub-prime habitats, and consider how variation in habitat affects detection. Studies so far have employed surveys of natural nests (Berg, 1996; Berg and Berg, 1998; Wolton, 2009; Ramakers et al., 2014) or nest tubes (Chanin and Woods, 2003; Ehlers, 2012; Dondina et al., 2016) to assess presence, which require dormice to reside in the habitat. Instead, we use footprint tunnels which have been shown to be faster (Mills et al., 2016; Bullion et al., 2018) and better for detecting dormice, with five times the occupancy rates from footprint tunnels compared to nest boxes or tubes (Melcore et al., 2020).

Methods

Site selection and permission

We selected survey sites based on the locations of National Dormouse Monitoring Programme (NDMP) sites in Cornwall and Devon in south-west England that had evidence of dormice activity in 2020/2021. This acted as a positive control, so that any absences were more likely to relate to habitat use than the wider landscape context. We identified landowners within 1 km of the NDMP site through online resources, and by contacting local businesses that might own land (e.g. farms). Having located landowners and secured survey permission, we selected hedges/scrub patches to cover different management stages (e.g., laid and intact hedges) and clear differences in structure. We define scrub as patches of shrub, for example gorse *Ulex europaeus* that are <5m in height, with no or only occasional trees.

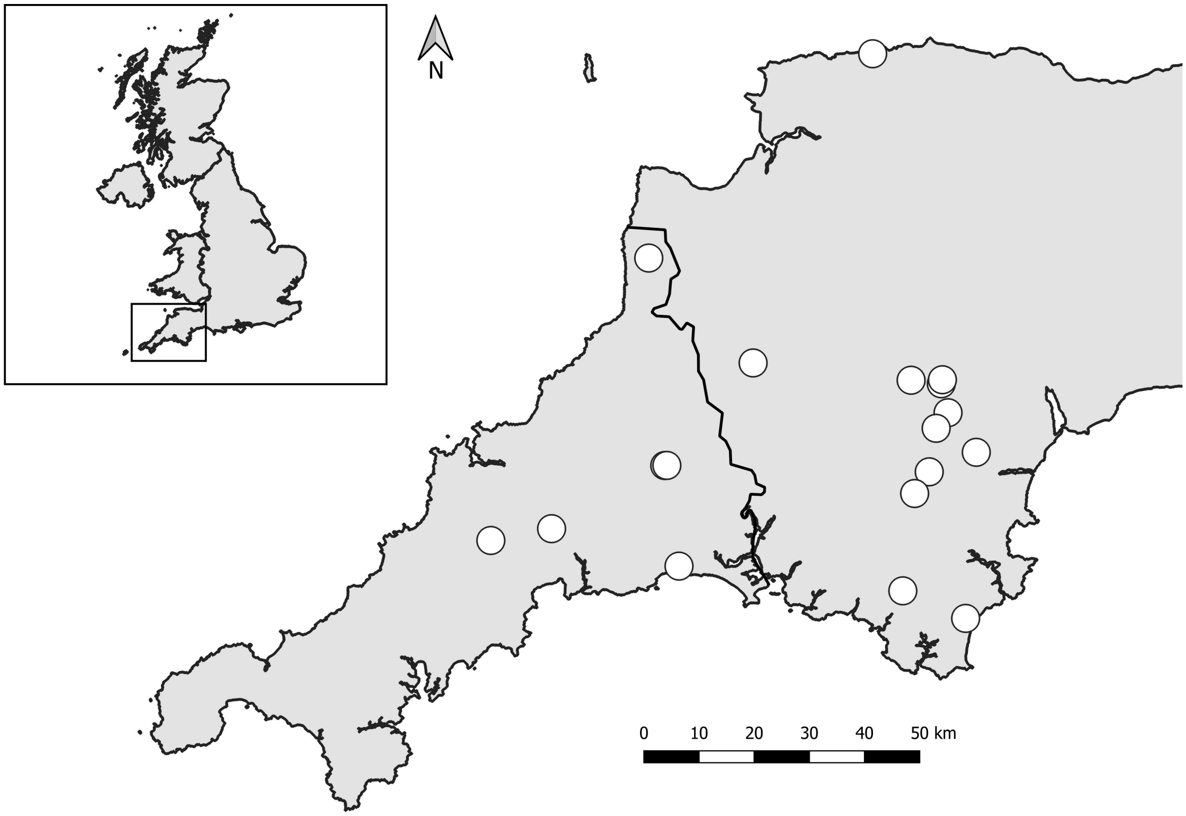

Figure 3.1. A map of the study area in the counties of Cornwall and Devon, with the locations of the National Dormouse Monitoring Programme sites (open circles) around which multiple hedges and scrub patches were surveyed. *Inset map shows the UK with a box outlining the location of the study area.*

Survey methods

Surveys took place with ethical approval from the College of Life and Environmental Sciences (Cornwall) Ethics Committee at the University of Exeter (Application ID: 513767). All surveys took place between June and November 2022. We surveyed hedge and scrub plots in the vicinity of 18 NDMP sites; 6 in Cornwall and 12 in Devon (Figure 3.1). Eleven sites were surveyed by volunteers, and the remaining seven were surveyed by ERS. Part-way through the survey, the tunnels in one hedge had to be moved to another to allow for habitat management, and these are treated as separate hedges. One volunteer withdrew from the study after one check, so this hedge was removed from the analysis.

Determination of dormouse presence was based on identification of their footprints recorded in a footprint tracking tunnel (Mills et al., 2016; Bullion et al., 2018). These tunnels comprise a square plastic pipe with a wooden insert on which to place card and ink made of edible charcoal and vegetable oil. Dormouse footprints can be distinguished from other small mammals by their unique pattern (Mills et al., 2016). We placed 20 tunnels in each hedge/scrub patch, with 10-15 m spacing between tunnels. The tunnels were placed in transects along hedges, and grids in scrub, though this was altered according to accessibility. Tunnels were also split across multiple hedges/scrub patches when one was insufficiently large to accommodate 20 tunnels (minimum seven in hedges, 10 in scrub). Such splits were noted as being in different hedges/scrub patches if the vegetation, management and/or structure of the habitat differed.

The tunnels were checked every two weeks to allow sufficient time for small mammals to use the tunnels, while not allowing the ink to dry out (Bullion et al., 2018), and were checked for two to five months. We recorded hazel dormouse and other small mammal footprints, not identified to species, for each tunnel at each check, and changed the footprint card if it had any footprints or was damaged. Checks were removed from the analysis if damage to the tunnels prevented us from ascertaining footprint presence, and damaged tunnels were replaced.

We trained volunteers initially using a protocol and footprint identification document, and then by meeting with them to set up the site. Volunteers were encouraged to identify footprints themselves but were also asked to collect in the footprint cards so we could check for footprints and species identification. As hazel dormice are not disturbed whilst footprint tunnels are checked, volunteers did not require a licence to participate. Volunteers had been instructed to stop surveys if a nest was found in a tunnel, however due to the timings of the surveys undertaken by volunteers, they did not find any nests. Those nests that were found in tunnels were at sites checked by ERS, who held the relevant protected species licence (Natural England, registration number 2020-49759-CLS-CLS). Nests were counted amongst dormouse presences for as long as the nest appeared used by dormice and not another small mammal species.

Habitat and population data

Habitat surveys were completed at the same time as the tunnels were placed, and by the same person for all sites. We collected data at both the tunnel-level and the hedge/scrub patch-level (referred to collectively as plot-level data). For each tunnel we noted the height of the tunnel from the ground, and ranked the five dominant vegetation species within 1 m of the tunnel. For tunnels in hedges we also noted if there was hedge gap within 1 m of the tunnel. For scrub tunnels we noted, as a single variable, whether the tunnel was in the interior of the patch, or the type of surrounding habitat (route/path, pasture, woodland) if it was on the edge.

For each hedge, we collected information based on the Great British Hedgerow Survey methodology (PTES, 2019b) relating to hedge structure and species composition, such as height and whether there was an earthen hedge bank (usually a constructed ridge of stone and soil on which a hedge sits). We also estimated the abundance of the plant species that previous research has indicated are important for dormice (Goodwin et al., 2018b), using the DAFOR index (Dominant >75%, Abundant 51–75%, Frequent 26–50%, Occasional 11–25%, Rare 1–10%, plus Absent). For scrub patches, we collected similar data to the hedge survey (Table 3.1), and other variables also relating to structure and management (Table 3.2). A full list of the data collected can be found in Appendix 2.

We also measured the length of each hedge using GIS and ESRI satellite imagery. Similarly, we measured the minimum distance a dormouse would have to travel from the nearest NDMP site to the hedge or scrub patch, via appropriate habitat such as hedges and woodland. We measured the closest distance, along a putative dormouse path, of each plot to any woodland, as defined by the National Forest Inventory 2020 (Anonymous, 2022). For hedges, we additionally considered the connecting habitat that a dormouse travelling outwards from the NDMP site would be going towards, either another woodland or more hedges. We used the tunnel-level data of the ranked vegetation species, which provided up to five species per tunnel position evenly distributed in the plot, to calculate plot-level Shannon diversity indices.

Finally, we included a measure of hazel dormouse abundance at the nearest NDMP site. We calculated an abundance index for each site using data from the NDMP surveys, where licensed volunteers count dormice in grids of nest boxes up to once a month from May until September. More information about the surveys can be found in the NDMP guidelines (PTES, 2019a). We used NDMP data from 1993 until 2021, including any site across the NDMP that had been surveyed for more than two years, and had found at least one dormouse. We used the approach initially applied by Goodwin et al. (2017) and updated by Scopes et al. (2023), where counts of adult dormice were modelled with a Poisson error structure against year, site and month of survey, with an offset of number of boxes to control for survey effort. This gives an index for each site indicating the number of dormice counted per unit of survey effort (per box) over the survey period 1993-2021. Not all the NDMP sites surveyed here had data for at least two years, so we used a subset for models utilising this data.

Statistical Analysis

All analyses were completed in R version 4.2.2 (R Core Team, 2022). We separately summarised variation in the presence of dormice and of other small mammals to compare their overall presence in hedges and scrub. To do so, we used a binomial generalised linear model (GLM) with the presence/absence of footprints as a binary response, and included habitat and distance to woodland as fixed effects, as scrub patches were on average closer to woodland than hedges. This is the only part of the analysis where hedge and scrub data were modelled together.

Next, and for each of the two habitats separately, we used two models, one at the level of the individual survey tunnel (tunnel-level model) and one at the hedge/scrub survey plot level (plot-level model) to explore how habitat factors at these two scales affect dormouse presence.

For the tunnel-level model, within each plot, we modelled the presence/absence of dormice at each check as a binary response, using a binomial GLM with a logit link function. All models included fixed effects of the plot and the day of the year the check occurred, which was scaled so that the first survey date (20th June) was day zero. We then tested whether habitat data at the tunnel-level improved the fit of these models and significantly affected dormouse presence, by including each variable as a fixed effect. We only included the first rank dominant species. We compared model performances using the Akaike information criterion (AIC), looking for models with the lowest AIC, providing the AIC differed by more than two (Burnham and Anderson, 2002). When we had finalised the variables, we used k-fold cross validation to identify the best polynomial shape for the relationship between the day of the year and detection, with a k=10 to avoid bias correction (Yates et al., 2023). This process gave a final, tunnel-level model for each habitat. To calculate a plot-level score of dormouse presence, we predicted the probability of dormouse presence for each plot when the other model variables (e.g. day of the year) were optimal for dormouse presence detection. Using the optimal conditions gave the most variation between plots, as detection rates were uniformly low across plots at intercept values (see Figure 3.2). These probabilities were the response data for the plot-level models.

For the next stage, for hedges and scrub separately, we used a quasi-binomial error structure to model the probabilities detailed above. To accommodate this error structure, and include random effects, we used a generalised linear mixed effect model (package gam, Hastie 2023). Our study design, with 20 tunnels and at least two months of checks, gives $>$90% probability of detecting dormice for all habitat types (PTES, unpublished data). This means we have similar confidence in our presences and absences and did not weight the response variables. We first fitted individual models for each variable we collected, testing 23 individual habitat factors against dormouse presence in hedges, and 24 factors in scrub. All these plot-level models included a random effect of the NDMP site, controlling for un-surveyed aspects of habitat, location and local hazel dormouse population. Given that scrub patches were usually closer to woodland than hedges, we tested an interaction term between the effects of each variable and the distance to woodland, however, there were no significant interactions so these were not included. We assessed whether the variable had some significant effect through analysis of variance (ANOVA) comparison between the model and a null model including only the random effect of site, using a chi-squared test. As this was the first step in variable selection and was exploratory, we used a significance threshold of p-value of <0.1. We then combined the variables that passed this threshold into two joint models, one for each habitat, to investigate whether significance of the factors was retained using a GLM summary (here p-value < 0.05). The multivariate models included a random effect of site and a random effect of surveyor (volunteer or ERS). This provided a final model for each habitat, from which to draw inference. We present the results as odds ratios, where an odds ratio of one indicates equal odds of detecting a dormouse.

Results

Footprint data

We completed 7560 individual tunnel checks in 38 hedges and 21 scrub patches, associated with 18 NDMP sites. All tunnels were checked on a minimum of four occasions (mean = 7.8), between 20th June and 3rd November 2022. 1266 checks were removed from the analysis as the tunnels were damaged or had fallen out of place. Of 3957 successful checks in hedges, hazel dormouse footprints were detected on 171 checks at 21 of 38 plots. Of 2337 successful checks in scrub, dormouse footprints were detected on 229 checks at 11 of 21 plots. The binomial model of all successful checks suggests there is a significant difference in detection of dormouse footprints between hedge and scrub habitat ($p < 0.0001$), with 4.5 (95% confidence interval: 3.2 - 5.8) detections per 100 tunnel checks in hedges and 9.3 (95% CI: 6.6 - 12.0) in scrub. For both habitats, the likelihood of detection decreased with increasing distance from woodland ($p = 0.001$).

Hazel dormouse nests were found at 20 tunnel checks (11.7% of checks with dormouse presences) in hedges and 11 checks (4.8%) in scrub.

Footprints of other small mammal species were frequently detected, with significantly greater frequency in hedges than in scrub ($p < 0.0001$). We found 1,556 checks with footprints of other small mammals in hedges, or 38.9 (95% CI: 35.8-42.1) detections of footprints per 100 tunnel checks. In scrub, there were 778 checks that detected footprints of other small mammals or 34.2 (95% CI: 30.0-38.4) detections per 100 tunnel checks.

Variation in hazel dormouse presence

Tunnel-level factors

For hedges, detection of dormouse footprints was significantly greater in tunnels placed higher in the hedge and in hedges with fewer gaps (Table S3.1, Figure 3.2A). Tunnels placed higher in scrub had greater detection of dormouse footprints, as did tunnels placed in the interior of the patch, or if they were on an edge, when that edge was next to a route (Table S3.1, Figure 3.2B). Though the relationships between check day and dormouse presence differed between habitats (Table S3.2), both showed increases across the season, peaking in late October (Figure 3.2). There was also significant variation between plots in both habitats (Table S4.1), which was analysed further in the plot-level models.

Plot-level factors

In hedges, nine factors passed the initial screening threshold: the abundances of bramble (*Rubus fruticosus*), hazel (*Corylus avellana*) and honeysuckle (*Lonicera periclymenum*), the Shannon diversity index, the distance to woodland (Table 3.1), the number of intersections, the percentage gaps in the hedge, the number of gaps wider than 5m, and the presence of an earthen hedge bank (Table 3.2). Combining these into the joint model, we found dormouse presence was significantly greater in hedges with high hazel and honeysuckle abundance, more intersections and without an earthen bank (Figure 3.3).

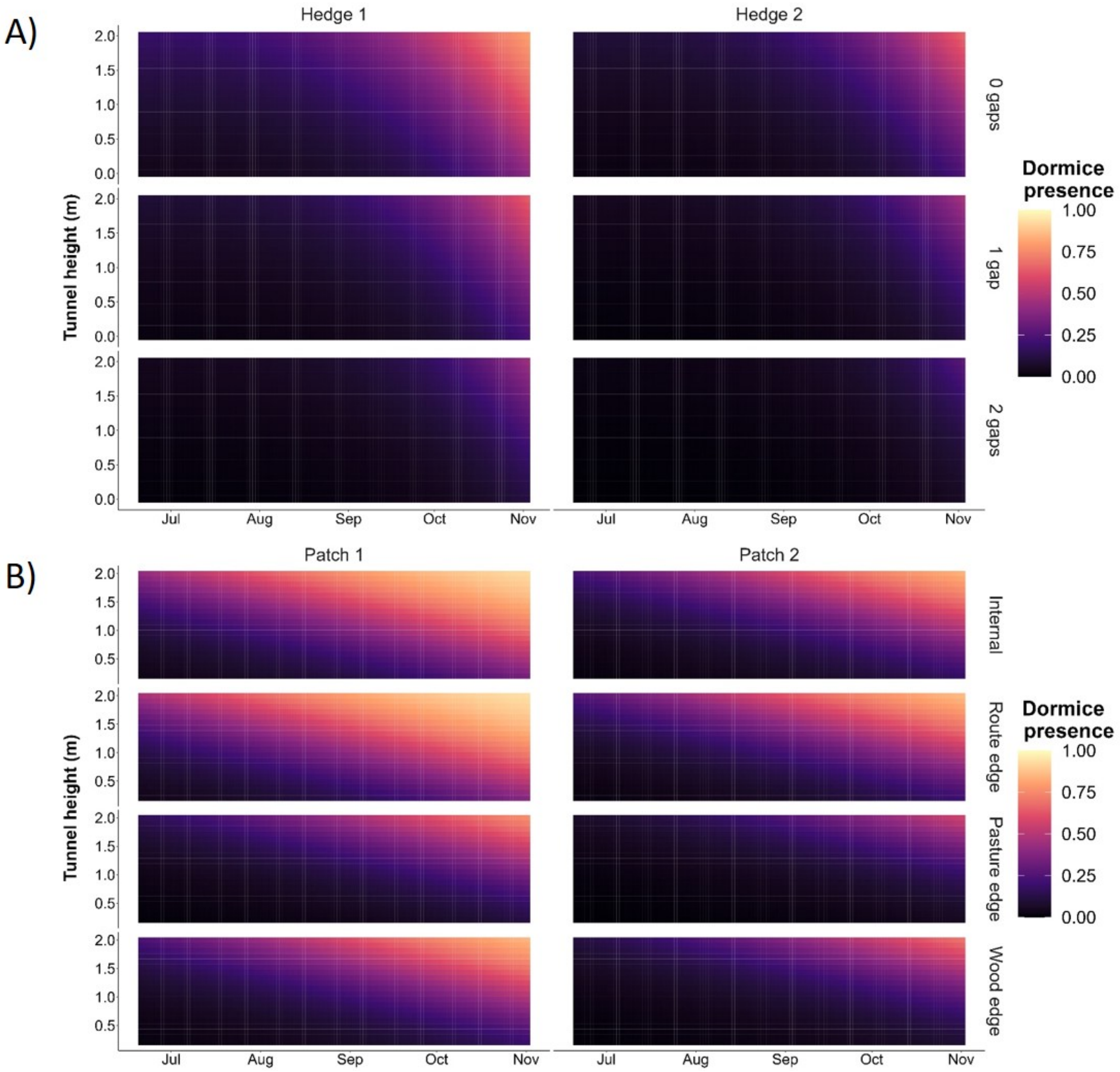

Figure 3.2. Dormouse presence at A) two exemplar hedge plots and B) two exemplar scrub plots. *Figure 2A is the best model from the AIC selection process for the hedge tunnel-level model, and figure 2B is the best model from the same selection process for the separate scrub tunnel-level model. For both figures, columns show two different plots (hedges or scrub patches) with differing frequencies of dormouse presence, and the colour of the squares indicates the frequency of dormouse presence. In plot A, the rows show the number of gaps, whilst in plot B rows show the different edge types.*

Table 3.1. A comparison of the exploratory analysis of variables affecting dormouse presence in hedge and scrub habitats, where habitat factors are directly comparable*. Each variable has been tested individually in a model that also contains a random effect of site, and compared through ANOVA to a null model which only contains a random effect of site, to give the p-value displayed here. An asterisk indicates p-values below 0.1, which was used as the threshold for the initial selection of variables that were used in the joint model for hedge and scrub respectively. A NA ANOVA p-value is due to a lack of degrees of freedom in the model for that variable. 'Ordinal DAFOR' refers to the abundance of a plant species using sequential categories (Dominant >75%, Abundant 51–75%, Frequent 26–50%, Occasional 11–25%, Rare 1–10%, plus Absent) and 'Abundance index' refers to the relative abundance of adult dormice at the nearest National Dormouse Monitoring Programme site.*

Model variable	**Hedge ANOVA p-value**	**Scrub ANOVA p-value**
Abundance Index (subset)	0.229	0.001*
Dormouse travel distance (m)	0.785	0.888
Number of emergent trees	NA	0.658
Bramble (ordinal DAFOR)	0.06*	0.466
Hazel (ordinal DAFOR)	0.002*	0.853
Honeysuckle (ordinal DAFOR)	0.079*	0.717
Willow (ordinal DAFOR)	0.156	0.487
Shannon diversity index	0.05*	0.501
Distance to woodland (m)	0.058*	0.466

In scrub, only three factors passed the initial threshold; the NDMP site Abundance Index (Table 3.1), the dominant mid-storey species, and the presence of management along scrub edges (Table 3.2). In the joint model with these variables, we found dormouse presence was significantly greater near NDMP sites with a greater Abundance Index and significantly reduced in plots with a bracken (*Pteridium aquilinum*) dominated mid-storey (in comparison to a gorse dominated mid-storey, Figure 3.3)

Table 3.2. A comparison of the exploratory analysis of variables affecting dormouse presence in hedge and scrub habitats, where habitat factors are not directly comparable. *Each variable has been tested individually in a model that also contains a random effect of site, and compared through ANOVA to a null model which only contains a random effect of site, to give the p-value displayed here. An asterisk indicates p-values below 0.1, which was used as the threshold for the initial selection of variables that were used in the joint model for hedge and scrub respectively. An NA ANOVA p-value is due to a lack of degrees of freedom in the model for that variable. 'Bank present' refers to the presence of an earthen hedge bank, 'ordinal DAFOR' refers to the abundance of a plant species using sequential categories (Dominant >75%, Abundant 51–75%, Frequent 26–50%, Occasional 11–25%, Rare 1–10%, plus Absent), 'land use percentage' refers to the percentage of the perimeter of the scrub with different land uses and 'DME scale' refers to the ground coverage of the scrub (dominant, medium or encroaching).*

Habitat	**Model variable**	**ANOVA p-value**
Hedge	Number of intersections	0.013*
	Percentage gaps	0.013*
	Number of gaps >5m	0.044*
	Bank (Y/N)	0.075*
	Knuckle (Y/N)	0.11
	Height group (m)	0.14
	Width (m)	0.18
	Connection type (hedge/wood)	0.21
	Bank height (m)	0.27
	Number of connections	0.35
	Sycamore (ordinal DAFOR)	0.35
	Number of gates	0.49
	Structure group	0.5
	Length (m)	0.86
Scrub	Dominant mid-storey species	0.0036*
	Managemnet at edges (Y/N)	0.0052*
	Land use percentage: woodland	0.12
	Land use percentage: route	0.12

Dominant upper storey species	0.13
Birch (ordinal DAFOR)	0.13
Dominant ground species	0.19
Managemnet internally (Y/N)	0.22
Land use percentage: pasture	0.32
DME scale	0.37
Height (m)	0.53
Land use percentage: arable	0.62
Number of paths >1m	0.94
Connection between shrubs (Y/N)	NA
Land use percentage: scrub	NA

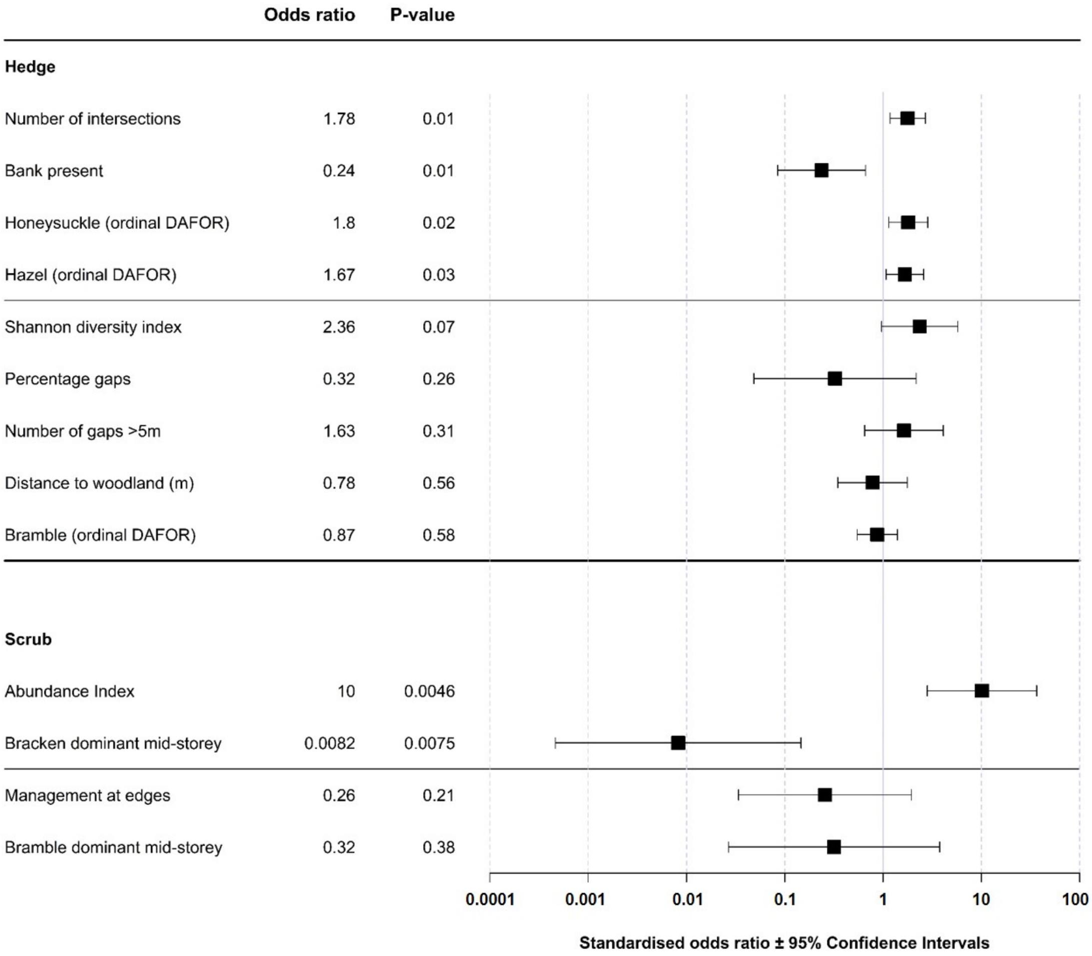

Figure 3.3. Relationships between habitat factors and dormouse presence in the joint models for hedges (top) and scrub (bottom). *Standardised odd ratios (with 95% confidence intervals) and the p-value from the joint model are shown. Dominant mid-storey species (bracken and bramble shown here) are in comparison to gorse. An odd ratio of 1 indicates similar odds of dormouse detection. Odds ratio are displayed on a log scale. 'Bank present' refers to the presence of an earthen hedge bank, 'ordinal DAFOR' refers to the abundance of a plant species using sequential categories (Dominant > 75%, Abundant 51–75%, Frequent 26–50%, Occasional 11–25%, Rare 1–10%, plus Absent) and 'Abundance index' refers to the relative abundance of adult dormice at the nearest National Dormouse Monitoring Programme site.*

Discussion

We undertook a targeted survey of the presence of hazel dormice in understudied hedge and scrub habitats in southwest England. We found more than double the frequency of dormouse presence in scrub habitats than in hedges, when controlling for distance to woodland. However, we did find more dormouse nests in hedges (11.7%) than in scrub (4.8%). Our study adds to the growing evidence that hazel dormice use and reside in these habitats, despite being generally viewed as sub-prime relative to broadleaf woodland.

In hedges, dormice were more frequently found, and so seemed to more frequently use, those with a greater abundance of hazel and honeysuckle, more intersections with other hedges and without an earthen hedge bank (Figure 3.3). Meanwhile, in scrub, dormice seem averse to areas with a bracken-dominant mid-storey, and were found more often in plots where the closest NDMP site had a greater population index (Figure 3.3).

The within-plot tunnel-level analysis suggests ways to refine future surveys using footprint tunnels (Figure 3.2). To maximise detection in either habitat, tunnels should be placed higher in the vegetation, up to 2 m to allow surveyors to access them, and surveys should take place in September/October. In hedges, placing tunnels away from gaps will further increase detection, while in scrub, placing tunnels within the patch or along routes will be most effective.

Given there is less research on dormice in scrub than in hedges (Phillips et al., 2022), it is revealing that our study found scrub to be the more frequently used habitat. This suggests that scrub may be more important than previously considered, and indicates additional opportunities for habitat restoration. For example, dense native scrub in a conifer landscape in Sweden can support high densities of hazel dormice (up to 6.7 per hectare, Berg and Berg 1999). In the UK, some experts were confident that scrub could sustain populations of dormice in the long-term, and that creating scrub would be a valuable conservation action (Phillips et al., 2022), which our surveys supports. Our study also agrees with the more extensive literature on hedges, including some evidence that hedges contribute to dormouse population viability at a landscape scale, not only by enabling connectivity, but also by hosting resident individuals (Schulz and Büchner, 2018). Hedges had a greater proportion of nests within tunnels than scrub, which might reflect better availability of natural nesting opportunities in scrub, such as dense bramble patches (Goodwin et al., 2018b).

In scrub, dormice might avoid bracken-dominated patches as it shades out other plants (Pakeman and Marrs, 1992), reducing food availability, compared to gorse which, though also shading, could provide nectar for much of the year. Our results differ from studies in Sweden, where hazel dormice were more often detected in scrub with greater number of shrub species and greater cover of shrub (Berg, 1996; Berg and Berg, 1998), whilst we found no effect of analogous variables (diversity and DME scale, Tables 1 and 2). In this Swedish study (Berg and Berg, 1998), dormice were also associated with areas with greater cover of hazel, which the authors considered important food sources in that conifer-dominated landscape. Differences between our findings and those of Berg and Berg (1998) might reflect the studies' wider landscape contexts of commercial conifer forests, with our scrub adjacent to broadleaved woodland, which may offer greater resources. However, the landscape of our study and Berg (1996) are similar, with deciduous woodland fragmented by farmland. We also did not find dormice more often in bramble-dominated mid-storey, compared to gorse (Figure 3.3), despite bramble being a preferred nesting habitat and associated with population stability (Goodwin et al., 2018b).

Greater abundances of dormice in the nearest NDMP site were associated with more frequent dormouse presence in scrub but not in hedges (Table 3.1). Scrub patches were also closer to woodland than the hedges surveyed, however, including distance to woodland as an interacting term with the other habitat variables did not contribute significantly to explained variance. One possible explanation is that scrub in this study might be predominantly used by resident hazel dormice, with their home ranges overlapping with woodland, whilst the more distant hedges are used by dispersing individuals.

Hazel nuts and honeysuckle provide a key resource for hazel dormice (Juškaitis, 2014), and are associated with greater breeding propensity and population abundance, respectively (Goodwin et al., 2018b). Other research has suggested high hedge density, and therefore high hedge connectivity, can support dormice populations in forest-poor landscapes (Ehlers, 2012; Schulz and Büchner, 2018), which is reflected in our findings. We also found that the presence of an earthen hedge bank decreased the probability of detecting dormice, which might be because tunnels had to be placed lower in hedges with banks, suggesting they would detect footprints less frequently (Figure 3.2). Dormice also appear to prefer wide hedgerows with a numerous native species and complex structure (Dondina et al., 2016), possibly requiring at least 12 woody species (Ehlers, 2012). Similarly, experts consider larger, fuller, more species-diverse hedges to be the most suitable for dormice (Phillips et al., 2022)), which has been evidenced by surveys in England (Bright and MacPherson, 2002). Though we found some support, in the tunnel-level analysis, that dormice avoid gaps, we did not find support for changes in dormouse detection in relation to hedge-level species diversity, width, height or indications of severe management (the presence of a ’knuckle’, vegetative scar tissue, indicating repeated trimming to the same point).

The differences between this study and the existing literature might be attributed to survey methods. Most of the previous research use natural nests (Berg, 1996; Berg and Berg, 1998; Wolton, 2009; Ramakers et al., 2014) or nest tubes (Chanin and Woods, 2003; Ehlers, 2012; Dondina et al., 2016) to assess hazel dormouse presence, whilst we employed footprint tunnels which have been shown to be faster (Mills et al., 2016; Bullion et al., 2018) and more effective methods of detecting dormice (Melcore et al., 2020). Techniques relying on nests highlight habitats preferred for nesting locations rather than for foraging or dispersal. For example, Wolton (2009) found blackthorn (*Prunus spinosa*) was favoured for nest locations over hazel, likely due to its thick thorny vegetation providing structure and protection for nests. Our study may therefore capture additional uses of these habitats.

Our study only surveyed during one season, and so cannot investigate any changes in habitat use that result from annual changes in weather or dormouse population. Nevertheless, the main aim here was to compare detection in hedges and scrub, which experienced the same conditions within the survey year. The summer of 2022 was marked by a drought in southwest England (Environment Agency, 2022), which might have reduced blackberry fruiting, explaining the lack of effect in our analysis. The drought could also have dried the ink faster and reduced detection, however, the high frequency of other small mammal footprints suggests that the method worked as expected. Finally, though our study indicates how dormice are using hedges and scrub, there is some confounding between detection and habitat use. We have accounted for this with the multi-level analysis, with the tunnel-level models controlling for some of the survey variables that could affect detection, and by using a method that gives high detection probabilities. However, future studies combining multiple survey techniques over several seasons might deal more fully with these issues.

Overall, our study reveals hazel dormice frequently use both scrub and hedge habitats, indicating additional targets, beyond the conventional focus on ‘prime’ broadleaf woodland habitat, for management to increase populations on a landscape scale. Scrub in particular, where we detected the most dormice, could be an easy way of increasing valuable habitat, if marginal areas are left to succeed naturally to scrub (Phillips et al., 2022). Practitioners did not have management suggestions, beyond creation, for improving scrub for dormice (Phillips et al., 2022). However, our study indicates that bracken suppression, in favour of other native flowering and fruiting species, may be a management option to increase scrub suitability. This study also suggests establishing new hedges, with abundant hazel and honeysuckle, and improving management of existing ones to increase connectivity would be beneficial for dormice, measures that are well-supported by existing literature and practitioner experience. The high availability of hedges and scrub in UK landscapes indicates a key opportunity to increase available habitat for hazel dormice, rather than focusing on woodland alone. Such actions could help slow and maybe reverse their chronic decline.

Chapter 4: Shifting baselines for species in chronic decline and assessment of conservation status. Are hazel dormice *Muscardinus avellanarius* Endangered?

Chapter 4: Shifting baselines for species in chronic decline and assessment of conservation status. Are hazel dormice *Muscardinus avellanarius* Endangered?

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Abstract

1. Long-term data are clearly beneficial for monitoring the conservation status of species. Assessments of population change over recent periods of fixed duration will, however, be subject to 'shifting baselines', where the accepted norm for the population at the start of the period already represents a reduction from historical levels. International Union for Conservation of Nature Red List criteria for categorising conservation threat rely on assessing declines against quantitative thresholds, generally measured over 10 years, as indications of the likelihood of extinction in the near future. By contrast, legal frameworks such as the European Habitats Directive require states to achieve and sustain 'Favourable Conservation Status' for protected species, while domestic conservation legislation can have more diverse objectives and mechanisms, based on local contexts that extend beyond biological or quantitative criteria.

2. We explore the challenges associated with assessing risk of extinction and the conservation status that arise from the availability of long-term monitoring data for hazel dormice *Muscardinus avellanarius* in the United Kingdom.

3. Numbers of adult dormice counted in the National Dormouse Monitoring Programme are in ongoing decline, amounting to an overall decline of 78% (95% confidence interval = 72–84%) over 27 years 1994–2020. If the observed annual rate of decline of 5.7% (95% CI = 4.7–6.8%) were to continue unabated, dormouse counts would decline by >90% from 1994 to 2033. Despite this, the species would never be categorised as Endangered, under IUCN criteria, which specify a reduction of >50% within 10 years.

4. While such chronic decline may not indicate imminent risk of extinction, justifying a higher Red List category, it is a demonstration of unfavourable conservation status at a national scale. Prioritisation based on demonstration of such chronic declines might direct more effective action towards species conservation at a point when their recovery is more attainable, rather than attempting later to reverse a journey to the brink of extinction when the species is finally 'Endangered'.

Introduction

Given the ongoing biodiversity crisis (IPBES, 2019), robustly assessing a species' risk of extinction has become an indispensable means of quantifying biodiversity loss and prioritising conservation actions. Long-term monitoring allows updates to species status, and continuing or accelerating declines can indicate targets for stepping up conservation action (Miller et al., 2006), while increasing populations might confirm the validity of actions or be celebrated as successes (Roman et al., 2015) Lists of threatened species inform conservation priorities (Miller et al., 2007), and focus scientific research upon knowledge gaps (Jarić et al., 2017). The International Union for Conservation of Nature (IUCN) Red List is the leading tool for categorising conservation threat (Rodrigues et al., 2006), and has helped substantiate and highlight risks of extinction, and identify conservation threats and actions that have averted extinction (Bolam et al., 2021).

Conservation is primarily enacted at the national level (Hunter and Hutchinson, 1994) and so threatened species lists are frequently compiled at this scale, to help inform national action and awareness. Most national lists are based on global IUCN Red List frameworks, adapted for regional assessments (Miller et al., 2007), where modified criteria provide for assessment of the extinction risk facing populations that form part of a species' wider range (IUCN, 2012a). IUCN criteria apply to assessment of extinction risk, based on recent population trend (criterion A), geographic range (B), population size (C and D) and projected probability of extinction (E; IUCN 2012b). Within each criterion there are thresholds and qualifying statements specifying threat level. For example, trend criteria (A) assess population reduction over three generations, or 10 years, whichever is longer, and include past data, as well as projections. Threshold levels of decline for each threat category are also qualified by whether the threats the species faces have ceased or are ongoing (IUCN, 2012b). These criteria are similar, whether applied globally or regionally, though regional populations may be accorded lower categories of threat if the risk of extinction is mitigated by reinforcement by other populations outside the focal region (IUCN, 2012a).

Despite the frequent use of threatened species lists in conservation planning, there is continuing debate about such application. Red List criteria and protocols are not designed for uses other than deriving measures of extinction risk, even if there is a persistent misconception that they measure conservation priority (Collen et al., 2016). Their unqualified use in planning and legislation can therefore often be inappropriate, as it is likely to be inefficient to allocate resources to species threatened with imminent risk of extinction, instead of preventing less severely threatened species from reaching that point (Possingham et al., 2002).

Because of these issues, several international conservation legislative measures have simpler, non-hierarchical approaches that assign priority to any species that is not thriving, shifting the focus from proximity to extinction and towards deviations from historical status. A key example is the idea of Favourable Conservation Status (FCS), which features in European Union legislative instruments, including the EC Habitats Directive (2017; Epstein et al. 2015) and member state transcriptions of this Directive. FCS encompasses standards for thriving species according to three aspects: a population that is maintaining itself on a long-term basis, the species' range is not being reduced, and there is sufficient habitat to maintain the species in the long-term. A species that does not meet one of these three definitions is considered a conservation priority as it is definitively in Unfavourable Conservation Status. FCS also differs from Red List categorisation, as it defines a positive state to reach, whilst the IUCN emphasises a state to avoid. The Red List defines species recovery as when they no longer qualify for any of the threat categories even if, for example, populations are still declining, albeit less steeply. It therefore seems easy for such a 'recovered' species to succumb once again to risk of extinction, especially if conservation priority is based on Red List status, and conservation action has ceased or reduced.

Most monitoring data used in assessing conservation status are based on direct or indirect counts that, even when repeated and standardised, are often intermittent or short term (Bonebrake et al., 2010; Mihoub et al., 2017). There are consistent calls for collection of longer-term data because baselines can affect perceptions of population trend, with shorter study periods potentially masking overall change (Bonebrake et al., 2010; Collins et al., 2020). Setting a baseline disregards the changes that occurred beforehand and, given consistency in patterns of biodiversity loss, use of more recent baselines is more likely to underestimate overall declines. This is a form of ‘shifting baseline’ syndrome, where contemporary losses are underestimated, as degraded populations are accepted as norms without historical context (Soga and Gaston, 2018). This syndrome can make people and processes more tolerant of declines, and produce confusion over which baselines or trends should be used (Soga and Gaston, 2018). Short monitoring periods, though able to indicate precipitous declines, are unable to capture more gradual, chronic losses, or identify extinction debt, where population decline and extinction are delayed after habitat destruction (Kuussaari et al., 2009).

Although the IUCN Red List categorisation process has been created to be as scientifically robust as possible, it has some limitations. Key among these is its stated primary application to determine risk of extinction, rather than conservation status, population change, need for actions, priority, or many other informative indicators for conservation. Furthermore, within the categorisation process, some terms in the category descriptions are deliberately vague, to enable their application in diverse contexts. This adds subjective elements to the interpretation of criteria that can introduce bias and uncertainty (Regan et al., 2000). IUCN criteria do provide guidance for dealing with uncertainty, though they focus less on statistical uncertainty, and more on instances where available evidence is limited (IUCN, 2012b). This is for the obvious reason that threatened species are often scarce, sparsely distributed and hard to monitor effectively. Hence, quantified statistical uncertainty does not often characterise the available information. Red List criteria do not encompass quantitative measures of uncertainty, only central estimates are compared to explicit, invariant thresholds to determine category of extinction risk. Several authors have proposed methods to incorporate statistical uncertainty (Akçakaya et al., 2000; Regan et al., 2000), but it has only recently been considered in formal assessments (Sherley et al., 2020). This means that better quantification of uncertainty, resulting from higher quality data or analyses, tends not to be accommodated in Red List assessment processes. Finally, choosing between analytical models to quantify trends, where this choice may be partly subjective, can also add uncertainty by producing slightly differing, but similarly valid, estimates of population trend. Thus, changes in threat category might result not from actual biological changes, but from minor statistical alterations or differences in approach (Possingham et al., 2002). On the other hand, determining FCS is concerned with whether a species' population, range or available habitat is declining or stable/increasing, which requires less statistical power and is less likely to be affected by statistical uncertainty than when measuring against discrete thresholds. Overall, maximising the value of scarce, hard-won long-term data by using appropriate analytical approaches and assessment criteria is important to account for long-term change in species status and, thereby, to identify conservation actions and priority.

Hazel dormice *Muscardinus avellanarius* in the U.K. are monitored primarily through a large citizen science project, the National Dormouse Monitoring Programme (NDMP). Licensed volunteers install and check nest boxes for dormice during the active season (in the U.K. hazel dormice are obligate hibernators). The Programme started with six sites in 1988, but has expanded considerably, achieving statistically useful scale in 1993, and reaching a maximum of 438 sites in 2016. Although the absolute time frame of monitoring is relatively short, compared to the ideal long-term data set (>100 years; Bonebrake et al. 2010), it is considerably longer than the 10-year period used for Red List assessment. This allows a robust comparison between trends over 10-year and longer periods, enabling us to examine how well assessment of extinction risk encompasses change in populations and in conservation status.

Previous analyses of NDMP data have demonstrated declines in counts of dormice, suggesting population decline of 72% between 1993 and 2014 (Goodwin et al., 2017) associated with reductions in habitat quality (Goodwin et al., 2018b). Based in part upon this analysis, the 2020 Red List for British mammals classified hazel dormice as Vulnerable, on the basis of criterion A2b (Mathews et al., 2020), i.e. an apparent decline of >30% but <50% (central estimate = 48% decline, 95% CI = 39–55%) over the most recently quantified 10-year period (2005 to 2014; Goodwin et al. 2017), where the reduction or its causes may not have ceased, or may not be understood, or may not be reversible (IUCN, 2012b). The most recent assessment of the conservation status of dormice in the UK, which the Statutory Nature Conservation Bodies had been required to report under Article 17 of the EU Habitats Directive, considered their status Unfavourable, based mainly on the declining counts (JNCC, 2019). Targets set by Natural England (the statutory body for England) for dormice to reach FCS are currently: to re-occupy 49 counties where dormice where known to be present in 1885, a reversal of the population decline to return the population to the level of 1993, and an increase in lowland mixed deciduous woodland with appropriate vegetative and structural composition (Morris, 2021). The decline of dormice in Great Britain is particularly troubling, given the legal protection (Conservation of Habitats and Species Regulations 2017, Wildlife and Countryside Act 1981, as amended) and conservation attention given to this species, suggesting that current actions may not be sufficiently effective to halt the decline. We use this large-scale and long-term dataset to explore the process of categorisation of extinction risk and the assessment of conservation status, and to highlight a conservation conundrum whereby the long-term trend obscures more recent losses, yet chronic declines are not reflected in assessment of extinction risk. We also explore how analytical model choice and statistical uncertainty become particularly important as population trends approach thresholds for threat categories. More specifically, given that estimates of dormouse population trends have run close to, but not passed, the threshold (50% decline over 10 years) that would support Red List categorisation as Endangered (Goodwin et al., 2017), we update trends with new data and ask if, or when, dormice might be Endangered in the U.K.

Methods

National Dormouse Monitoring Programme

The NDMP includes sites across England and Wales, spanning the current range for dormice in the U.K. Sites are predominantly located in broadleaf and mixed woodlands. Each site is equipped with a grid of dormouse nest boxes that are checked up to once a month in the active season from May to October, with at least one check post-hibernation in May/June and another after breeding in September/October. Volunteers monitor the number of dormice, along with basic biometric data such as sex, age class and weight. From 1988 to 2021, sites have been monitored for 1–34 years, and have different numbers of boxes, from <10 up to 750. More detailed survey methods can be found in NDMP guidelines (PTES, 2019a). The NDMP only surveys a sub-sample of the dormouse population, i.e. those using boxes on monitoring sites, meaning the derived trends may not be representative of the entire population, or of all habitats. Most potential biases, however, have either previously been evaluated, such as variation in survey effort within and among sites (Goodwin et al., 2017), or are unlikely to affect population trends by systematically changing across the course of monitoring; for example, the habitats covered by the programme change as sites are added or abandoned, but this is likely to be random as it is driven by volunteer availability. For the time-being and in the absence of evidence to the contrary or from other non-woodland habitats, we take the trends in counts presented here to be representative of the wider dormouse population.

Data analysis

We are interested in modelling variation in dormouse counts from sites where they have been recorded, taking into account recording effort and variation in time. Inclusion of data in this analysis follows the approach established in Goodwin et al. (2017). We excluded data from 1988 to 1992, as only a few sites were surveyed in this period, and excluded data from sites that had been surveyed for two years or less, so any site effects could be separated in part from time effects. We also excluded sites that recorded only one dormouse, or none, in the duration of their operation, to avoid zero inflating the data with sites where dormice are not present. Several sites had more than one survey section, which were grouped to reduce the non-independence of related samples. We used the counts of adult dormice in the analyses, as the numbers of younger age-class individuals are not consistently recorded, since they are harder to detect and count, especially as some volunteers dislike disturbing breeding nests. We included data from all months in which surveys took place, to reduce between-month variation impacting yearly trends. Earlier analyses did not find spatial auto-correlation among sites (Goodwin et al., 2017) and this was not included in current models.

All statistical analyses used R version 4.0.2 (R Core Team, 2020). Dormouse counts in nest boxes from 1993 to 2021 were analysed with generalised additive models (GAMs), using the package mgcv (Wood, 2010). The model we employed differs slightly from that in Goodwin et al. (2017), in which we had employed a negative binomial model to deal with overdispersion of data. Overdispersion was measured using the Pearson estimate from the residuals of each model; the Poisson model was overdispersed (estimate: 2.54, greater than 1), and this was effectively reduced by the negative binomial model (estimate: 1.12). We then investigated two potential model distributions, Poisson and negative binomial, by simulating datasets with different distributions, and seeing if the two models could recover the true decline values. We found that the negative binomial model exhibited some negative bias, leading to a slight overestimation (3-4%) of the overall decline, when the data was simulated using any distribution other than negative binomial. Meanwhile, the Poisson model showed low levels of bias irrespective of the actual data distribution, suggesting it is more applicable to this analysis, where an unbiased trend is necessary to assess conservation priority and the underlying distribution of the data is uncertain. We therefore used the Poisson distribution in the model. Again, differing slightly from the earlier analyses, we included month as a fixed effect, with 6 levels for the months May to October, as we found that, after inclusion of additional years of new data, trends varied among months. For consistency and to enable direct comparability, we also applied our earlier (Goodwin et al., 2017) model to the updated data. Thus, we present two models, the current model using Poisson distribution and a fixed effect of month, and the earlier model using a negative binomial distribution without an effect of month, akin to the earlier analysis (Goodwin et al., 2017). In all other respects the models are similar. Comparing these two models also highlights the role of choice in statistical approach, enabling us to compare how two similarly valid modelling approaches affect estimates of population trends and the consequent assessment of threat category.

Both GAMs included a fixed effect of site, to account for site-specific variation in counts, and the number of boxes as an offset variable, to account for varying survey effort. We used fixed effects as our wider ecological analyses focus on site-level variation (Goodwin et al., 2018b). Time was included in the model by including the calendar year in a smoothing function formulated by penalised regression splines. The level of smoothing was determined by qualitative assessment as the number of degrees of freedom (seven), which produced the long-term population signal. To account for the period when the GAM is least reliable (Hewson and Noble, 2009), we do not report trends extending to the first (1993) and last (2021) survey years. Changes for each consecutive year are therefore reported for the 27-year period, 1994 to 2020, with overall changes relative to a baseline in 1994. Bootstrapping with 1000 replicates at the site level, with replacement, was used to calculate the 95% confidence intervals for each model (Fewster et al., 2000).

Because conservation policy is devolved within the U.K., in addition to a U.K. trend, we calculated separate trends for England and Wales by including the country in which the site was located as an interaction term within the smoothing function, as degrees of freedom are not penalised. This was an extension of the Poisson model. Bootstrapping was stratified by country and three null bootstrap samples for Wales, which were likely produced when the limited sites available at the beginning of the time series were not randomly sampled, were removed from the confidence interval calculation.

We calculated 10-year sliding windows of dormouse population change, in line with the 10-year basis for IUCN Red List criteria (IUCN, 2012b). Dormouse population change over the entire 27-year programme was thus divided into sixteen 10-year windows, using the same Poisson model as above. For each window, we calculated change in population size by year 10, relative to year 1, starting with 1994 to 2003, and ending with 2011 to 2020. Bootstrapping was used to calculate 95% confidence intervals as before. To explore how 10-year windows compared to the overall 27-year trend, we plotted all 10-year windows on the same scale as the overall trend, with results relative to an arbitrary value of one at the starting point for each time frame, thereby explicitly identifying the shifting baseline. We applied this sliding window analysis to data from England and Wales separately, and, for comparability, to the earlier negative binomial model (Goodwin et al., 2017).

Results

Survey summary

Between 1993 and 2021, 838 NDMP sites were monitored. 602 (72%) sites recorded more than one adult dormouse: 534 in England and 68 in Wales. The number of sites that recorded more than one dormouse in any one year ranged from 33 in 1995 to 383 in 2016 (Table 4.1). The mean number of boxes per site was 74.6 (SE = 0.4 boxes), and the mean duration of monitoring was 10.1 years (SE = 0.26). The annual mean number of adult dormice counted per site for these 602 sites varied from a high of 8.8 (SE = 0.96) in 1995 to a low of 1.6 (SE = 0.08) in 2021 (Table 4.1).

Table 4.1. Summary of annual records of dormouse counts from the National Dormouse Monitoring Programme from 1993 to 2021. *These data are for all sites where more than one dormouse was recorded and includes the number of sites, the mean (SE mean) numbers of adult dormice counted in nest boxes per site from May to October inclusive, and the mean (SE mean) number of nest boxes per site.*

Year	Number of sites	Mean count of adult dormice (SE Mean)	Mean number of nest boxes (SE Mean)
1993	34	6.2 (0.55)	85 (4.1)
1994	36	5.7 (0.58)	90 (4.8)
1995	33	8.8 (0.96)	97 (5.4)
1996	44	6.6 (0.53)	93 (4.1)
1997	53	6.3 (0.56)	93 (4.2)
1998	70	4.4 (0.35)	75 (3.1)
1999	78	4.9 (0.34)	81 (3.3)
2000	109	4.6 (0.32)	71 (2.4)
2001	111	3.6 (0.24)	78 (2.6)
2002	103	4.2 (0.35)	86 (3.5)
2003	145	3.5 (0.18)	82 (2.8)
2004	153	4.5 (0.32)	78 (2.6)
2005	167	3.4 (0.21)	76 (2.6)
2006	191	3.6 (0.25)	75 (2.5)
2007	192	4.1 (0.23)	81 (2.6)
2008	215	3.0 (0.15)	76 (2.4)
2009	238	3.2 (0.16)	77 (2.1)
2010	268	3.2 (0.15)	74 (1.9)
2011	300	3.5 (0.16)	73 (1.8)
2012	338	2.7 (0.10)	71 (1.7)
2013	344	2.1 (0.08)	71 (1.5)
2014	365	2.4 (0.10)	73 (1.6)
2015	374	2.3 (0.08)	73 (1.7)
2016	383	2.0 (0.08)	72 (1.6)
2017	370	2.0 (0.08)	72 (1.5)
2018	383	1.9 (0.07)	71 (1.4)
2019	369	2.0 (0.08)	72 (1.5)
2020	292	2.0 (0.10)	74 (2.0)
2021	319	1.6 (0.08)	71 (1.6)

Dormouse population change

552 sites had been surveyed for more than two years and were used in analysis. Hazel dormouse counts in nest boxes declined by 78% (95% confidence interval = 72–84% decline; Figure 4.1) over the 27-year period from 1994 to 2020, according to the Poisson model. This model had an adjusted R-squared value of 0.506, and explained 49.2% of model deviance, reflecting the dominance of the trend in time explaining variation in dormouse counts. This equates to a mean annual decline of 5.7% (95% CI = 4.7–6.8%). While confidence intervals overlap, the central estimate of decline, on which Red List criteria are based, has worsened since the previous analysis, which estimated a decline of 72% (95% CI = 62–79%) from 1993 to 2014 (Goodwin et al., 2017). The mean annual decline, however, is similar to the earlier estimate of 5.8% (95% CI = 4.5–7.1%; Goodwin et al. 2017). Applying the model from the earlier analysis (Goodwin et al., 2017) to the new data, with a negative binomial distribution and no inclusion of month, resulted in a slightly greater estimate of 83% decline (95% CI = 75–86%) in the period 1994–2018 (Figure 4.1). This negative binomial model also had a lower adjusted R-squared value of 0.424, and explained only 41.2% of model deviance. This is a mean annual decline of 6.5% (95% CI = 5.2–7.2%). Patterns of decline in the two models are similar, though estimates of decline in the negative binomial model are consistently slightly greater, as expected from our model testing. Furthermore, for the model comparisons the confidence intervals overlap the central estimates.

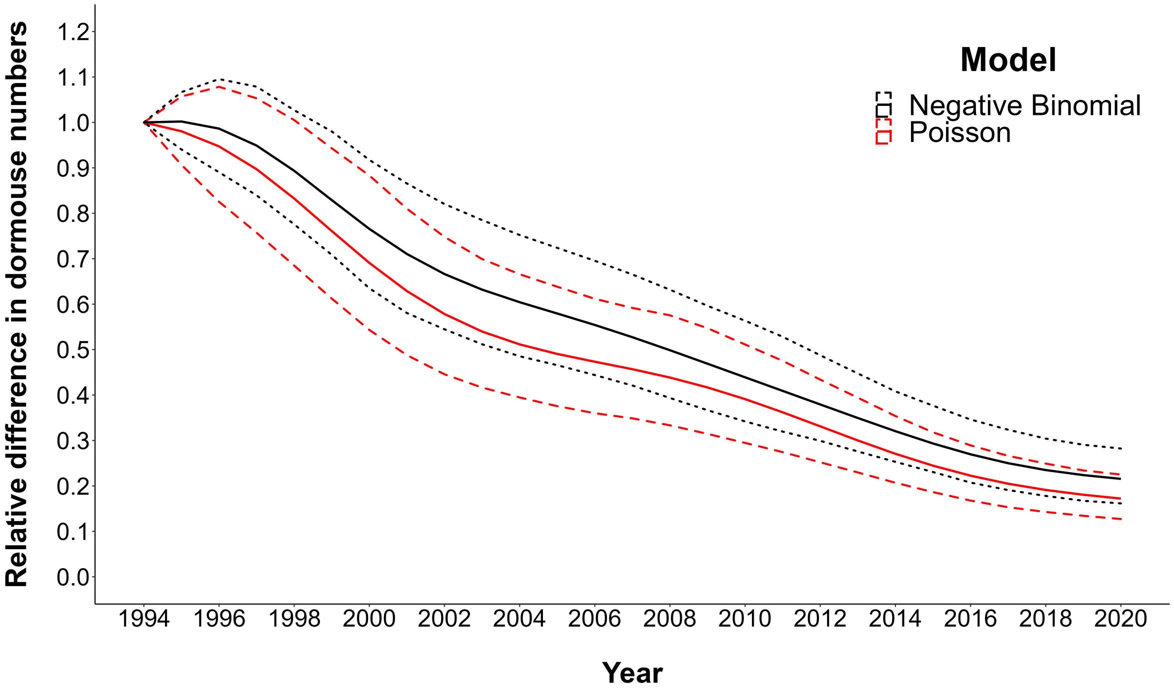


Figure 4.1. Trends in counts of adult hazel dormice from the U.K. National Dormouse Monitoring Programme. *The current Poisson model is in black, and the earlier negative binomial model (Goodwin et al., 2017) is in red. The 27-year period 1994 to 2020 is shown because the first (1993) and last (2021) survey years, when the model is least accurate, have been removed. Population indices are scaled to a value of one in the first year. The area between the dashed lines shows the 95% confidence intervals for each model, calculated by bootstrapping. All NDMP sites (n = 552) used for this analysis recorded more than one adult dormouse and were surveyed for more than two years.*

The overall decline in counts has implications for returning dormice to FCS in the U.K. Favourable status would entail a return to the population size at the start of NDMP monitoring in 1993 (Morris, 2021). With an estimated current population size of 757,000 individuals (Mathews et al., 2018), to reverse the 78% decline in the Poisson model would mean increasing the population to approximately 3,441,000, whilst reversing the 83% decline of the negative binomial model would mean returning to 4,453,000. Practically, this means at least doubling the current population in the next 10 years, then doubling the population again in the subsequent 10 years.

Estimates of overall decline in Wales are greater (89%; 95% CI = 67–95%), than in England (78%; 95% CI = 70–83%), though uncertainty associated with smaller

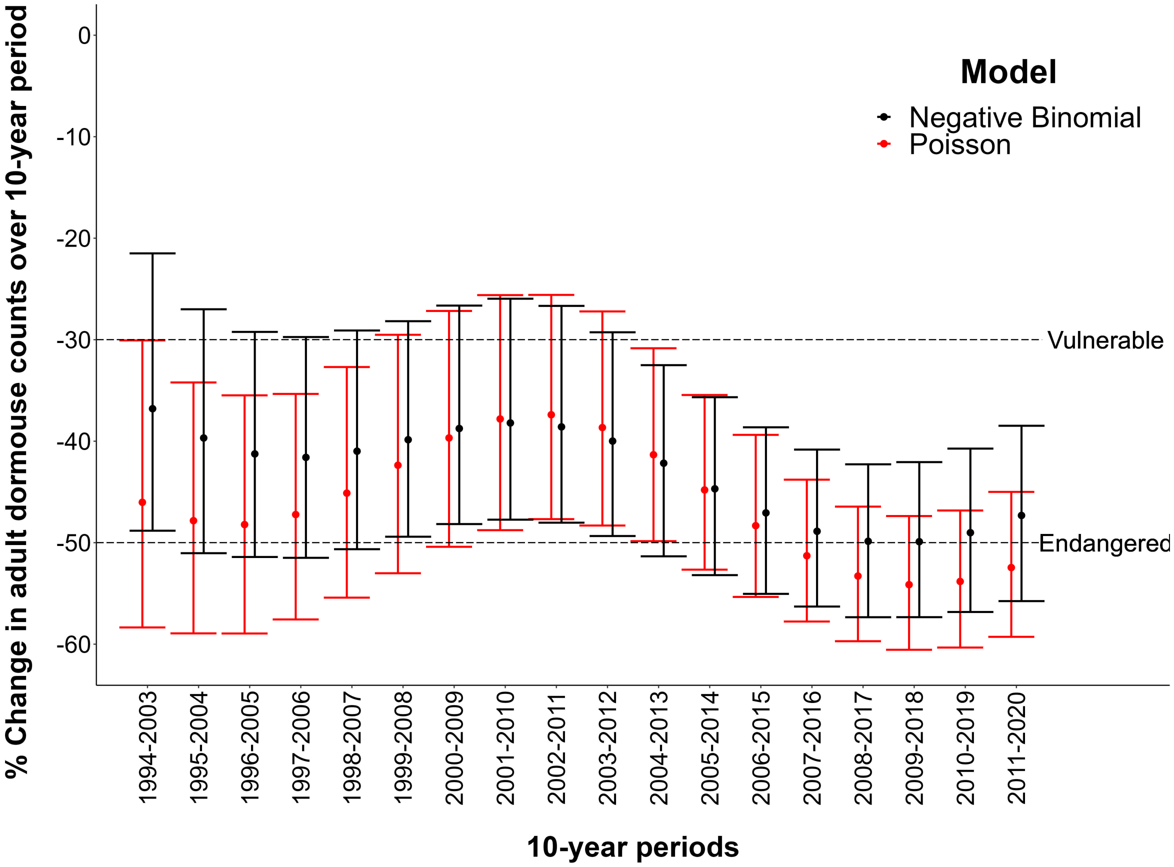


Figure 4.2. Estimates of changes in counts of adult hazel dormice from the U.K. National Dormouse Monitoring Programme over 10-year sliding window periods between 1994 and 2020*. Points from the central estimates of the current Poisson model are in black and the earlier negative binomial model (Goodwin et al., 2017) are in red. Bars represent 95% confidence intervals for each model calculated using bootstrapping. No population change over a 10-year period would be zero on the graph, whilst 50% decline is represented by 50. The thresholds for IUCN Red List criteria for changes in population size over a 10-year period for the categories Vulnerable and Endangered are indicated.*

sample sizes in Wales means 95% confidence intervals for estimates of decline in the two countries overlap.

The model shows declines in hazel dormouse counts have continued apace since the last analysis (Goodwin et al., 2017), with a further 27% decline (95% CI = 18–35%) in the period 2015–2020. The additional six 10-year windows support a picture of continuing decline, as they contain the highest central estimates of decline (49.9%;

2009–2018), and the windows most closely approaching the 50% threshold, of the whole 27-year period (Figure 4.2). This suggests that the decline has accelerated slightly at a decadal scale since 2001. Overall, of the eighteen 10-year windows, only six differ significantly from 50%, while the most recent window (2011-2020) suggests a decline of 47% (95% CI = 38–56%). The negative binomial model also shows the same patterns, though the magnitudes of declines in each 10-year window tend to be greater (Figure 4.2). Specifically, the central estimates of the five most recent 10-year windows exceed the 50% threshold and the most recent window indicates a 53% decline (95% CI = 45–59%).

Comparison of the magnitudes of the declines in each 10-year window, relative to the full 27-year trend (Figure 4.3), shows how the extent of recent declines is obscured when a long-term view of the data is presented. At the same time, the shifting 10-year baseline also obscures the severe chronic decline in the overall, long-term trend. If the estimated mean annual decline (5.7%) were to continue, by 2034 counts of dormice in the U.K. would have declined by $>$90% since 1994. Yet the decline over any 10-year period would never have exceeded the $>$50% threshold required for dormice to be categorised in a Red List assessment as Endangered. The mean annual decline would have to accelerate to 7.4% per year to surpass a threshold of $>$50% in a 10-year period.

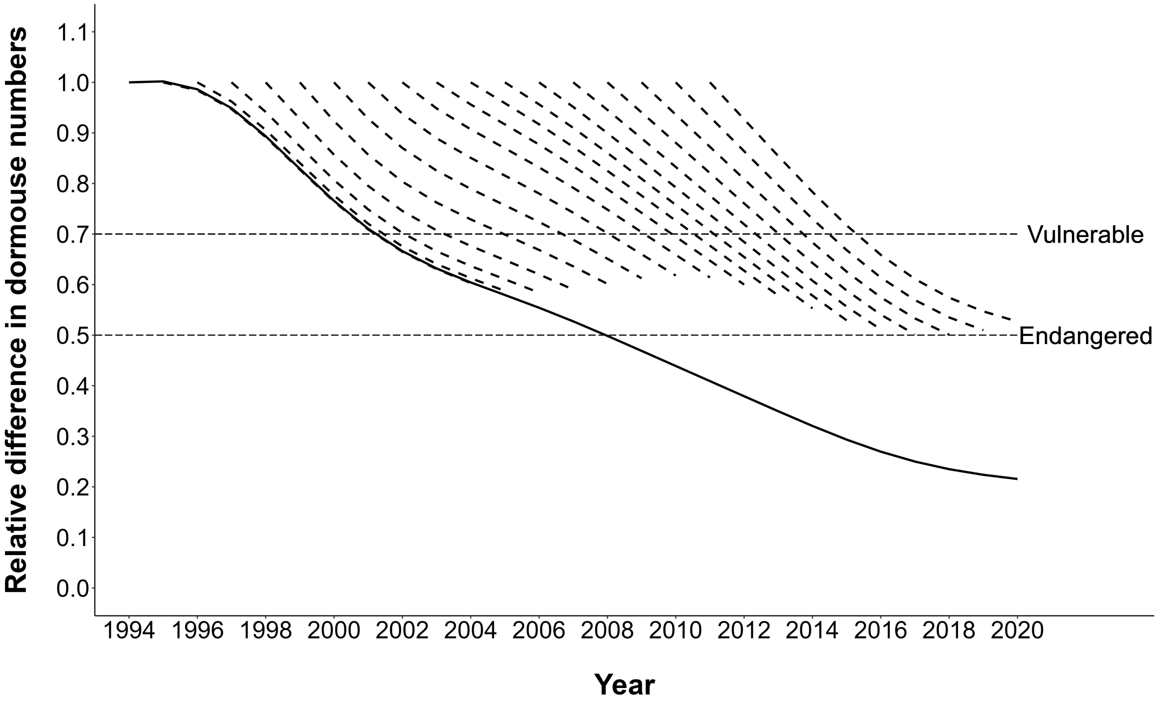


Figure 4.3. Trends in counts of adult hazel dormice from the U.K. National Dormouse Monitoring Programme from 1994 to 2020. *The overall trend is shown as a solid line and trends over each 10-year sliding window are shown as dashed lines. Each trend is set to the same scale to show how the change of scale effects perception of the trend. Data are from the Poisson model. Population indices are scaled to a value of one in the first year of the full 27-year period or the initial year of each 10-year window. The first 10-year window (1994 to 2003) is shown but as this window and the full 27-year trend share the same starting point they overlap completely. The thresholds for IUCN criteria for changes in population size over a 10-year period for the categories Vulnerable and Endangered are indicated.*

Discussion

The National Dormouse Monitoring Programme provides unusually extensive, consistent surveillance data, which allow for statistically robust estimates of trends in hazel dormouse counts in woodland habitats across England and Wales (Goodwin et al., 2017). Here we have found counts of adult dormice in the NDMP have declined by 78% in the 27 years from 1994 to 2020, and declines have continued apace since the earlier analysis (Goodwin et al., 2017). A series of 10-year sliding windows indicate acceleration in the rate of decline when measured over this timeframe. The trends differ between England and Wales, with Welsh counts suggesting a more severe decline. Overall annual rates of decline are sustained, with a mean of 5.7% per year, which, if it were to continue, would mean the dormouse population would decrease by >90% by 2034, some 40 years after the 1994 baseline.

When the full 27-year view is taken, the decline appears to be flattening compared to the initial reduction (Figure 4.1), and on the face of it, the estimate of overall decline of 78% up to 2020 differs very little from the estimate of 72% up to 2014. However, when the full period and 10-year windows are set to the same scale (Figure 4.3), it is clear that the long term view obscures the magnitude of changes in decadal periods, especially the most recent. This indicates how the scale and presentation of the decline can affect its perception. Although recent declines represent the loss of a small proportion of the starting counts, they represent a significant proportional reduction in those remaining 10 years previously. Without analyses of the 10-year windows, there might be a false perception of recent abatement in the rate of decline, which supports the merits of the focus in IUCN Red List categorisation on short, recent time frames.

Conversely, however, concentrating on the shorter period means the longer term, chronic decline contributes little to threat assessment. The sustained decline, if it remains at its current level, would never surpass the threshold of 50% decline in a 10-year period, as required for the species to be categorised on the Red List as Endangered, even if counts had declined by >90% over the entire monitoring period. This conundrum is recognised in the background for the development of IUCN criteria, which explains that a population declining by the same proportion each year will never qualify for higher threat category under criterion A, even as it goes extinct, but must instead qualify under the other criteria B-E (Mace et al., 2008). This is because a chronically declining population does not fit with the declining species paradigm

(Caughley, 1994), which is the basis for criterion A (Mace et al., 2008), as the imminent risk of extinction is low. This challenge of responding to chronic declines has yet to be explicitly explored. In simulations of hip-pocket frog *Assa darlingtoni* populations, the species mostly qualifies for threatened status when its range becomes small (criterion B) or based on extinction probability (criterion E), despite consistent declines (Keith et al., 2014). The Vancouver Island marmot *Marmota vancouverensis* declined by 90% between 1973 and 2006 (Lindenmayer et al., 2013), but was initially only recognised as Endangered due to small and restricted populations (criteria C and D; Nagorsen 2000).

While the Red List does as it intends, in assessing and collating imminent risks of extinction, evidence of chronic declines is material to broader assessment of conservation status, for national and international legislation. Measures of change over otherwise somewhat arbitrary (10-year) periods may particularly underplay the importance of declines in species that have short generation lengths but low productivity, which cannot recover their populations as quickly as might be expected for ‘R-selected’ species. For example, hibernators such as dormice, have relatively low productivity and slower life histories in general compared to similar sized non-hibernators (Turbill et al., 2011). Such species with a slower life history may be less able to recover from chronic declines and so could therefore be considered to be in particular need of conservation prioritisation and action, even where not categorised as Endangered by Red List criteria.

Despite IUCN guidance to the contrary, Red Lists are frequently used at least to inform conservation priority (Miller et al., 2007), stemming from the misconception that the IUCN assessment is itself a prioritisation scheme (Collen et al., 2016). This misuse may be reinforced by the way the IUCN Red List also understandably dominates public discourse on conservation issues, which may also create risks for species that are no longer categorised as Threatened, losing public interest when they still require conservation actions. This can also be seen with chronic declines, as with the hazel dormouse, which do not lead to categorisation as high risk of extinction, but would be beneficial to incorporate into conservation prioritisation and enactment of effective conservation measures.

On the other hand, FCS can take into account chronic declines and the associated issues for conservation prioritisation. Any amount of population decline $>1\%$ per year is considered Unfavourable (JNCC, 2019), which is consistent with both chronic and acute declines. The amount of decline can be taken into account when defining FCS for the species, as this often requires a reversal of the known declines. By focusing on deviations from evolutionary viability, instead of the proximity of extinction, FCS is broader in assigning the value of conservation action, and does so earlier.

Waiting for a species with known chronic decline to dwindle to the extremely small range or population size required to attain a higher category on the Red List, before they are given conservation priority, may restrict the ability to address obligations to attain Favourable Conservation Status. Recovery may be easier to secure with earlier action as there is more time for research and to trial alternative actions, and there are likely more options for conservation before a species reaches a small population size. The conservation actions will likely cost less, as there is less need for expensive procedures like ex situ conservation. Fundamentally, allocating resources to less threatened species, when populations are reduced but remain able to respond to effective conservation measures, is more efficient than reversing a journey to the brink of extinction when a species is finally categorised as Endangered (Possingham et al., 2002). This can be seen with dormice in the U.K.; although there is high awareness of their conservation need and of their legal protection, our analysis suggests this has not been sufficient to stabilise or increase the population. Current conservation actions, like habitat management, reintroductions and mitigation of developments are usually undertaken at very local scales, whilst broad scale actions primarily focus on monitoring within woodland habitats. Practitioners have highlighted the need for more proactive landscape-scale approaches to create and improve habitat whilst promoting connectivity (Phillips et al., 2022). Such measures are needed imminently to prevent the population deviating further from Favourable Conservation Status.

Systematic monitoring of threatened species has only recently been established, and follows decades, if not centuries, of anthropogenic threat, and population decline (Mihoub et al., 2017). This includes dormice in the U.K., as the NDMP monitoring was established after well-described declines in range and population, relative to historical data (Bright and Morris, 1996). Thus, the ongoing declines shown here must be set in the context of prior historical losses of unquantified magnitude. Similarly, though truly long-term data (>100 years) are rare (Bonebrake et al., 2010), where available they tend to show greater losses than expected. For several hunted North America mammals, using 1970 as a baseline indicates recent population increases, but a historical baseline of 1850 reveals overall decreases (Collins et al., 2020). Such populations, depleted from their pre-anthropogenic state, may be less resilient and at greater risk of extinction (Mace et al., 2008), or even in extinction debt.

Assessments of conservation status and priority, like FCS, can incorporate this longer-term view with the aim of returning species to an earlier baseline, and have the advantage of more readily integrating qualitative information, as the criteria do not include thresholds. Including long-term data could also combat shifting baseline syndrome (Soga and Gaston, 2018), but would require wider dissemination and use of FCS, and its equivalents, in the public discourse.

For hazel dormice in the U.K., the available evidence from a robust monitoring scheme, albeit one confined to the distinct set of habitats where NDMP sites are established, suggests a continuation of their chronic decline. Dormice therefore remain in unfavourable status. However, there is further ambiguity in the threat assessment process by considering uncertainty stemming from analytical model choice. The IUCN threshold for Endangered (50%) is missed by most recent decadal declines in the Poisson model (47%), but exceeded by those in the negative binomial model (53%). Both models are valid, and the estimates do not differ statistically, but the 6% difference between these central estimates spans the threshold between Vulnerable and Endangered. Currently, statistical uncertainty is not incorporated in the IUCN criteria, though it is starting to be discussed in formal assessments (Sherley et al., 2020). Instead, the criteria allow assessors to deal subjectively with uncertainty, providing they are precautionary, favouring the higher threat level when there is evidence for it, and the decision is well-documented (IUCN Standards and Petitions Committee 2019, Section 3.2). For dormice, this would suggest using the negative binomial model as evidence of the higher threat level, and classifying dormice as Endangered. Whether using this shift in Red List category, or considering the widening gap between current populations and the 1993 reference population for Favourable Conservation Status, our work suggests hazel dormice should be a target for further and more effective conservation action. Considerable effort will be required to return hazel dormice to Favourable Conservation Status in a meaningful time frame, requiring doubling the population in the next 10 years, and again in the following 10 years.

Chapter 5: Trends in occupancy and abundance, and environmental drivers of local colonisation and extinction, at hazel dormouse (*Muscardinus avellanarius*) nest box sites whilst accounting for preferential sampling

Chapter 5: Trends in occupancy and abundance, and environmental drivers of local colonisation and extinction, at hazel dormouse (*Muscardinus avellanarius*) nest box sites whilst accounting for preferential sampling

Abstract

1. Citizen science may be key for spatially and temporally extensive species monitoring programmes, but the resulting data can be prone to biases. This includes preferential sampling, where ecological variables such as species presence are correlated with the probability a site is surveyed. However, explicitly modelling sampling probability can effectively account for this issue.

2. We use data on hazel dormice *Muscardinus avellanarius* nest box sites in Britain to investigate trends in occupancy and abundance, and the environmental drivers of local colonisation and extinction probability, whilst accounting for potential preferential sampling biases.

3. We find substantial influence of preferential sampling on models of both occupancy and abundance. Accounting for this bias, we estimate a 33.3% (95% CI: 23.7% - 41.8%) decline in the occupancy of nest box sites between 2000 and 2021.

4. We also estimate a decline of 68.1% (95% CI: 52.0% - 78.7%) in the prebreeding adult abundance between 1993 and 2021. We estimate the current British population to be 178,869 (95% CI: 136,474 - 239,089) dormice, which is considerably lower than previous estimates.

5. However, we find the model with preferential sampling produces reduced between site variation in persistence/extinction probability by ascribing the drivers of extinction to changes in sampling. It may therefore be more informative to explore environmental drivers of occupancy changes through models that do not account for this bias, which in this study reveal increased local extinction probability as late winter (February and March) temperature range increases, and as the area of woodland within 1km of the nest box site decreases.

Introduction

The current biodiversity crisis derives not only from species extinctions, but also declines and extirpation of constituent populations (Ceballos et al., 2020). Although monitoring programmes are vital for understanding this conservation crisis, they can only benefit species if they lead to conservation action (Lindenmayer et al., 2013). Such programmes, especially at regional scales, contain essential information on changes to local populations, revealing the dynamic processes such as local extinction and recolonisation, which determine trends (Fandos et al., 2021). Understanding how environmental factors drive these dynamics can reveal appropriate management solutions to help reverse populations declines (Pressey et al., 2007). In particular, it is important to untangle threats conservation practitioners can tackle directly, such as habitat loss, from those, such as climate change, which need broader indirect approaches.

Monitoring programmes often rely on volunteers for data collection, leveraging public engagement to survey at geographical scales that would be difficult to achieve using professionals alone (McKinley et al., 2017). These programmes can generate large datasets but tend to produce unstructured or semi-structured data with biases that can make analysis challenging (Johnston et al., 2023; McClure and Rolek, 2023). Key issues include false positives and reporting preferences, where volunteers might only report the species they are most interested in (Johnston et al., 2023). Citizen scientists also tend to be limited by by the accessibility of the environment, preferring areas close to urban centres and roads/trails (Cretois et al., 2021). Biases in citizen science data, particularly opportunistic sightings, can mean this data is less sensitive to changes (Kamp et al., 2016).

However, many biases can be reduced through protocol design and volunteer training (McKinley et al., 2017). For example, training can reduce or eliminate false positives, whilst a standardised technique, such as requiring full species lists, can reduce volunteer reporting preferences. Within such a programme, volunteers can collect data with the power to detect declines at key threat thresholds (Barlow et al., 2015). However, some biases remain including preferential sampling; when ecological variables, such as occupancy, are correlated with the probability of a site being surveyed (Emmet et al., 2023). Volunteers may select sites based on previous records of threatened species (Tulloch et al., 2013), which entangles the probabilities of occupancy and sampling. Volunteers may also stop surveying a site if species of interest become absent or less abundant (Kéry et al., 2021), missing recolonisation events (McClure and Rolek, 2023). This form of preferential sampling can lead to an overestimation of abundance at low quality sites (Pennino et al., 2019) and so inflation of the overall population size (Fandos et al., 2021). Modelling preferential sampling biases directly can effectively handle this issue, usually resulting in lower abundance and occupancy estimates (Pennino et al., 2019; Fandos et al., 2021; Kéry et al., 2021).

Hazel dormice (*Muscardinus avellanarius*) in Britain are in chronic decline, having decreased by 78% between 1994 and 2020 (Scopes et al., 2023). Previous research suggests dormice are particularly vulnerable to habitat fragmentation through loss of woodland, due to their low dispersal capability (Bright and Morris, 1996). There is also evidence that dormice are sensitive to climate, preferring warmer sunnier summers for foraging, and consistently cold winter for efficient hibernation (Goodwin et al., 2018b). In Britain, hazel dormice are monitored by a large citizen science project, the National Dormouse Monitoring Programme (NDMP). The NDMP has a standardised protocol for conducting surveys using dormouse next boxes (PTES, 2019a) and volunteers must have a licence from their relevant Statutory Nature Conservation Body, which is acquired through training. However, volunteers choose their survey sites and when, or if, to survey, leading to possible preferential sampling biases. In this study, we investigate how dormouse occupancy and abundance has changed in Britain, alongside the environmental drivers of occupancy transitions, whilst accounting for potential preferential sampling biases.

Methods

Dormouse data

We used data from the NDMP, which has sites across the current dormouse range in England and Wales (Mathews et al., 2018), predominantly located in broadleaf woodland. Each site has a grid of nest boxes that are checked by licensed volunteers mostly between May and October. As a minimum, volunteers are asked to check the boxes at least once in May/June and again in September/October. At each check, the volunteers monitor the number of dormice, as well as each individual's sex, age and weight. More information on the surveys can be found in the NDMP guidelines (PTES, 2019a).

Sites can have more than one survey section, due to multiple locations of nest boxes within the wood, which were grouped by site to increase the sample independence. For the occupancy modelling, we only considered the presence or absence of dormice at each site and monthly check, and did not include dormouse nests, as these are easily misidentified risking false positives. As volunteers have extensive training to obtain survey licences, we assume that false positives are not possible with this data. For the abundance modelling, we used the counts of adult dormice as used in previous studies (Goodwin et al., 2017; Scopes et al., 2023).

Although monitoring started in 1988, we initially only included data from 1993 when over 30 sites were part of the programme (Scopes et al., 2023), until 2021. We included sites that had two or more years of data, so that at least one occupancy transition had occurred. We removed sites that were part of the reintroduction programme, or could only have been colonised from these sites, allowing us to focus on the drivers of natural local colonisation and extinction. A subset of NDMP sites have polygon data showing the survey area, which were used to gather habitat and climate data, and this subset was used in the analysis of environmental drivers of occupancy.

Habitat data

We used the site polygon data and the National Forest Inventory (NFI; 2010-2020; Anonymous 2022) to ascertain the woodland in which each site was located. The NFI data also allowed us to calculate area of woodland at a site each year. From 2011, the NFI also classifies woodland into habitat type, with which we calculated the proportion of the woodland that was dominated by broadleaved trees each year, by including areas classified as ’Broadleaved’ and ’Mixed mostly Broadleaved’. We also calculated the proportion of the most recent woodland area (2020) that was classified as ancient woodland (Spencer and Kirby, 1992).

We calculated the average elevation, aspect and slope for each nest box polygon using data from Ordinance Survey (Ordinance Survey, 2022). Aspect and slope were used to calculate solar index, a measure of the potential solar radiation an area receives based on its incline, for each site and year, using the package ’microclima’ (Maclean et al., 2019). The index was calculated for 12pm on the first day of each month, which was averaged to provide a value for each site per year.

For measures of connectivity, we use a 1km radius circle originating from the centroid of the nest box polygon, giving the same area (3.14km^2) for each site. Within this circle we calculated the area that was woodland (2010-2020), broadleaved woodland (2011-2020) and ancient woodland (single value).

Climate data

We obtained daily climate data from the UK Met Office at a 1km resolution (Hollis et al., 2018) and included variables which previous work had found to be important for dormice; minimum temperature, temperature range and total rainfall (Goodwin et al., 2018b). We derived climate data for each site based on the closest grid square to the centroid of the site polygon. For the detection portion of the model, we used the minimum temperature and total rainfall on the day of the survey, and calculated the mean minimum temperature and total rainfall for the week previous. These variables were standardised across sites and years, allowing imputation of the mean (now 0) for site and year combinations where surveys did not take place. For the ecological part of the model, we calculated the mean minimum temperature, mean temperature range (difference between mean maximum and mean minimum) and total rainfall for every early (December, January) and late (February, March) winter.

Statistical analysis

All analysis was completed in R version 4.3.0 (R Core Team, 2022). We used the JAGS modelling language through the package ’R2jags’ version 4-14 (Su and Yajima, 2022) for the occupancy models, and the Nimble language through the package ’nimble’ version 1.0.1 (de Valpine et al., 2017) for the abundance models.

Dynamic occupancy model: trend and drivers of occupancy

We used a Bayesian dynamic site occupancy model, which can account for imperfect detection (MacKenzie et al., 2003). This model is hierarchical; the ecological submodel explores the latent ’true’ occupancy of the site, whilst the detection sub-model links the observed data to the latent state. Occupancy transitions are modelled via colonisation and site persistence, the probability of dormice remaining present at a site. Table 5.1 shows the occupancy states and transitions; as each row must sum to one, extinction is the inverse of persistence and absence is the inverse of colonisation.

We assumed that site occupancy was stable within a year, only changing between years when dormice disperse shortly before/after hibernation (Juškaitis, 2014). The monthly site checks within a year were used to estimate the probability of detection. We used a model framework that included posterior predictive checks using chi-squared goodness of fit (GOF) measures comparing observed and model-generated values (Kéry and Royle, 2021b), which were calculated for the open (ecological) and

Table 5.1. The possible occupancy states (presence or absence) of a site, and the four possible transitions between these states that could occur each year (extinction, persistence, colonisation and absence). *The left column denotes the possible states for a site in year t, either occupied by dormice (presence) or not (absence), with the other two columns showing the possible transitions to the same states the following year (t+1). As a site must either have dormice present or not, the probabilities of the two possible transitions (rows) must sum to one. Hence, defining the transition from presence to presence (persistence) as ϕ, then the other transition, presence to absence (extinction), must equal 1 - ϕ. Equally, defining the transition from absence to presence (colonisation) as γ, then the other transition, absence to absence (absence), must equal 1 - γ. Thus, extinction and persistence are inversely related, as are colonisation and absence.*

		State in year t + 1	
		Absence	Presence
State in year t	Presence	1 - ϕ *Extinction*	ϕ *Persistence*
	Absence	1 - γ *Absence*	γ *Colonisation*

closed (detection) sub-models. A model with the optimal GOF would have a chi-squared value of 0.5. We ensured that all models had good mixing and convergence between chains by visually inspecting the model and confirming the Gelman-Rubin statistic was $<$1.1 (Gelman and Rubin, 1992).

We first devised the detection sub-model, starting with a base model containing a random effect of year and an annual varying site random effect, after initial analyses suggested this had the best GOF and lowest deviance information criterion (DIC; Spiegelhalter et al. 2002, Table S5.1). We then added continuous effects of both the number of boxes at a site, to control for differing survey effort, and the week of the year the survey took place, to account for seasonal changes. We trialled several polynomial shapes for the relationships between detection and these variables, selecting the best model based on GOF and DIC. We then tested whether the minimum temperature and total rainfall on the day of the survey, or the week before the survey, effected detection. These four variables were included in separate models as linear effects on detection. Here, and throughout, we considered variables non-significant if the 95% confidence interval of the slope included zero. Only significant variables were retained in the final detection model, which was used in all following models.

As we considered 14 habitat and climate variables, we initially investigated their effects on site persistence and colonisation through single models; one for each covariate. Each model included the covariate as a linear effect with a random year intercept for persistence and colonisation separately. We combined significant variables into a joint model for colonisation and persistence, with variables standardised to enable comparison of linear effects.

We added an inclusion parameter (w) for each covariate in the joint model. This is a latent binary variable with an uninformative prior, such that when $w = 1$ the covariate has an effect on the transition probability equal to the slope parameter and when $w = 0$ the covariate has no effect (Santos et al., 2018). As such the posterior probability of each inclusion parameter indicates the probability that each covariate is included in the ”best” model, with a probability $>$0.5 indicating it should be considered (Barbieri and Berger, 2004). This methodology allows the calculation of model-averaged estimates across all the models present in the posterior sample. We calculated model-averaged estimates of occupancy and detection across the whole posterior sample, but for covariate slopes only used the samples where the corresponding $w = 1$ (Santos et al., 2018). We checked for negative correlations between the inclusion parameters, indicating covariates that frequently displaced each other in the model, and removed the covariate with the least contribution.

We included preferential sampling as the last step, and present identical final joint models with and without preferential sampling. Following the framework in Kéry and Royle (2021b), preferential sampling was included by modelling site visitation each year in relation to four effects. We included a linear effect of year, as sites have been added to the NDMP over time, and an effect of COVID-19 restrictions in 2020 and 2021 which limited volunteer access to sites. We used an indicator variable to make the visitation probability zero before the site was added to the NDMP. Finally, we modelled how site occupancy affected visitation probability, as sites with few or no dormice might be abandoned by volunteers, by using a linear effect of the mean occupancy in the previous five years. For the first year, this effect was not included, and the mean of all previous years was used from year two until five previous years were available.

Binomial mixture model: abundance trend

We used a Bayesian binomial mixture model to explore trends in abundance (Kéry and Royle, 2021a) in relation to preferential sampling. This model has a similar hierarchical structure to the above model, with the latent ’true’ abundance linked to the observed data through a detection model. We calculated pre-breeding and post-breeding adult dormouse population sizes, assuming the population size did not change between May and June, or between September and October respectively. Young of the year may mature if born early in the season, in July or August (Juškaitis, 2014), and be counted amongst the autumn adult population. As this is considerably less data from which to estimate detection probability (two months compared to eight above), we simplified the detection model to retain only a random year intercept and linear effects of the number of boxes and week of the year. Abundance was modelled with a site fixed effect intercept and a correlated random walk over time using a conditional auto-regressive prior. As above, we present pre- and post-breeding models both with and without preferential sampling. Visitation probability is modelled identically to above, except the substitution of mean abundance instead of occupancy.

We used the area of each site polygon to estimate the mean adult dormouse density for each year across all NDMP sites, and across those in woodland that was majority broadleaved and majority conifer separately. The habitat specific densities allowed us to estimate the total number of dormice in Britain, using the areas of each habitat within the species British range and the estimated occupancy of this habitat published in Mathews et al. (2018).

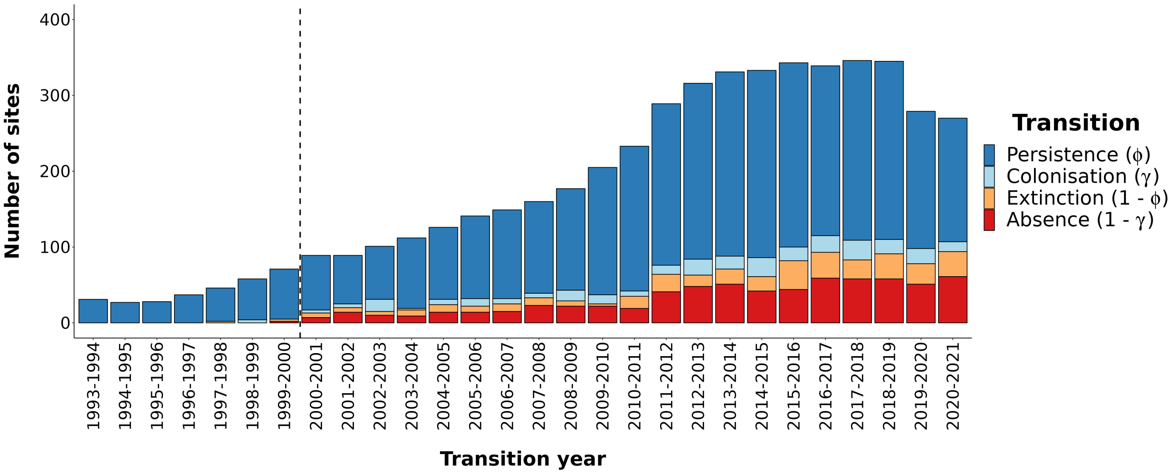


Figure 5.1. The observed transitions between occupancy states at 679 National Dormouse Monitoring Programme sites between 1993 and 2021. *Sites were included if they had at least two years of surveying in this period, and were not either reintroduction sites or could only have been colonised via a reintroduction site. Transitions are described in Table 5.1, with colours showing persistence (presence-presence), extinction (presence-absence), colonisation (absence-presence) and absence (absence-absence). To the left of the dotted line are years removed from the study due to a lack of transitions in the data. Years to the right of the dotted line (2000 until 2021) were included.*

Results

There were 728 sites in the NDMP with at least two years of data between 1993 and 2021. Of these, 58 were removed as they were reintroduction sites, or could only be colonised from reintroduction sites. This left 679 sites for our initial investigation of the number of observed transitions within the data. Figure 5.1 shows the number of sites with each of the four possible transitions (Table 5.1), and demonstrates that there are mostly persistence transitions in the first few years. We therefore decided to analyse data from 2000 until 2021, as the period 2000-2001 is the first time all four transitions are present (Figure 5.1).

Of the above, only 446 sites had polygons with which to gather habitat data, and were included in occupancy analysis. The number of sites added to the NDMP increases steeply over time, and most sites have missing surveys after they have been added to the programme (Figure 5.2). There is also an impact of the 2020 and 2021 COVID-19 lockdowns, with many sites lacking surveys in this year (Figure 5.2).

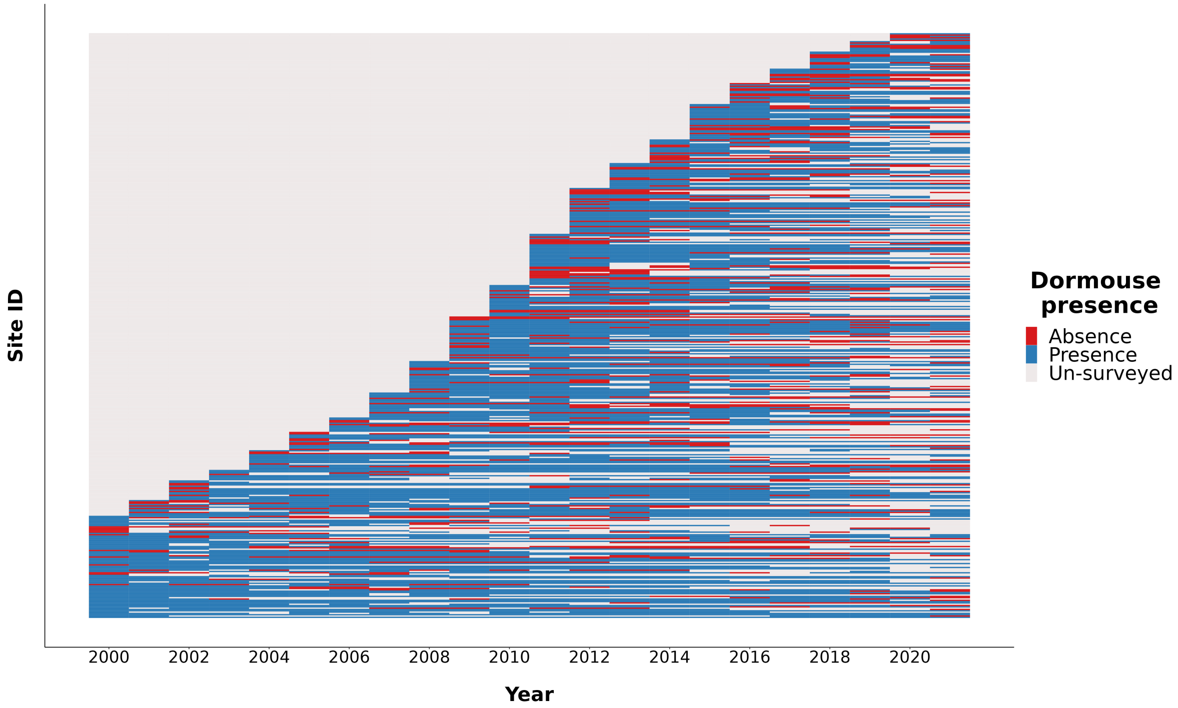


Figure 5.2. The observed presences (blue) and absences (red) of dormice, and years without surveying (grey), at 446 National Dormouse Monitoring Programme sites between 2000 and 2021. *Sites were included if they had at least two years of surveying in this period, had polygon data on the location of the nest boxes, and were not either reintroduction sites or could only have been colonised via a reintroduction site. The effects of COVID-19 lock-downs can be observed through the increase in un-surveyed sites (grey) in 2020 and 2021.*

Detection model

For the detection sub-model, a linear effect of the number of boxes and quartic polynomial effect for the week of the year the check occurred were the best supported models (Appendix 5). We then investigated possible climatic effects, with only the sum of rainfall in the previous week of the survey having a significant effect on detection (Appendix 5).

The number of boxes had a significant positive effect on detection probability, reaching a plateau at around 250 boxes (Figure 5.3A). The detection probability at 50 boxes, which is the guideline number for an NDMP site (PTES, 2019a), is 0.68 (95%

confidence interval: 0.64 - 0.72), though this is only for a single survey when the other variables are at their mean. With two surveys, the probability of detecting at least one dormouse with 50 boxes rises to >0.9. There are two peaks in detection probability over the year, the first in May and the second in October, with only a small decrease in detection between these points (Figure 5.3B). The larger peak in October may be due to juveniles becoming independent and so more likely to be found in boxes on their own (Juškaitis, 2014). There is a positive relation between the sum of rainfall in previous week and detection probability (Figure 5.3C), possibly because dormice are more likely to sheltering in boxes in prolonged adverse weather, and are more likely to be torpid (Armitage et al., prep).

Occupancy modelling

There are significant negative effects of year and COVID-19 restrictions, and a significant positive effect of the mean occupancy in the previous five years, on the probability of visiting a site (Table 5.2, Figure 5.4). Mean occupancy has the biggest impact on visitation probability, with a less than 50% probability that a site will be visited if no dormice occupy the site the previous 5 years (Figure 5.4). This effect indicates preferential sampling has substantial impact on the NDMP data and therefore estimates of occupancy.

Without preferential sampling, there is an estimated 16.9% (95% CI: 7.2% - 25.7%) decline in the proportion of sites occupied between 2000 and 2021. Meanwhile, with the addition of preferential sampling the decline is almost doubled to 33.3% (95% CI: 23.7% - 41.8%). The models only appear to diverge recently, with the differences becoming significant from 2017 onwards (Figure 5.5).

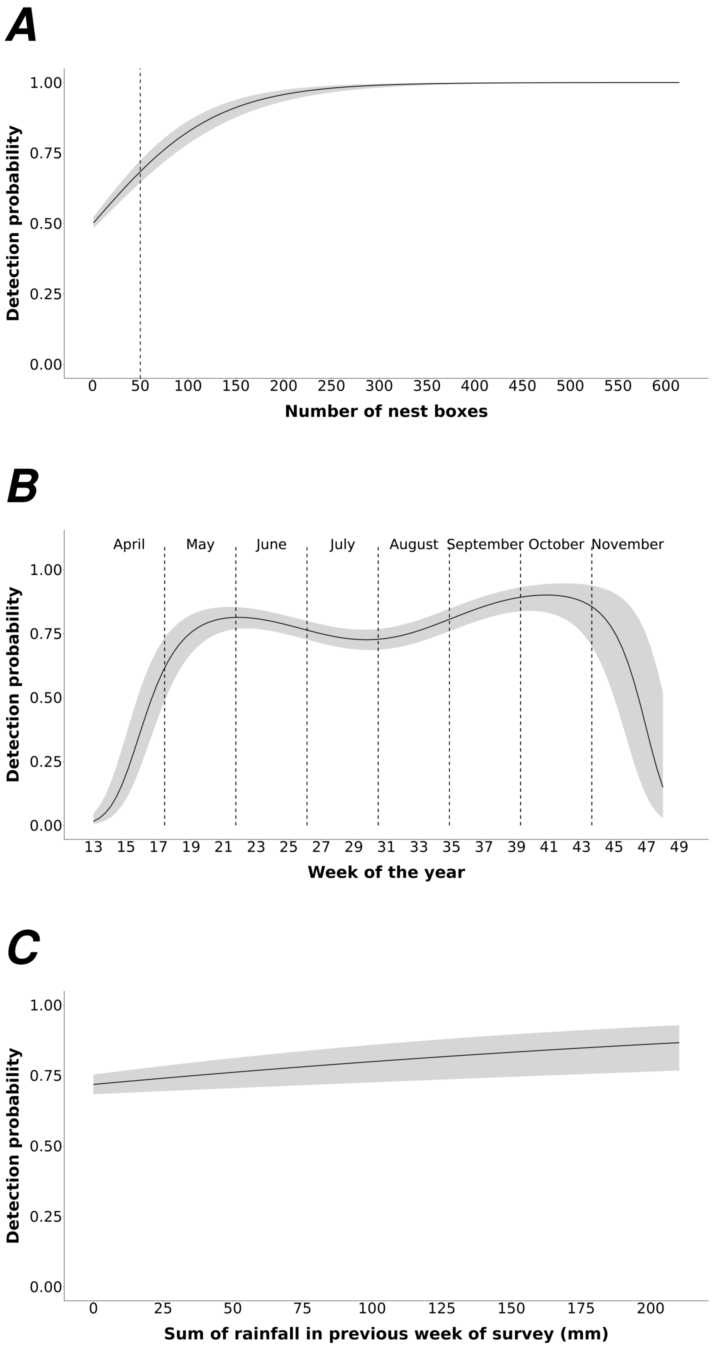


Figure 5.3. The relationship between A) the number of boxes (linear), B) the week of the year the survey occurred (quartic polynomial) and C) the sum of rainfall the week before the survey (linear), and the detection probability in the final detection model. *Lines represent the mean of the posterior distribution, and the grey area the 95% confidence interval. Each graph shows the relationship when the other variables are at their mean. The dotted line on graph A represents 50 boxes, which is guideline number for NDMP site set-up (PTES, 2019a). Graph B uses dotted lines to split the period into the months of the year.*

***Table 5.2. A comparison of the drivers of preferential sampling across models**. The columns show the estimated slope for the effect of year (Year slope), COVID-19 restrictions (Lockdown slope) and the mean occupancy or abundance in the previous five years (Past 5-years slope) on the probability of a volunteer visiting a site. The mean and 95% confidence interval of the posterior distribution of each slope is provided.*

Model	**Year slope**	**Lockdown slope**	**Past 5-years slope**
Occupancy	-0.51	-0.054	3.5
	(95% CI: -0.63 - -0.38)	(95% CI: -0.09 - -0.019)	(95% CI: 3.2 - 3.8)
Pre-Breeding	-0.31	-0.98	0.096
Abundance	(95% CI: -0.41 - -0.21)	(95% CI: -1.2 - -0.79)	(95% CI: 0.081 - 0.11)
Post-Breeding	-0.42	-0.012	0.036
Abundance	(95% CI: -0.53 - -0.3)	(95% CI: -0.21 - 0.19)	(95% CI: 0.029 - 0.043)

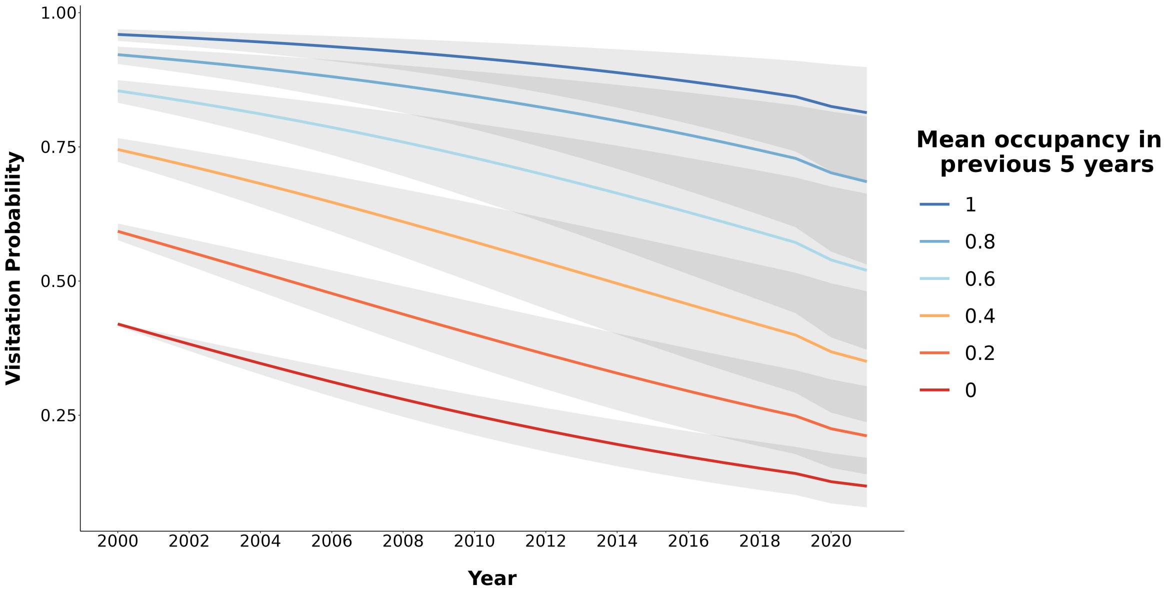


***Figure 5.4. NDMP site visitation probability in relation to the year of surveys, the occurrence of COVID-19 restrictions in 2020 and 2021, and the mean occupancy in the previous five years (line colour).** The graph shows values for a site where surveying has started, as otherwise visitation probability is zero. A mean occupancy of one in the previous five years indicates the site had dormice each year, whilst a value of zero means there were no dormice at the site in this period. The lines show the mean of the posterior distribution, and the grey area the 95% confidence interval.*

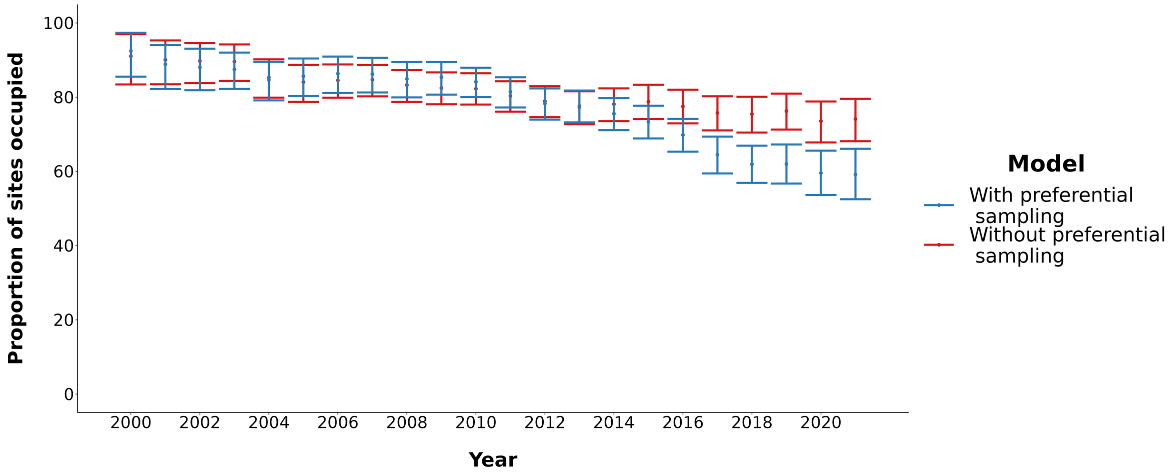


Figure 5.5. The estimated proportion of occupied National Dormouse Monitoring Programme sites (n = 446) between 2000 and 2021 from joint occupancy models with (blue) and without (red) preferential sampling. *The points show the mean of the posterior distribution, and the error bars show the 95% confidence interval.*

Drivers of occupancy dynamics

The exploration of the 14 single variable models revealed a sub-sample of the habitat and climate covariates to combine in the joint model (Appendix 6). Three significant effects were included in the colonisation model: solar index, proportion of broadleaved woodland at the site, and the sum of late winter rainfall. We found negative correlations for some inclusion parameters in the persistence model, and so removed the area of woodland and the area of ancient woodland within 1km to retain the area of all woodland within 1km. This meant eight effects were included in the persistence model: solar index, late winter temperature range, early and late winter rainfall, elevation, area of all and broadleaved woodland within 1km, and proportion ancient woodland at the site.

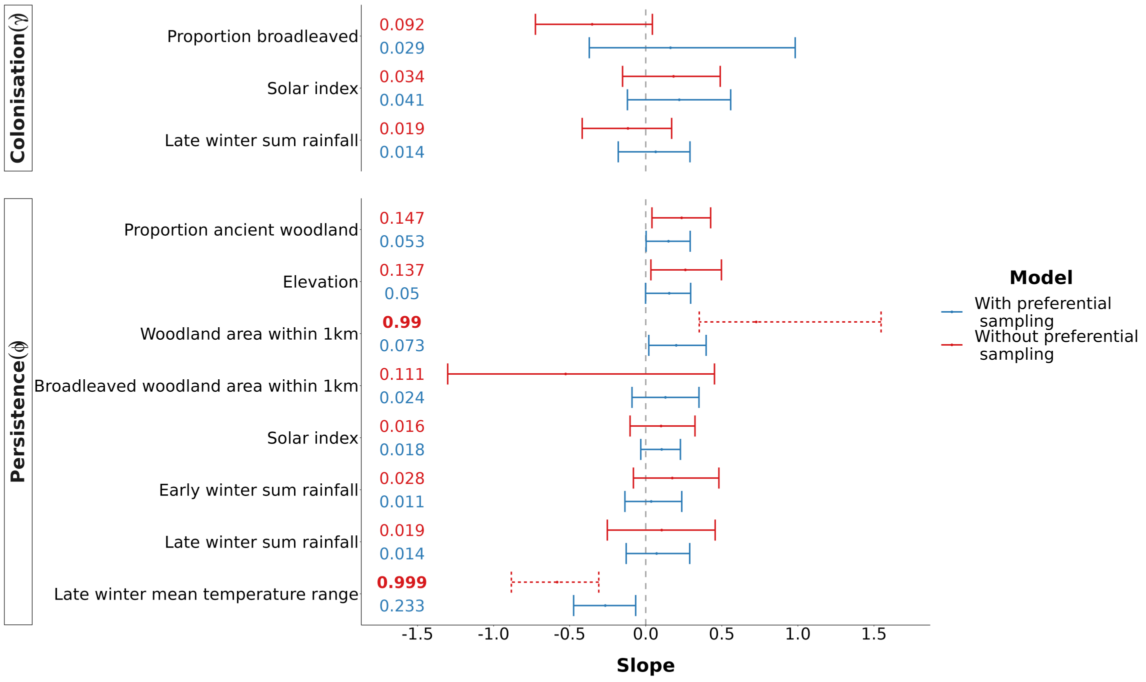


Figure 5.6. The estimated linear effects (points) and inclusion parameters (numbers) of each variable included in the joint models of occupancy both with (blue) and without (red) preferential sampling. *We show the linear effect mean and 95% confidence interval (error bars) of the posterior distribution when the corresponding inclusion parameter* $w = 1$. *Variables with a* $w > 0.5$ *are considered included in the 'best' model and are shown with inclusion parameter in bold and the corresponding linear effect dashed. The dashed line indicates zero.*

We tested these habitat and climate variables together in two final models, one with and the other without preferential sampling which gave different results (Figure 5.6). The model with preferential sampling suggests that the 'best' model is the null with only a year-specific intercept, as all inclusion parameters are <0.5 (Barbieri and Berger 2004; Figure 5.6). Meanwhile, the model without preferential sampling has strong evidence for the inclusion of late winter mean temperature range and the area of woodland within 1km of the site centroid within the persistence model, with inclusion parameters of 0.99 (Figure 5.6). This loss of significance between the two models can be explained by a reduction in between site variation in persistence probability in the preferential sampling model. Figure 5.7 shows the mean estimate

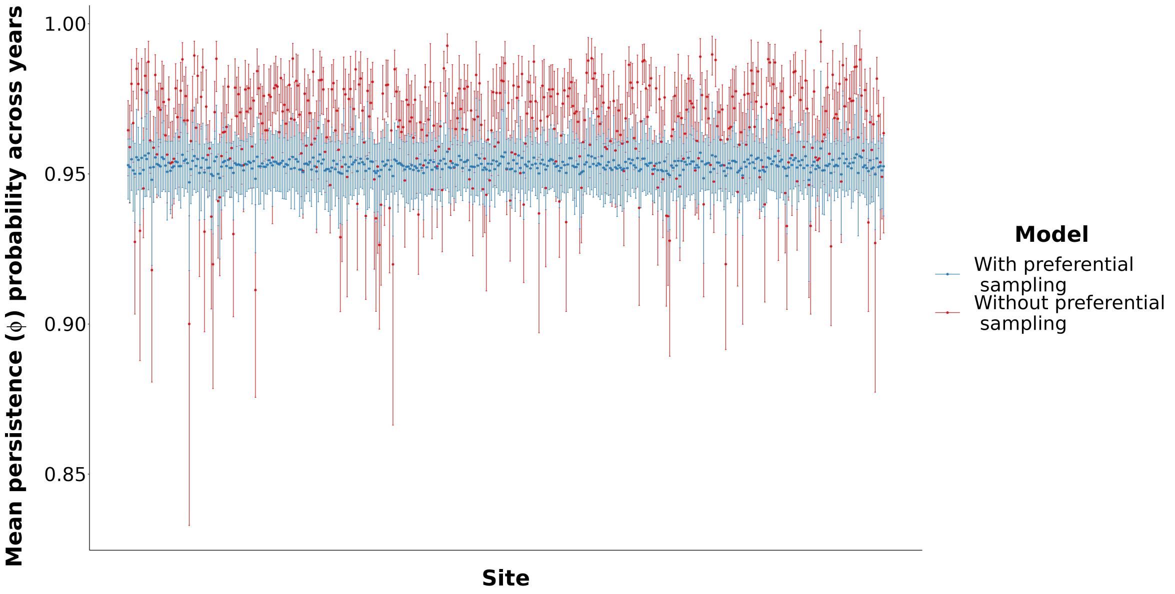


Figure 5.7. The mean persistence (ϕ) from 2000 to 2021 at each National Dormouse Monitoring Programme site as estimated by models with (blue) and without (red) preferential sampling. *The average persistence mean and 95% confidence interval (error bars) from the posterior distribution is shown.*

of persistence probability across years for each site, and clearly demonstrates a homogenisation of estimated mean between sites in the model with preferential sampling compared to the model without. The preferential sampling model lacks the variation in persistence to disentangle any effects of habitat or climate.

Considering the model without preferential sampling, with the indication of significant effects, we find late winter (February and March) temperature range has a significant negative relation with persistence and so a significant positive relation with its inverse, local extinction (Figure 5.8A). Though there is considerable uncertainty due to the reduced number of observations at higher ranges, local extinction probability begins to increase when the temperature range exceeds 7°C. There is also a slight significant negative relation between the area of woodland within 1km of a site and local extinction (Figure 5.8B), where extinction probability becomes negligible when there is around 1km^2 of woodland in the circle area.

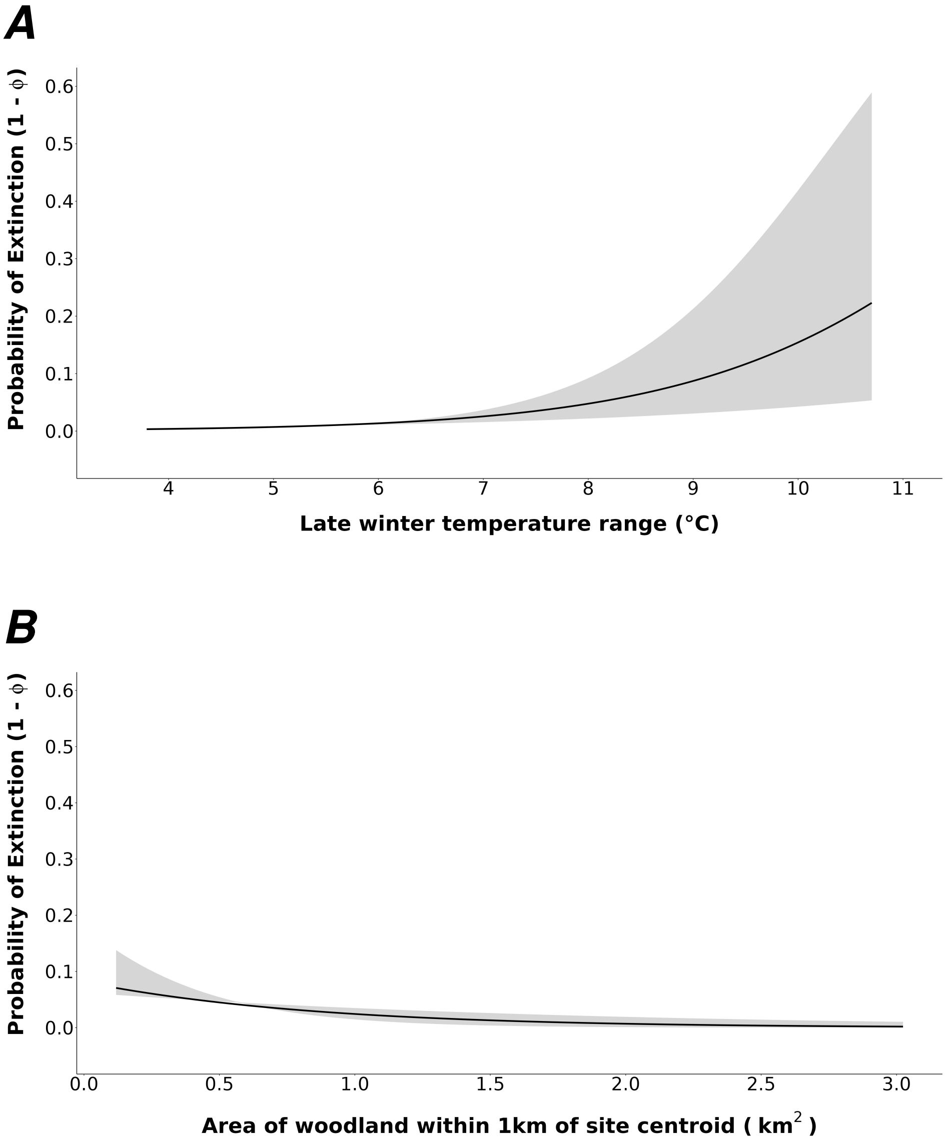


Figure 5.8. The significant relationship between A) mean late winter (February and March) temperature range and B) the area of woodland within 1km of the site centroid with the probability of extinction (1 - ϕ), from the joint model of occupancy without preferential sampling. *These are the only significant effects found in either model. The lines shows the mean of the posterior distribution, and the shaded area the 95% confidence interval. All other variables in the model are held at their mean. The intercept is the mean of the random effect of year.*

Abundance modelling

For the abundance modelling, we started with the same sites as the occupancy analysis (446), and removed sites with insufficient data in the pre- and post-breeding periods (May/June and September/October respectively). 385 sites were included in the pre-breeding model, and 425 sites in the post-breeding model. As these models did not rely on occupancy transitions, we included all data from 1993 until 2021. For the estimation of mean density in conifer and broadleaf habitat, there were 384 broadleaf sites and 32 conifer sites in the post-breeding model, and 347 and 30 respectively in the pre-breeding model.

As with the occupancy model, we found significant effects for all parameters influencing visitation probability, with effects in the same direction but different magnitudes (Table 5.2). Across all three models, the negative effect of year was similar. There was a slightly greater negative effect of COVID-19 lockdown restrictions in the pre-breeding abundance model than the other two models. There is also a dramatic difference in the positive effect of mean occupancy/abundance in the past five years, with much greater impact on the occupancy model than the abundance model (Table 5.2).

Similarly, the addition of preferential sampling also impacts the estimated trend in dormouse abundance, though much less so than with the occupancy model (Figure 5.9). For the pre-breeding models, there is an estimated decline of 74.0% (95% CI: 57.0% - 85.3%) in the model without preferential sampling, and a slightly lesser decline of 68.1% (95% CI: 52.0% - 78.7%) with preferential sampling. The post-breeding model with preferential sampling shows a slightly lesser decline at 70.3% (95% CI: 43.9% - 84.0%) than the model without at 72.3% (95% CI: 43.8% - 86.0%).

Though the confidence intervals all overlap, the slightly lesser decline in the models with preferential sampling is consistent with an overestimation of site abundance when less sites are visited in the early part of the time period.

Noticeably, the post-breeding abundance estimates for the number of dormice in Britain are an order of magnitude greater than the pre-breeding estimates (Figure 5.9), despite the focus on adult dormice. For the estimation of population sizes, pre-breeding estimates are preferred, and here we would also focus on the preferential sampling model as we have evidence of significant biases. As such, this model suggests there are 178,869 (95% CI: 136,474 - 239,089) adult dormice in Britain in 2021, and a 68.1% (95% CI: 52.0% - 78.7%) decline between 1993 and 2021.

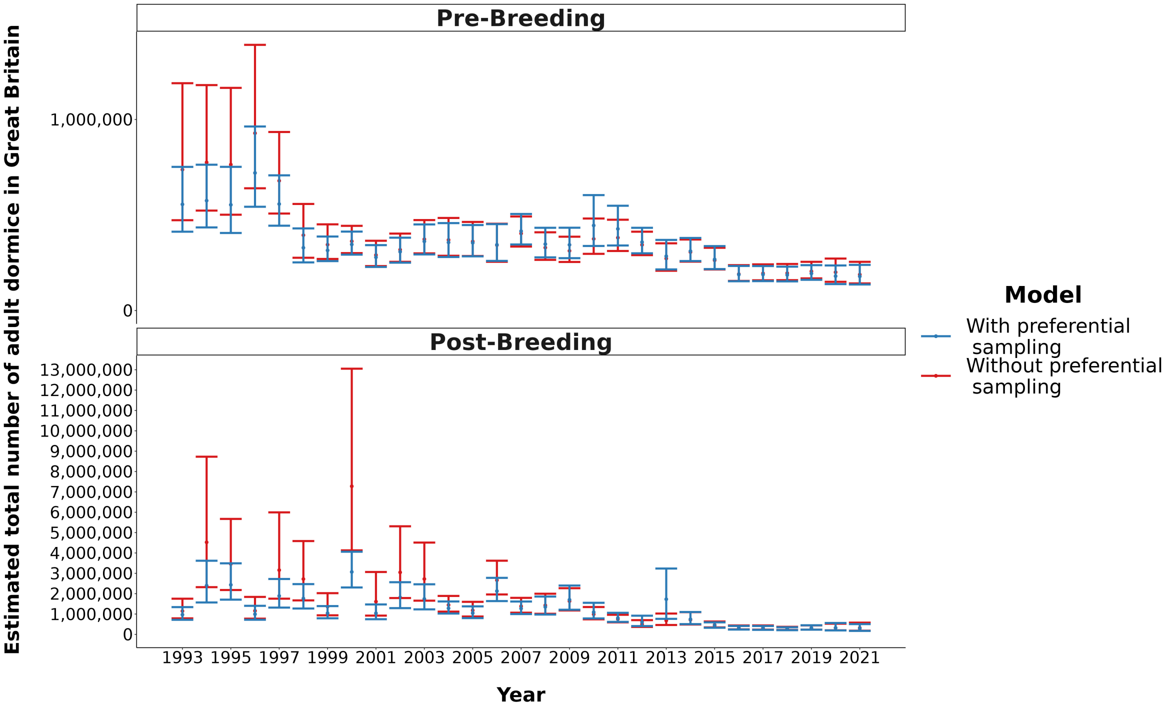


Figure 5.9. The estimated total abundance of adult hazel dormice in Great Britain at National Dormouse Monitoring Programme sites, both pre- (n = 385) and post-breeding (n = 425), between 1993 and 2021 from abundance models with (blue) and without (red) preferential sampling. *The points show the mean of the posterior distribution, and the error bars show the 95% confidence interval.*

Chapter 5

Discussion

We use the extensive National Dormouse Monitoring Programme data to investigate the occupancy and abundance of dormice in nest boxes whilst accounting for potential preferential sampling biases. In modelling the probability of visiting a site, we found positive effects of the mean occupancy or abundance in the past five years indicating significant preferential sampling bias in the NDMP. After accounting for this sampling bias, we find a decline of 33.3% (95% CI: 23.7% - 41.8%) in the occupancy of sites between 2000 and 2021, and a decline of 68.1% (95% CI: 52.0% - 78.7%) in the pre-breeding adult abundance between 1993 and 2021. We also investigate the climate and habitat drivers of local colonisation and extinction, but find that accounting for preferential sampling reduces between site variation in occupancy transitions such as persistence. As such, we rely on the model that does not include visitation probability, and find that local extinction probability increases with increasing late winter temperature range and decreasing area of woodland within 1km.

Our results reflect the literature, which has shown through simulation (Conn et al., 2017; McClure and Rolek, 2023) and applied studies of observed data (Fandos et al., 2021; Kéry et al., 2021) that not accounting for preferential sampling produces larger abundances and higher occupancy due to overestimation of the abundance/occupancy of the un-surveyed sites (Pennino et al., 2019). As such, investigations of drivers of occupancy have based their conclusions on the model accounting for preferential sampling (Kéry and Royle, 2021c). However, we struggled to gain inference about drivers in the preferential sampling model, as it seems that explicitly linking past occupancy and visitation probability explains much of the between site variation in occupancy and it's transitions. In our model, if sampling ceases at a site it is very likely dormice have gone locally extinct and are absent, compared to a site where sampling persists. In effect, sampling probability strongly explains occupancy probability, leaving little residual variation to be explained by environmental effects. Therefore, when investigating environmental drivers of occupancy changes, it may be more informative to implement a model without preferential sampling. This is because it is a stronger hypothesis that dormice go locally extinct because of environmental variables, and then people stop looking, rather than that all local extinction is driven by sampling bias. Future work, using simulations of different strengths and methods of accounting for preferential sampling, will be needed to further elucidate the entanglement between sampling and occupancy probability.

The link between sampling bias and occupancy may be particularly strong in the NDMP, compared with other systems where preferential sampling models have allowed inference (e.g. Kéry and Royle 2021c). Mean historical occupancy has a large positive effect on visitation probability, and may reflect the high investment of time (multiple surveys per year of usually at least 50 nest boxes) and resources (supplying and maintaining boxes and survey equipment) required for NDMP surveys; its simply not worth it for the volunteers to continue if they are not expecting to see a dormouse. This is supported by the stronger preferential sampling bias in the occupancy model compared to the abundance models, which indicates that volunteers are more sensitive to the presence of dormice, rather than their abundance. Continuing surveys in the absence of dormice may reduce the issues highlighted here. Such a protocol may also detect more recolonisation events, which are minimally observed in the data (Figure 5.1) and thus prevent any drivers of recolonisation being identified in either model. To persuade volunteers to do this, education on the importance of continued surveys, or even volunteer incentives (Tulloch et al., 2013), could be added to the programme, and should be considered when establishing other monitoring programmes.

For all models, the probability of visiting a site declines over time, likely due to the expansion of the programme. Sites added more recently could have been lower quality leading to earlier abandonment by volunteers, however, Goodwin et al. (2017) did not find significant differences between NDMP sites added at different times. Alternatively, as the programme became more well-known, the newer volunteers may have been more sensitive to the changes in dormouse occupancy/abundance. There is an additional effect of COVID-19 lockdowns on all models, though particularly strongly for the pre-breeding abundance model. The lockdowns would have prevented many volunteers from visiting sites during 2020 and 2021, especially in the early months of the survey year which is the focus of the pre-breeding model.

As well as the issues with preferential sampling, we have the additional caveat that the NDMP only comprises dormice using nest boxes in, predominantly broadleaved, woodland. Therefore, trends in occupancy and abundance may not reflect trends in the wider population that do not use the nest boxes or are found in other habitats. That being said, the NDMP is our only monitoring dataset for dormouse populations in Britain, and its spatial and temporal coverage is far greater than exists for many other British mammal species (Coomber et al., 2021) or hazel dormice in other countries (Juškaitis, 2014). Therefore, the NDMP can give important insights into the drivers of local colonisation and extinction.

The model without preferential sampling suggests two drivers of site persistence/extinction. Increasing late winter (February and March) temperature range increases the risk of local extinction at a nest box site, which matches existing literature on dormouse preference for consistent cold winters (Goodwin et al., 2018b). Temperature variation can have a detrimental impact on hibernation success, as individuals must expend more energy to remain at an ideal temperature which can mean they exhaust their stored fat resources too quickly (Scopes et al., 2024). With climate change likely to increase temperature variation over seasonal time periods (Guo et al., 2021), local extinction of nest box sites may increase in the future.

We also found local extinction probability decreased as the area of woodland within 1km of the site increased. This habitat variable was correlated with both the site's area of woodland and the area of ancient woodland within 1km of the site centroid, suggesting that this variable combines these effects and is an amalgamation of the patch size and connectivity of the NDMP site. Our findings reflects multiple studies highlighting the importance of habitat connectivity for dormouse populations (Iannarilli et al., 2017; Goodwin et al., 2018b; Dietz et al., 2018). In Britain, a study suggesting dormice require 20ha of woodland to persist (Bright et al., 1994) has become a threshold in forestry guidelines below which dormice are frequently assumed not to occur (Forestry Commission, 2019). Our study, where the is strong persistence probability for 12ha of observed woodland within 1km, corroborates other studies that find thriving dormouse population in smaller woodlands (Büchner, 2008). The 20ha threshold in forestry guidelines therefore needs to be altered to ensure forestry practice accounts for the presence of this protected species in more woodlands. Our results also indicate that planting woodland within 1km of known dormouse populations may aid in their persistence.

We estimate a 68% decline in the pre-breeding dormouse abundance between 1993 and 2021, which significantly differs from previous work which found 78% (95% CI: 72%–84%) over a similar period of 1994 to 2020 (Scopes et al., 2023). This difference is likely due to the latter study including a greater number of sites, as we only used sites with polygon information here, and our focus on the pre-breeding population rather than the whole adult population. We can also compare our abundance estimates to others used in British dormouse conservation. Harris et al. (1995) estimates a total pre-breeding population of 500,000 dormice in 1995. This is remarkably similar to our estimate, despite methodological differences, with a population size of 553,466 (95% CI: 405,995 - 752,102) in 1995. However, our estimate of current population size at 178,869 adult dormice is considerably smaller than Mathews et al. (2018) estimate of 930,000 (95% CI: 389,000 - 2,640,000). This difference is because we estimate current density in broadleaved woodland to be 0.5/ha (95% CI: 0.38/ha - 0.67/ha) and in conifer 0.69/ha (95% CI: 0.51/ha - 0.94/ha), compared to the values used by Mathews et al. (2018) of 3/ha and 2/ha respectively which were based on previous work, usually from small studies, or expert opinion. Though the NDMP may only sample part of the population, as discussed above, previous studies have found that providing high densities of nest boxes, which is commonly found in the NDMP, can increase the rate of dormouse detection and therefore estimated density compared to wider spacing (Juškaitis, 2006). This may mean dormouse densities are lower at sites without nest boxes, reducing our population estimate further.

Sampling biases are present throughout citizen science data, even in those, such as the NDMP, with rigorous training and a well-designed protocol. Analysis techniques can go some way to compensate for these biases, allowing important inferences on population trends. However, in this study, we highlight that accounting for preferential sampling bias reduces between site variation in modelled persistence probability, preventing the model from drawing conclusions on the environmental drivers that are clearly influential in the model without this addition. Further work is required to indicate in which systems or modelling structures this reduction in variation can become an issue and guide future applications of these models.

For hazel dormice in Britain, we present further evidence of population decline and a smaller current population estimate than previously considered. Our models also indicate key effects of winter temperature range and patch size and connectivity for dormouse persistence, highlighting both the species' vulnerability to climate change and possible management actions to increase woodland area.

Chapter 6: A seasonal integrated population model reveals the vital rates, and associated climate variables, driving population change in hazel dormouse *Muscardinus avellanarius*

Chapter 6: A seasonal integrated population model reveals the vital rates, and associated climate variables, driving population change in hazel dormouse *Muscardinus avellanarius*

Abstract

1. Integrated population models combine multiple datasets to estimate demographic rates and population sizes, which can be used in life table response experiments to ascertain the contributions of individual vital rates to population growth. This can reveal causes of population declines and targets for conservation actions.

2. We use data from two individually marked hazel dormouse (*Muscardinus avellanarius*) populations, one in Lithuania and one in Britain, to build an integrated population model for three age classes: early-born juveniles, late-born juveniles and adults. This model estimates monthly active season survival and yearly hibernation survival for all three classes, as well as recruitment for each juveniles class.

3. We found significant differences in estimates of demographic parameters between sites, with dormice in Britain having lower early-born juvenile recruitment and late-born juvenile active season survival than those in Lithuania. Hibernation survival was higher across all classes in Britain, though only significantly so for late-born juveniles.

4. There is a large contribution from demographic stochasticity to the realised variance in population growth rate in both of these small populations. Within

the demographic rates, the largest contributions to growth rate come from recruitment for both sites. Hibernation survival has a greater contribution to population growth in Lithuania, and there are also differences in the age classes with the largest contribution. This suggests alternative targets for conservation actions to improve population growth, for example recruitment of both juveniles in Britain but focusing on early-born juveniles recruitment in Lithuania.

5. We found strong correlations between seasonal and monthly climate variables and demographic parameters in Britain but not Lithuania. For example, early winter (December, January) total precipitation was negatively correlated with early-born juvenile recruitment and autumn mean temperature range was negatively correlated with late-born juvenile hibernation survival. Climate change is expected to improve conditions for dormice in autumn but worsen them in winter, making it difficult to predict the response at the population level.

Introduction

With growing threats it becomes increasingly important to understand the drivers of population changes to forecast future extinction risk and help target conservation management more effectively. Long term monitoring projects can provide information for population models which can indicate the demographic parameters (e.g. adult survival, productivity) to target to maintain or increase population growth rates (Caswell, 2000; Wilson et al., 2016), elucidate the effects of current management practices (Wilson et al., 2016), and suggest future options for conservation actions (Johnson et al., 2010). For example, a study of whooping cranes (*Grus americana*) population dynamics between 1977 and 2013 revealed that conservation goals could be met by maintaining high adult survival and increasing breeding output, and also suggests that egg collection for captive rearing did not affect population growth rate or productivity (Wilson et al., 2016).

Integrated population models (IPMs) combine multiple datasets, usually population counts and demographic data such a capture-mark recapture (CMR) and productivity data, to estimate and project demographic parameters (Schaub et al., 2007). By integrating information across shared parameters in each dataset, estimates from IPMs are more precise and less biased than other methods (Abadi et al., 2010). IPMs can also estimate parameters that could not be obtained from each dataset separately, such as immigration and productivity rates, and cope with missing data and unequal temporal coverage which is common with monitoring data (Schaub and Abadi, 2011). Adaptive management strategies can also benefit from IPMs as they can link management actions to population demographics, incorporating uncertainty in all parameters and allowing the outputs to be checked against monitoring data (Duarte et al., 2017).

IPMs can also be useful in current applications of sensitivity analysis, which investigate how changes in demographic parameters affect population growth. Traditional sensitivity analyses, through 'life table response experiments' (LTRE), have focused on asymptotic population growth; the growth when a population is at its stable age distribution when the environment is either constant or varying around a stationary mean (Caswell, 2000; Koons et al., 2016). However, this method cannot cope with non-stationary environmental variation, where there are changes in the mean, variance or both, which is common under current anthropogenic threats such as climate change (Koons et al., 2016). Recently developed methods therefore consider the past realised population growth rates, incorporating any environmental changes, and separate the contributions of each demographic parameter and population structure (e.g. proportion of population that are adults or juveniles, Koons et al. 2016). To do so, this 'transient' LTRE analysis requires estimates of the population structure at every time step, which are easily accessible using IPMs (Koons et al., 2017). Further extensions can investigate the contribution of environmental covariates, if their influence on demographic parameters is modelled within IPMs, and explore the relative contribution of environmental and demographic stochasticity as a whole (Knape et al., 2023). These improvements to sensitivity analysis are important for understanding how populations are responding to current shifts in environmental conditions.

Hazel dormice (*Muscardinus avellanarius*) are arboreal rodents which hibernate throughout most of their range (Juškaitis, 2014). Though dormice are considered Least Concern on the Global Red List (Hutterer et al., 2021), they are listed as threatened in several countries near the edge of its range (Juškaitis, 2018), including Britain, where they have declined by 78% between 1994 and 2020 (Scopes et al., 2023). Dormice are threatened by habitat destruction, due to the loss of species-diverse and structurally complex wooded habitats (Hutterer et al., 2021), and are sensitive to changes in temperature and precipitation during key seasons (Goodwin et al., 2018b; Combe et al., 2023). Previous work has estimated demographic parameters for dormice using multiple methods (Juškaitis, 1999; Bieber et al., 2012; Combe et al., 2023). An IPM utilising an annual structure has also revealed the negative effects of density dependence, precipitation and winter temperature (Combe et al., 2023). However, the yearly structure of this model could not distinguish between different survival periods, for example active season and hibernation survival, limiting our understanding of dormouse population ecology and their climate sensitivities. Conservation and habitat management planning also requires a finer scale understanding of how seasonal changes in demographic parameters affects population growth. For example, the structurally complex woodland preferred by dormice can be maintained by traditional management such as coppicing (Goodwin et al., 2018b), however the timing of this habitat management must be carefully considered to reduce its impacts on population growth.

In this study, we construct a temporally fine scale IPM with monthly transitions from April to October each year. In doing so, we distinguish hibernation and active season survival, and the recruitment of early-born and late-born juveniles. Dormice can have one or two litters per year, with young of the year able to breed late in the active season if conditions are favourable, which has implications for population growth. Though detailed information on seasonal survival is available for Lithuania (Bieber et al., 2012), British populations are less well-studied, and may differ as this is the north-western edge of the dormouse range (Juškaitis, 2014). Demographic rates are expected to be lower on range margins, where population performance is low, though this has not always been found in studies (Pironon et al., 2017). We use data from Lithuania to underlie and lend strength to more sparse British data, whilst allowing for site-specific differences to investigate any disparities between these sites. We use the outputs of the IPM to investigate the contribution of seasonal demographic parameters to variance in population growth, and how key demographic parameters are influenced by climate.

Methods

Data sources

Data for this study were collected from two dormouse populations; Bontuchel (North Wales, Britain) and Šakiai (South West Lithuania, Figure 6.1). Each site consists of a grid of around 250 nest boxes. Bontuchel is part of the National Dormouse Monitoring Programme (NDMP) with spacing between nest boxes of 10-20m (PTES, 2023), whilst a 50m spacing is used in Lithuania.

Dormice were individually marked using passive implanted transponder (PIT) tags in Britain, and aluminium leg rings in Lithuania. At each nest box check, the age class, weight and sex of individually marked dormice was recorded, and any young too small to be marked were counted. In Britain, nest box checks occurred once a month in May, June, September and October, from 2005 until 2020, though there were a few surveys in July and August in 2005 and 2006. In Lithuania, checks occurred every three weeks from April to October, but were collapsed into monthly bins for the analysis, and data was available from 1999 until 2021. Only data from female dormice were included in the model.

Integrated Population Model

All analysis was conducted in R version 4.3.0 (R Core Team, 2022).

Data structure

The individually marked dormouse data provided the capture histories for a capture-mark-recapture (CMR) model and the population totals, which also included individid-

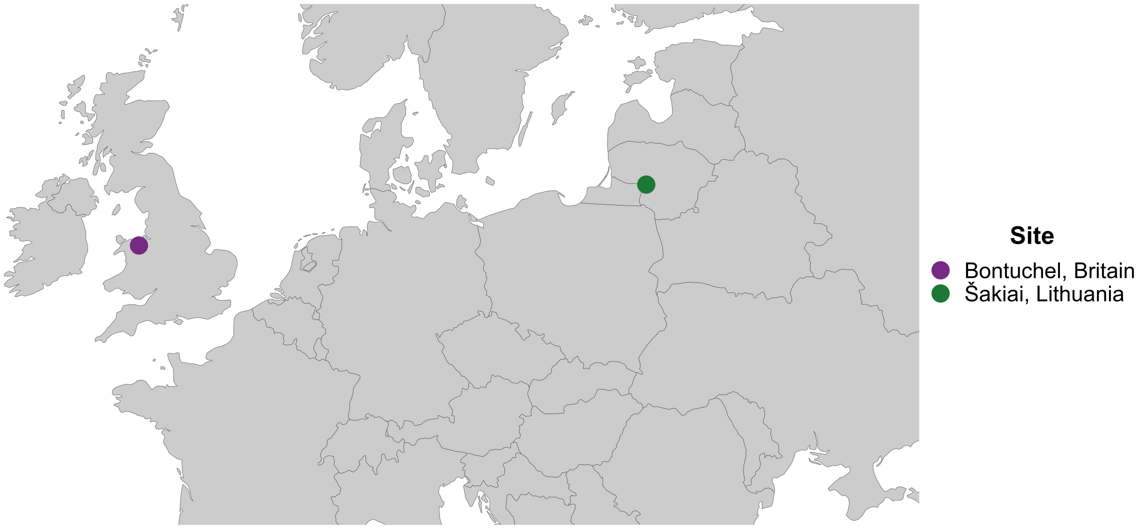


Figure 6.1. A map showing the locations of the two capture-mark-recapture data collection sites: *Bontuchel in North Wales, Britain (purple) and Šakiai in South West Lithuania (green).*

uals that could not be marked (e.g. escapees). This is a high level of data overlap, where multiple individuals occur in both datasets. IPMs rely on the assumption that individual datasets are independent, allowing joint likelihood to be derived from the product of individual data likelihoods (Abadi et al., 2010). However, extensive simulation studies show that even complete data overlap does not produce bias or change the uncertainty of estimated parameters (Abadi et al., 2010; Weegman et al., 2021). We are therefore able to generate our IPM with these interdependent datasets.

Our model included three age classes: early-born juveniles, late-born juveniles and adults. Adults were dormice that have survived their first hibernation, and can be distinguished by the golden fur from their first moult (PTES, 2023). Juveniles were assigned to early- and late-born classes based on when they were first captured and their weight, according to known growth curves (Juškaitis, 2014). Early-born juveniles were those seen for the first time in May, June or July, were $>$10g in August, $>$11g in the first half of September, $>$14g in second half of September, and $>$17g in

October. Juveniles that could not be assigned, for example those that were not weighed, were removed from the analysis. Early-born juveniles exist in the model from May until October, whilst Late-born juveniles only exist from August to October. Early-born juveniles can sometimes breed the year of their birth (Juškaitis, 2014) to produce late-born juveniles, which we have included in our models.

Model structure

Our female-only IPM consisted of a population state-space model and a Cormack-Jolly-Seber (CJS) model formulated in an M-array structure (Schaub and Kéry, 2022a). For each model, seven months (April to October) were nested within each year (Figure 6.2). We had four demographic parameters: active season survival, hibernation survival, recruitment, and recapture (Table 6.1, Figure 6.2). As this is a closed pop-

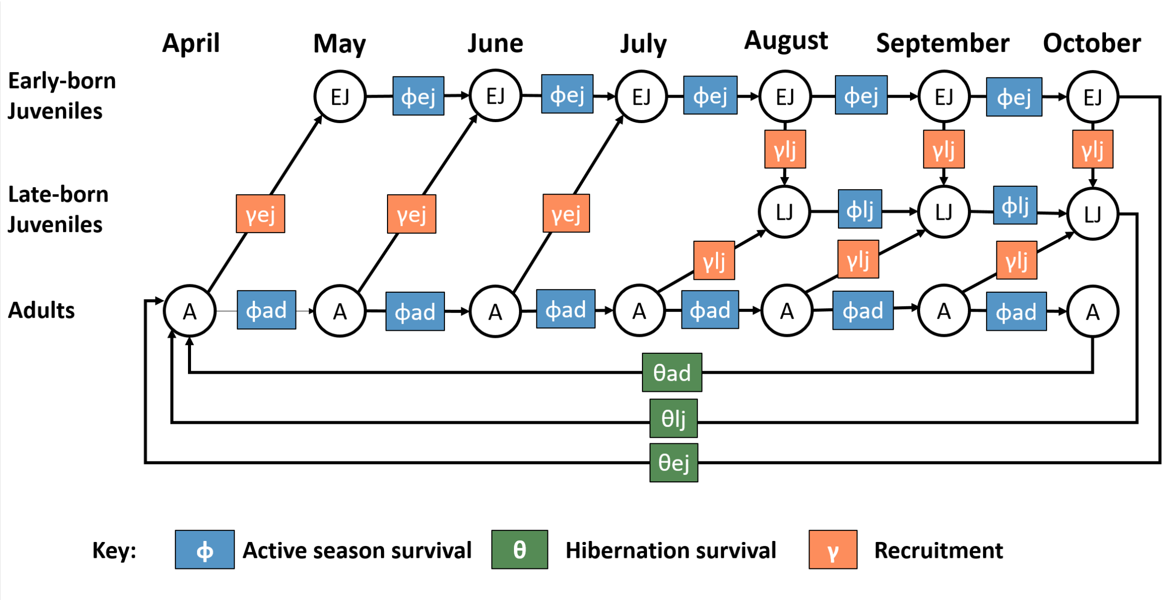


Figure 6.2. A diagram of the integrated population model structure for each year cycle. *Circles show the 3 stage classes: adults, early- and late-born juveniles. Each of the seven months is depicted, with the associated stage classes possible in that month. Between months, arrows depict the transitions between stages, which are labelled with coloured boxes showing active season survival (blue), hibernation survival (green) and recruitment (orange). The subscript of each arrow label shows the stage class of the transition.*

ulation model, survival parameters represent apparent survival, as emigration could be included in the variable, and recruitment could also include immigration. Active season survival (ϕ) is the survival between months of the same year, whilst the dormice are active. Meanwhile, hibernation survival (θ) encapsulates the survival over the hibernation period between years (October to April) and the transition of both juvenile age classes into adults. Recruitment (γ) is the number of female juveniles produced by each adult female that month for early-born juveniles, and each adult or early-born female for late-born juveniles (Figure 6.2). Recruitment may also include immigration as there is no direct information on productivity. There is a separate parameter for the recruitment of early- and late-born juveniles (Table 6.1). In our results, we assume an equal sex ratio and multiply recruitment by two to give the recruitment of both sexes. Recapture (ρ) is the probability of recapturing an individual that month in the CJS model. Active season survival, hibernation survival, and recapture all have separate parameters for each of the three age classes (Table 6.1, Figure 6.2).

Each time step transition (between months or between years from October to April) consisted of a different combination of parameters, depending on dormouse life history (Figure 6.2). For example, the transition of April to May includes active season survival for adults, and recruitment of the first litters of early-born juveniles. Recapture in May only includes adults, whilst both age classes exist in the population totals. British data had fewer recapture parameters than Lithuania, as fewer surveys occurred at this site which effects the structure of the CMR model. The population equations and CJS transition tables can be found in Appendix 7.

This model links population counts to the observed counts using a Poisson distribution, allowing the observed data to be both above and below the estimated counts.

This is usually appropriate for count data, as individuals can be missed or double counted. However, in this system it is unlikely that double counting occurs as all nest boxes are surveyed at the same time, and all individuals are marked. Therefore, observed values should always be smaller than estimates, as individuals in the population can only be missed during the surveys. We therefore tried implementing a binomial observation model which would better reflect the survey method. However, this model was incapable of estimating parameters as it produced flat posterior chains for several variables, which we were not able to fix by changing the model initialisation or samplers. We therefore returned to presenting the Poisson model here.

To test goodness-of-fit for this IPM, we produce posterior predictive checks for both sub-models (Schaub and Kéry, 2022c). These checks compare the expected population values from the demographic parameters in the model to both the observed data and data replicated from the model. Differences between the expected and observed/replicated data are quantified by a discrepancy statistic, with good fit if the discrepancy statistics from each of the comparisons are similar. For the state-space model we used mean absolute error as the discrepancy measure between observed and expected data, and a Freeman-Tukey statistic for the CJS model (Schaub and Kéry, 2022c).

Site and time effects

The Lithuanian data contain more information on monthly changes in the population parameters due to greater coverage of months and its longer time period of surveys (1999-2020). To share information between Lithuanian and British data, whilst allowing for differences between the sites, we included site random effects for every parameter.

Table 6.1. The demographic parameters, for each age class, included in the integrated population model. *The mathematical notation and the period over which the parameter varies in time is shown.*

Parameter	Age class	Notation	Time Variation
Active season survival	Adult	$\phi ad_{t,m}$	Year, month
Active season survival	Early-born juvenile	$\phi ej_{t,m}$	Year, month
Active season survival	Late-born juvenile	$\phi lj_{t,m}$	Year, month
Hibernation survival	Adult	θad_t	Year
Hibernation survival	Early-born juvenile	θej_t	Year
Hibernation survival	Late-born juvenile	θlj_t	Year
Recruitment	Early-born juvenile	γej_t	Year
Recruitment	Late-born juvenile	γlj_t	Year
Recapture	Adult	ρad_m	Month
Recapture	Early-born juvenile	ρej_m	Month
Recapture	Late-born juvenile	ρlj_m	Month

To incorporate variation over time, we also included time-specific random effects (Table 6.1), which were shared across sites in the same time period by matching corresponding months/years. Sites therefore shared a global mean and temporal variation and differed only by site random effects. This structure was chosen to maximise shared information between the data, and to focus on identifying any differences between the sites on average.

Active season survival varied over every year and month time step, hibernation survival and recruitment only over years (same recruitment for each month of the same year), whilst recapture only varied over months (same recapture for each year for the same month). This reflects likely variation in biology, for example dormice becoming more detectable in autumn as they increase foraging activities and disperse before hibernation, but without including excessive variation which could make parameters unidentifiable.

Model Implementation

The posterior distribution for the IPM was estimated using Markov chain Monte Carlo (MCMC) simulations implemented using the package 'nimble' version 1.0.1 (de Valpine et al., 2017). We used vague priors for all parameters (Appendix 8). We used the default samplers for all parameters, but imposed slice samplers for the global means and site/time random effects for each demographic parameter and the initial adult population at each site, as this produced better mixing. We ran three chains of 250,000 iterations, discarding the first 100,000 iterations as the burn-in period and thinning every 10 iterations to produce 45,000 posterior samples. We confirmed convergence of this model by visually inspecting the chain outputs and confirming that the Gelman-Rubin statistic was <1.1 (Gelman and Rubin, 1992). We summarise all parameters using the mean and 95% confidence interval of the posterior distribution.

Contributions to population growth

We then complete a 'transient' LTRE (tLTRE) analysis documented in Koons et al. (2016), with an extension to consider contributions of environmental and demographic stochasticity to variance in realised population growth rate documented in Knape et al. (2023). In this context, where we do not directly model the effect of any environmental covariates within the IPM, environmental stochasticity is the temporal fluctuations in demographic parameters, whilst demographic stochasticity results from chance events in individual outcomes (Knape et al., 2023). Thus, demographic stochasticity may have more influence on growth variance in small populations. We consider population growth rate on a yearly scale (from April to April), matching the perception of conservation practitioners, whilst maintaining seasonal differences in demographic parameters. We calculate the average growth rate for each site using the geometric mean of growth rates for the periods of survey.

We further decompose the contribution of environmental stochasticity into the individual contributions of each demographic parameter and population structure using tLTRE analysis Koons et al. (2016). A large contribution indicates a parameter has: A) a large growth rate sensitivity, B) a large variance and/or C) a large covariance with another parameter with a large sensitivity. This tLTRE method uses Taylor approximations to estimate the sensitivity of population growth rate to each parameter (Koons et al., 2016). We therefore checked for error from this approximation by calculating the relative percentage error between the realised variance in growth rate from environmental stochasticity and the sum of the individual parameter contributions. If the approximation is completely correct these values should be equal, though some error is expected.

Climate correlations of demographic parameters

We investigated how climate influenced each demographic parameter with large contribution to population growth rate and/or that were significantly different between sites. This analysis was completed post-hoc through calculating Pearson rank correlations between climate and demographic parameters. We accessed historical monthly climate data for Britain and Lithuania from CRU-TS 4.06 (Harris et al., 2020) down-scaled with WorldClim 2.1 (Fick and Hijmans, 2017), using the highest resolution data at 2.5 minutes (˜21km^2). This provided monthly temperature minimum and maximums, from which we calculated temperature range, and total precipitation. For active season survival, which varied over months, we consider the short term effects of climate by considering the temperature and precipitation in the month previous to the survival transition. For hibernation survival and recruitment, where only one value is calculated per year, we investigated the effects of season previous to the demographic parameters effect, considering the effect of autumn weather on hibernation survival, winter weather on early-born juvenile recruitment and spring weather on late-born juvenile recruitment. Seasonal values where calculated as the mean of temperature parameters and the total sum of precipitation. Seasons were categorised to match previous dormouse analysis of early and late winter (**Chapter 5**); early winter (Dec, Jan), late winter (Feb, Mar), spring (Apr, May), summer (June, July, Aug) and autumn (Sep, Oct. Nov).

Results

Survey summaries

The data collected in Lithuania was available from 1999 until 2021. During this period there were 3576 captures of 1565 individual dormice. Most of these individuals were first captured and marked as early-born (n = 852) or late-born juveniles (n = 566), though some were caught initially as adults (n = 147). On average, individuals were caught 2.3 (standard deviation: 2.1) times including initial marking, suggesting that individuals on average were recaptured at least once. The individual with the longest capture history was recaptured for five years after being initially marked as an early-born juvenile. This is similar to Britain where three individuals were recaptured after five years, though one was initially marked as an adult suggesting it could have been older.

In Britain, data was available from 2005 until 2020, with 1098 captures of 565 individuals in this time. Here, more individuals were initially captured as late-born (n = 230) than early-born juveniles (n = 103), and a larger proportion of individuals were marked as adults (n = 232). Individuals were caught 1.9 (SD: 1.8) times on average, suggesting much of the population was not recaptured after initial marking.

IPM estimates

The posterior predictive checks of the IPM sub-models suggests there is good fit for the state-space model of the British data, however it also suggests there is lack of fit for the state-space model of the Lithuanian data, and the CMR models for both countries (Appendix 9).

Population estimates

The IPM produces estimates of all three stage class female population size, as well as overall totals. The IPM is closer to the observed data in Britain than in Lithuania (Figure 6.3), reflecting the GOF results. We expected some difference between estimates and observed data as the Poisson structure of the observation can account for both imperfect detection and double counting. Both errors can be observed in Figure 6.3, especially in Lithuania where observed counts are occasionally much higher than estimated population size. The lack of fit in Lithuanian count data may be due to the larger population sizes and therefore larger Poisson variance allowing estimated counts to differ more from the observed values. Overall, the IPM is able to capture the seasonal increases within each year, and the trend in population size over each survey period.

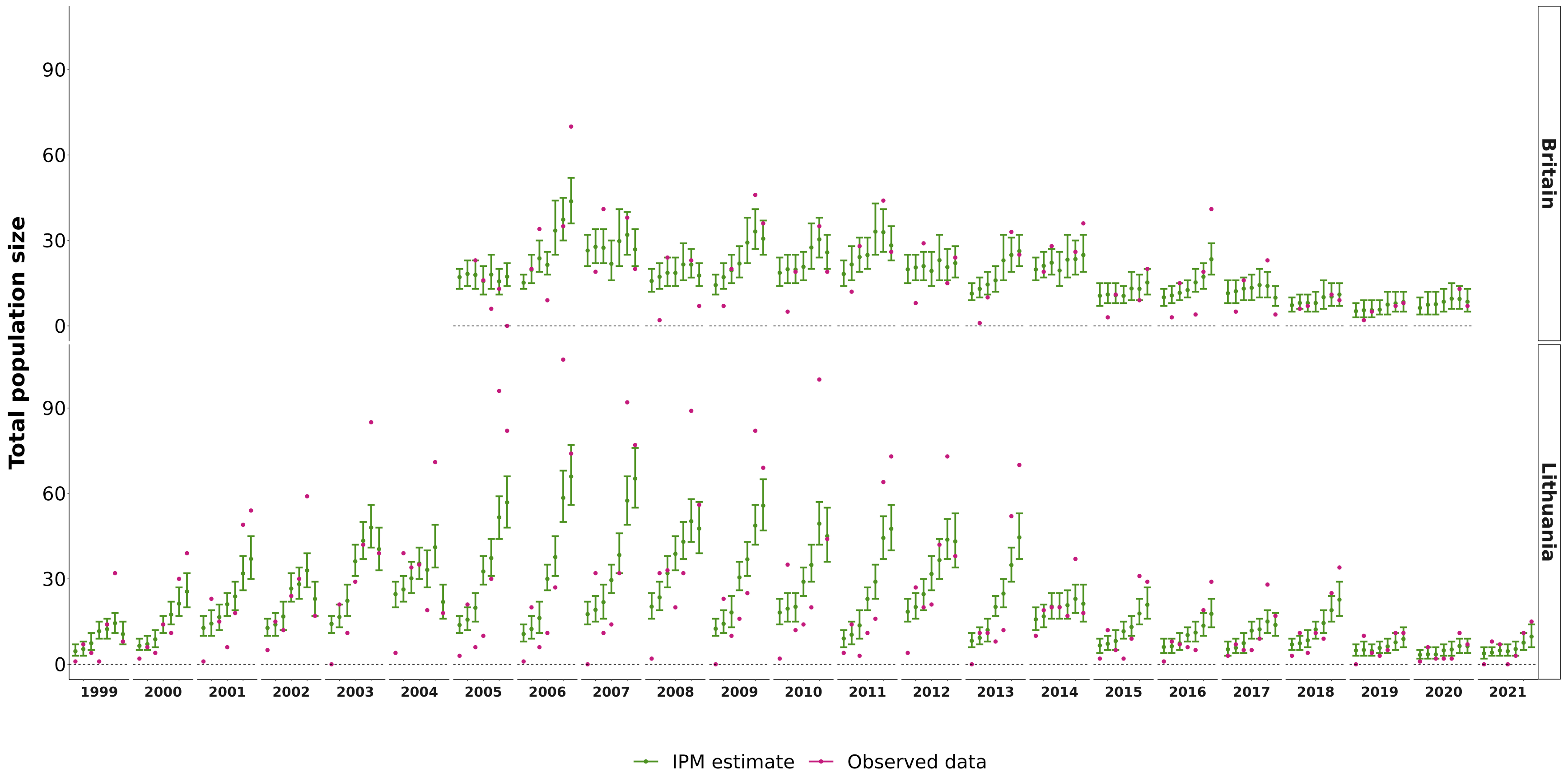


Figure 6.3. A comparison of the estimated total population size (green) and the observed data (pink) for both Britain and Lithuania. *For the model, estimates of the mean (points) and 95% confidence interval (error bars) are shown. The dashed lines mark zero population size to aid visualisation. Britain has less observed data but the model produces estimates for each month.*

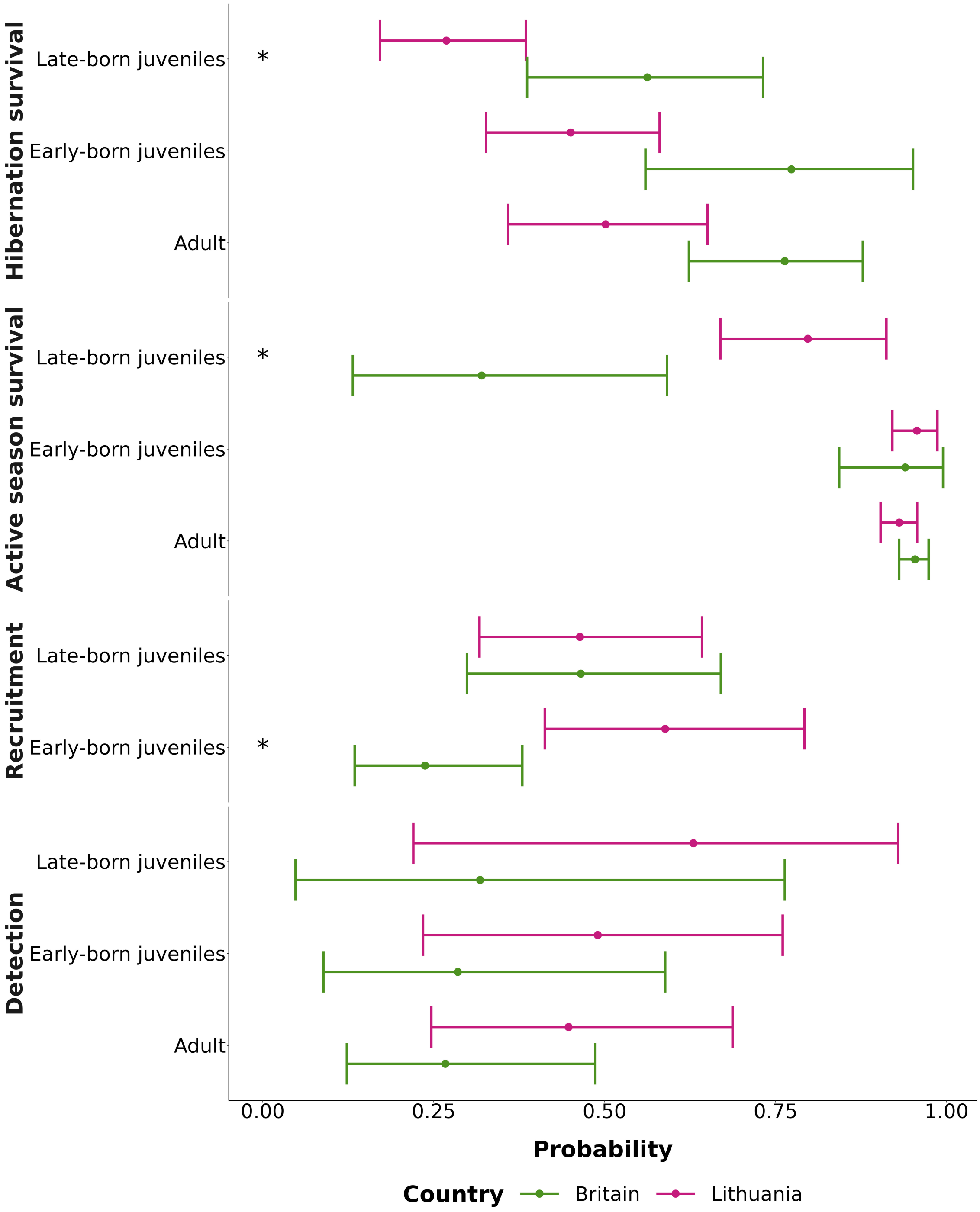


Figure 6.4. The mean of each demographic parameter for both countries, Britain (green) and Lithuania (pink), around which there is temporal variation. *The mean (points) and 95% confidence interval (error bars) of the posterior distribution is shown. An asterisk indicates a significant difference between sites, where the confidence intervals do not overlap. Hibernation survival covers a longer period (October to April) than active season survival (one month steps).*

Demographic parameter estimates

The estimates of the site-specific mean for each demographic parameter are shown in Figure 6.4. There are significant differences between sites for three parameters: the British site has lower early-born juvenile recruitment and late-born juvenile active season survival, and higher late-born juvenile hibernation survival than Lithuania. On the whole, there is more uncertainty around the juvenile parameter estimates than the adult ones, reflecting the reduced amount of data, especially for late-born juveniles, that is available in the model.

Comparing parameters within sites, we find that recruitment of both juveniles classes is similar in Lithuania, but early-born recruitment is lower (though not significantly) in Britain. To compare between hibernation and active season survival, the parameters must be placed on the same scale (see Appendix 10). Hibernation survival is equal or higher than active season survival for the same stage class.

tLTRE analysis

Both populations have periods of growth, decrease and stability throughout the time periods analysed (Figure 6.5). The mean population growth rate for Lithuania is 0.99 (95% CI: 0.96 - 1.02) suggesting the population is overall stable, whilst for Britain it is 0.93 (95% CI: 0.90 - 0.97) suggesting a slight decline on average.

The variance in the realised growth rates in Figure 6.5 can be decomposed into contributions from demographic and environmental stochasticity. For Britain, the contributions from each form of stochasticity are relatively equal, environmental factors contribute 48.6% (95% CI: 24.4% - 75.7%) and demographic 51.4% (95% CI: 24.3% - 75.6%) of the variance. In Lithuania, environmental stochasticity contributes more

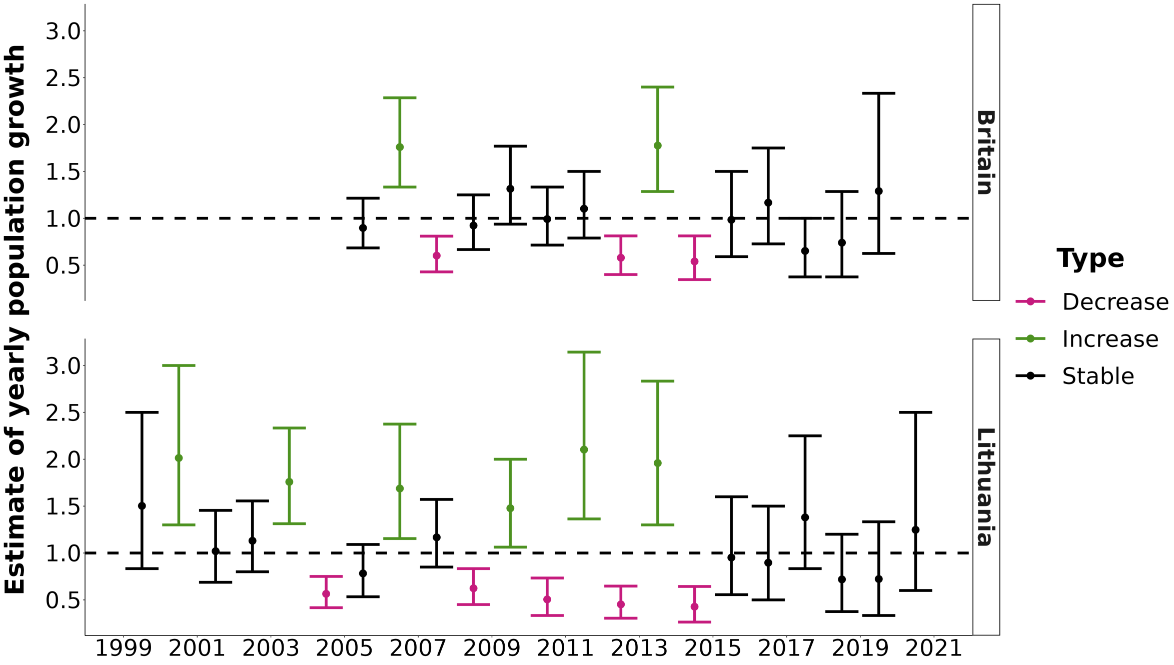


Figure 6.5. Estimated yearly population growth rates for Lithuania and Britain. *The mean (points) and 95% confidence interval (error bars) of the posterior distribution is shown. The dashed line shows a population growth of one, which is a stable population. The colours indicate population growth (green) if the estimate and confidence intervals are greater than one, population decrease (pink) if they are less than one, or population stability (black) if the confidence intervals cross one.*

to variance with 62.9% (95% CI: 39.5% - 90.0%), compared to demographic stochasticity with 37.1% (10.0% - 60.5%). These are both relatively large contributions from demographic stochasticity (Knape et al., 2023).

The contributions from environmental stochasticity can be further decomposed into contributions from temporal fluctuations in individual demographic parameters (Figure 6.6). We used Taylor approximation for these calculations but find a low percentage error between the sum of these demographic parameter contributions and the total environmental contribution for each site, with a mean relative error of 3.6% (standard deviation: 18.2%) in Lithuania and 0.5% (SD: 12.7%) in Britain. There are similar large contributions from recruitment at both sites, whilst there is a stronger contribution from hibernation survival in Lithuania than Britain (Figure 6.6). The population structure in April has no impact on growth rate as it is the same every year with only adults in the population at this time. There are further differences when the age class and seasonal rates are considered (Figure 6.7). Early-born juvenile recruitment contributes more in Lithuania than Britain, whilst the opposite is true for late-born juvenile recruitment. Early-born juvenile hibernation survival contributes more in Lithuania than Britain, but there are stronger contributions from active season survival in Britain particularly from adult survival between June-July and September-October, and early-born juvenile survival between August-September. Therefore the parameters with significant differences between sites (Figure 6.4) are not necessarily those with the largest contributions or different contributions between sites (Figure 6.7). The large individual contributions are mainly due to high sensitivity of growth rate to the vital rate, rather than high variance or covariance.

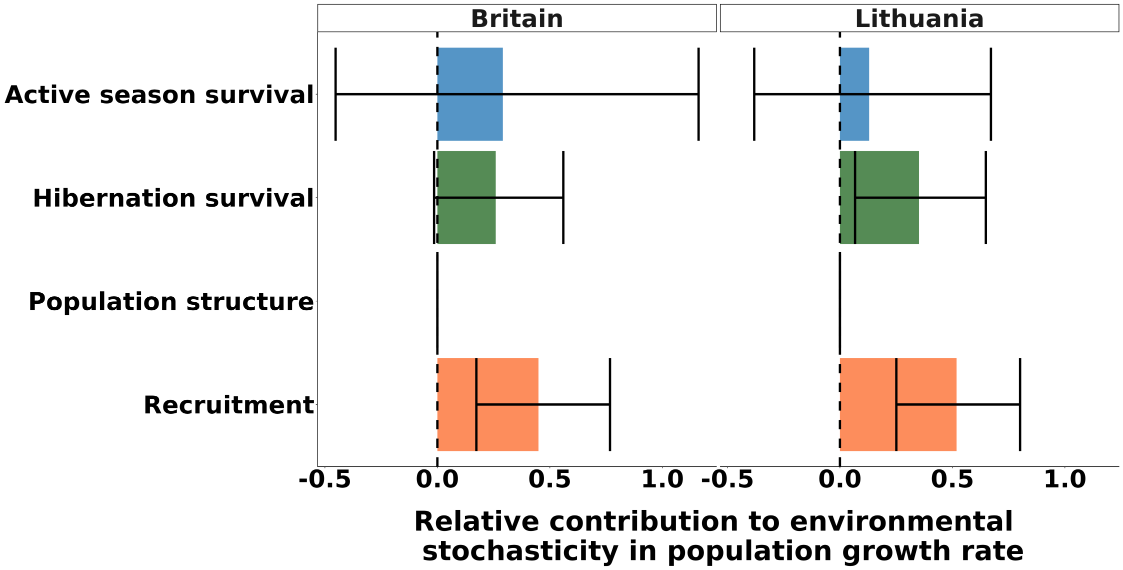


Figure 6.6. Relative contribution of the three categories of demographic parameter to environmental stochasticity in realised population growth rate in Lithuania and Britain. *The mean (bars) and 95% confidence interval (error bars) of the posterior distribution is shown. The colours indicate the demographic rates: Recruitment (orange), hibernation survival (green) and active season survival (blue). A dashed line indicates zero, helping distinguish parameters with negative and positive contributions.*

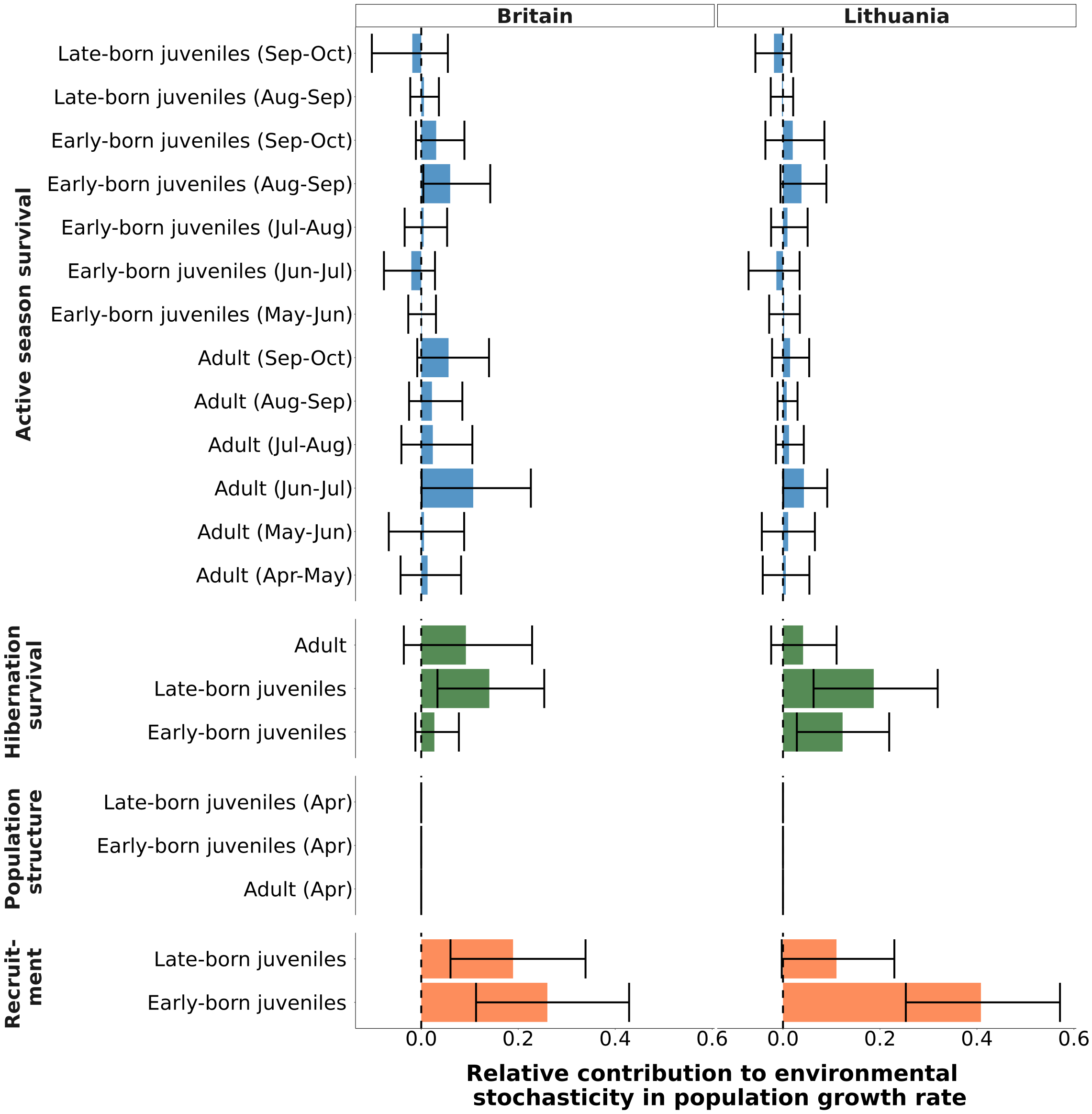


Figure 6.7. Relative contribution of each demographic parameter to environmental stochasticity in realised population growth rate in Lithuania and Britain. *The mean (bars) and 95% confidence interval (error bars) of the posterior distribution is shown. The colours indicate the demographic rates: Recruitment (orange), hibernation survival (green) and active season survival (blue). A dashed line indicates zero, helping distinguish parameters with negative and positive contributions.*

Climatic influences

We tested the climate correlations for all demographic parameters, as all had either strong contribution to environmental stochasticity (Figure 6.7) or were significantly different between sites (Figure 6.4). Table 6.2 shows the variables with absolute correlations greater than 0.5, with all correlations tested available in Appendix 11. Notably, we only found strong correlations for parameters in Britain.

For recruitment, which had some of the greatest contribution to environmental stochasticity, we did not find strong correlation between the climate the previous spring and late-born juvenile recruitment (Appendix 11). However, we did find a negative correlation between early winter (December, January) total precipitation and early-born juvenile recruitment. For hibernation survival, we found no correlations for adult parameters, but found temperature correlated with both juvenile classes. Finally for active season survival, we found several correlates for adults, but only one for early-born juveniles. There were correlates for two of the adult active season survivals with strong contributions to environmental stochasticity (Sept-Oct, and Jun-Jul), but also for variables with weak contributions.

Table 6.2. Correlations between demographic parameters and climate variables in the previous month or season. *Only absolute Pearson rank correlations greater than 0.5 are shown. The time period refers to the period over which the climate variables are calculated, and are previous to the respective demographic parameter.*

Site	Parameter	Age class	Time period	Climate variable	Correlation
Britain	Active season survival	Adult	September	Temp. range	-0.62
Britain	Active season survival	Adult	June	Temp. range	0.55
Britain	Active season survival	Adult	August	Precipitation	-0.51
Britain	Active season survival	Early-born juv.	September	Precipitation	-0.53
Britain	Hibernation survival	Early-born juv.	Autumn	Mean min. temp.	0.58
Britain	Hibernation survival	Early-born juv.	Autumn	Mean max. temp.	0.54
Britain	Hibernation survival	Late-born juv.	Autumn	Mean temp. range	-0.57
Britain	Recruitment	Early-born juv.	Early winter	Total precipitation	-0.55

Discussion

We found significant differences between British and Lithuania populations for late-born juvenile survival in both the hibernation and active season, and for early-born juvenile recruitment. Both sites have large contributions of demographic stochasticity to realised population growth rates, and large contributions of juvenile recruitment to environmental stochasticity in growth rate. Hibernation survival has more impact on growth rates in Lithuania than Britain, and the sites also differ in the age classes and months with the greatest contributions. Finally, we considered the climate correlations with important demographic parameters, but only find strong effects at the British site.

It can be difficult to assess the goodness-of-fit in an IPM with a hidden parameter, such as our model (Schaub and Kéry, 2022c). A hidden parameter is a vital rate that can only be estimated from the population model, and does not have any other data contributing to its estimation, for example, recruitment in our model. When a hidden parameter is included, the power to detect a lack of fit is greatly reduced, as the hidden parameter can compensate for most model issues (Schaub and Kéry, 2022c).

That being said, we were able to detect a lack of fit in this IPM. This can also be seen when comparing the estimated population sizes to the observed size (Figure 6.3), where the observed values are both above and below the confidence intervals due to the Poisson structure of the observation model. This is a closed population model, but there is likely immigration and emigration occurring between the nest boxes and other parts of the wood. We can account for emigration in the survival parameters and juvenile immigration in recruitment, however, there is no mechanism in our model to allow for adult immigration which could be contributing to the lack of fit. Adding adult immigration to the model would mean adding another hidden parameter. Usually only one hidden parameter can be estimated in IPMs as they are inferred from a single population count (Schaub and Kéry, 2022b). Here, we are able to estimate two hidden recruitment parameters as we have separate counts for both juvenile age classes. It would therefore be possible to add a hidden parameter relating to the adult population count. However, additional hidden parameters are likely to reduce the ability of the model to mix and greatly increase time until convergence.

There are similarities between this model and others in the literature that suggest our estimates of demographic parameters are reasonable. Data from the Lithuanian site, between 2001 and 2006, was used to estimate survival parameters in the early (May–August) and late active season (August–October), and over the hibernation period (October–May) for early- and late-born juveniles and adults (Bieber et al., 2012). This analysis, despite the shorter time frame and different modelling approach, shows similar estimates of survivals when compared to our estimated site-specific means for Lithuania for all values except early-born juvenile active season survival which we estimate to be higher than Bieber et al. (2012). The Lithuanian data has also been used to estimate yearly survival of different age classes using life tables (Juškaitis, 1999), and again our results are similar for adults, which are directly comparable, when converted to a yearly scale. There are fewer estimates for survival in Britain, however data from both sites were used to build a yearly IPM by Combe et al. (2023), which estimates higher yearly survival for adults. Combe et al. (2023) did not share information between sites and had shorter time frames of data available, which may account for these differences. Similarity between our estimates and those in the literature suggests we can be more confident in the robustness of these results, despite the lack of model fit.

Our model has several strengths, including distinguishing early- and late-born juvenile recruitment, estimating survival in different seasons and estimating population size for the British site when no surveys have taken place. This allows us to investigate in some detail the differences between the sites. The lower growth rate in Britain, at the range margin, suggests poorer population performance compared to the range centre, which matches expectations (Pironon et al., 2017). Early-born recruitment is lower in Britain than Lithuania, though late-born recruitment is the same.

The method used to split juveniles into these classes was based on data from Lithuania (Juškaitis, 2014), where there are two peaks of births within the early (May-July) and late (August-October) period (Juškaitis, 2003). However, in Britain, there is a single peak of breeding in July and August (Bright and Morris, 1996) which spans the division. Our results suggest there are fewer births in the early period in Britain, with most breeding occurring in the late period. Our estimates also suggest there is less recruitment overall in Britain, which might explain the lower mean growth rate, given the large contribution of recruitment to growth. Late-born juvenile active season survival is low in Britain which may be because juveniles are not able to access enough resources in the autumn. Another possibility is juveniles in Britain are emigrating during the active season, rather than the hibernation season. The higher early-born juvenile active season survival in Britain suggests that when young are infrequently recruited early, they survive well, likely as the decision to breed early hinges on the adults having sufficient resources to support them.

Hibernation survival is higher in Britain for all age classes, though only significantly so for late-born juveniles. Hibernation survival depends on both energy use during hibernation and the resources gathered beforehand (Scopes et al., 2024), suggesting British dormice may have access to more resources or have a more favourable hibernation conditions. Lithuania winters are likely colder than those in Britain, which should favour hibernation (Scopes et al., 2024), however they are also longer (Juškaitis, 2014), so perhaps resources are frequently insufficient for the length of hibernation period required. Another possibility is emigration in Lithuania occurs more frequently over the hibernation season than in Britain. Dormice are thought to disperse shortly before and after hibernation (Juškaitis, 2014) but dispersal is difficult to study and so there could be behavioural differences across the dormouse range.

Demographic stochasticity has a large contribution to variance in growth rate of both sites. This is likely due to the small population sizes at both sites, especially more recently (Knape et al., 2023). Large amounts of demographic stochasticity can increase the extinction risk of the population, as it can lower population growth and slow adaptation (Steiner et al., 2021). Population growth is on average low in Britain, indicating population decline, which may be the result of the larger demographic stochasticity. There is a circular relationship between small population size, demographic stochasticity and lower population growth, which contributes to the 'extinction vortex', where small populations continue to decline as a consequence of being small (Caughley, 1994). Though we did not project population sizes forward in time, the low population growth rates and small population sizes suggest a high risk of local extinction for both populations in the near future.

The sites differ in how demographic rates contribute to environmental stochasticity, though there are some similarities. These differences are likely driven by disparities in sensitivity between sites, which has the largest impact on the contribution estimate. For example, early-born juvenile recruitment and hibernation survival contribute less in Britain, matching the low production of these juveniles compared to Lithuania.

Conservation management targeting juvenile recruitment would have the biggest impacts on population growth at both sites. This might mean increasing the abundance of food resources by planting species associated with breeding, such as hazel (*Corylus avellana*) and willow (*Salix spp.*, Goodwin et al. 2018b). Woodland management could also be planned to avoid disturbing breeding dormice. The differences between the contributions of early- and late-born juveniles suggests that management should be avoided throughout the season in Britain, but should mainly avoid the early season in Lithuania. However, the greater contribution of hibernation survival to population growth in Lithuania suggests that woodland management in winter, and the destruction of hibernation nests, could be more harmful to populations than in Britain. More work is needed to quantify the impact of management on survival and recruitment, however this work suggests that management regimes may need to differ across the dormouse range to minimise the effects on growth rate and population persistence.

We only found strong correlations between climate and demographic variables in Britain. Britain is at the north-western edge of the hazel dormouse range in Europe (Juškaitis, 2014) and so may have a more marginal climate for the species compared to Lithuania. Small climate variations can have large demographic effects at range margins where conditions are less favourable (Westerbom et al., 2019), which is reflected here. Adult active season survival has opposing correlation with temperature range depending on the time of year; in June increased temperature may have positive effects on insect growth (Colinet et al., 2015) providing more resources for adult survival, meanwhile in September large daily temperature ranges can advance leaf senescence (Wang and Liu, 2023) which may advance the cessation of fruit production. This would also explain the negative correlation between late-born juvenile survival and temperature range in autumn, as juveniles would enter hibernation with less stored energy. Early-born juvenile hibernation survival correlates positively with warmer autumn temperatures possibly as this can advance fruit ripening (Gallinat et al., 2015). The difference between early- and late-born juveniles here may be because early juveniles are already independent in autumn and able to take advantage of early ripening fruit, whilst late-born juveniles become independent later in the season so are more sensitive to the ending of fruiting and beginning of winter. Heavy precipitation in the active season reduces dormouse activity (Bright et al., 1996a) and so reduces the amount of time available for foraging. Meanwhile, precipitation during hibernation can increase energy loss if fur becomes damp (Scopes et al., 2024), suggesting that during wet years adults could emerge from hibernation in poorer condition, reducing the recruitment of early-born juveniles.

Given the contributions to population growth, the effects of early winter precipitation on early-born juvenile recruitment and temperature range of late-born juvenile hibernation survival are likely to have the biggest impacts on population growth in Britain. Future work could model these relationships explicitly within the IPM, allowing the contribution of the climate variables to growth to be measured explicitly (Knape et al., 2023). Climate change is expected to increase both mean precipitation and the frequency of extreme rainfalls in winter in Britain (Watts et al., 2015), which may further reduce early-born juvenile recruitment going forward. It is more difficult to predict changes in temperature range, however asymmetry in the expected changes in winter daily maximum and minimum suggest temperature ranges may decrease in the cooler part of the year (Murphy et al., 2009), which could benefit the survival of late-born juveniles over winter. It is therefore uncertain how dormice in Britain may respond to climate change, though future work could elucidate this further by using this model and estimated changes in climate variables to forecast population size and extinction risk.

In conclusion, we reveal differences in dormouse population ecology between Lithuania and the edge of their range in Britain. We provide monthly estimates of survival probabilities, which were not previously available for either site, and allow comparison between hibernation and active seasons, as well as early- and late-born juveniles for the first time for a British population. In doing so, we reveal different demographic targets for conservation actions to increase population growth and add to our understanding of dormouse climate sensitivity in Britain, including possible effects of climate change. The results of this model could inform population management as part of adaptive management strategies to test conservation actions as they occur in the field, particularly woodland management at different times of the year.

Chapter 7: Discussion

Chapter 7: Discussion

Overview

Conserving locally rare but globally common species has a number of benefits including preventing the species from becoming threatened and creating ’umbrella’ species for conserving important habitats (Hunter and Hutchinson, 1994). Conservation science can be effectively informed by the study of species’ population ecology, which can identify extinction risk, targets for future conservation actions, and evaluate existing management practices (Norris, 2004). Such inferences from population ecology are only available for species with detailed observational, or even experimental, studies (Gotelli and Ellison, 2006), or with long-term and spatially extensive monitoring data. Such monitoring programmes often rely on citizen scientists to generate these large datasets, which are more possible for local charismatic species which engender strong public support.

In the UK many species are declining due to anthropogenic threats such as intensive agricultural land use, over-exploitation and climate change (Burns et al., 2023). I focus on the hazel dormouse, a charismatic small mammal with an extensive dedicated volunteer monitoring programme which has provided evidence for Red Listing as Vulnerable in Britain (Mathews et al., 2020). Understanding the population ecology, life history and wider habitat requirements of this species is vital for guiding future conservation efforts. This is especially important for a species like dormice which despite high levels of conservation awareness and protective legislation, is still in decline.

In this thesis, I investigate in detail how hazel dormice are declining in the UK and identify the possible causes and future conversation options. I focus on investigating multiple aspects of dormouse ecology and habitat use using demographic models, observational surveys and literature review. I start the thesis by exploring how hibernation biology impacts mammals as a whole, and how this can both help and hinder conservation actions (**Chapter 2**). I then surveyed hedges and scrub (which has rarely been studied as dormouse habitat) in Southwest England to investigate habitat associations with dormouse detection, revealing extensive use of these habitats and highlighting future targets for conservation action to increase landscape connectivity (**Chapter 3**). I updated our understanding of dormouse decline in the UK, providing evidence for Endangered status whilst considering how conservation priorities are created more broadly (**Chapter 4**). Using Bayesian occupancy models, I then investigated how occupancy and abundance of dormouse nest boxes has changed over time, and how habitat and climate variables may drive local extinction rates. Here, I reveal the influence of preferential sampling biases on the UK dormouse monitoring programme and its implications for our understanding of dormouse ecology derived from this data (**Chapter 5**). Finally, I used individually marked dormouse data from Britain and Lithuania to create a monthly-structured integrated population model. This highlights the key demographic contributions to population growth rate which can be targeted by future conservation actions, and how these are themselves influenced by climate (**Chapter 6**).

In this chapter, I review my work in relation to dormouse conservation in the UK and within the wider context of citizen science and population ecology.

Implications for other taxa

In **Chapter 2** I explore the how hibernation can protect species from some current threats, such as invasive predators and some diseases, whilst introducing new threats from disturbance during this period. Importantly, hibernators show distinct outcomes to the multiple threats associated with climate change (Wells et al., 2022), which makes it difficult to generalise to species that have not been well-studied, particularly those in the tropics. Conservation actions can also successfully accommodate hibernation biology, though there is a clear need for further research, as many actions elicit unexpected and sometimes detrimental results. By synthesising this literature, my thesis highlights the importance of considering hibernation within conservation practice and identifies threats to examine when first considering why a hibernator might be declining. The synthesis of conservation actions relating to hibernation biology provides a foundation of effective actions to apply to other species, and highlights ineffective actions to be avoided or cautiously applied and evaluated.

In **Chapter 4** I use hazel dormice as an example of a chronically declining species, and discuss how this is accommodated by the IUCN Red List and other conservation legislation. The Red List functions as intended, in that it solely evaluates extinction risk and appropriately assesses chronically declining species with large population sizes as low risk. The issues arise when this threat assessment is used in conservation prioritisation, as this would require waiting for the species to contract to a small population size before acting, which will likely make population recovery more difficult to achieve. My findings therefore support the existing literature (Possingham et al., 2002; Collen et al., 2016) that the Red List is not suitable for conservation prioritisation despite its persistent use in this area (Miller et al., 2007).

Finally, the integrated population model presented in **Chapter 6** is a novel model in which demographic parameters are estimated on a monthly (rather than annual) basis during the active season. Some existing models have decomposed years into seasonal cycles (Rushing et al., 2017), however my model is able to produce additional resolution which might be more applicable to conservation management timescales. This model can be used, as shown in **Chapter 6**, to investigate how monthly changes in demographic parameters can contribute to yearly population growth, identifying key times when reductions in parameters, for example from habitat management, or increases from conservation actions could be particularly influential. For example, my results suggest that practitioners might avoid woodland management that disturbs recruitment of juveniles between May and October. Within an adaptive management framework, this model could evaluate both the short-term monthly and the longer-term annual impacts of specific conservation actions or disruptions. The benefits of this model could be applied to other taxa, with similar monitoring data, by using the same model structure.

Citizen science and the NDMP

Citizen science is vital for monitoring programmes which contribute extensive data to conservation science (McKinley et al., 2017). Volunteer programmes are adept at collecting data on species distribution and abundance, which are vital for population models, and more detailed behavioural traits such as phenology (Chandler et al., 2017). However, the majority of citizen science projects globally focus on birds (Chandler et al., 2017). The National Dormouse Monitoring Programme (NDMP) defies this taxonomic trend by providing large-scale abundance and biometric monitoring of a small mammal. The NDMP provides far greater temporal and taxonomic coverage than is available for many other GB mammal species, especially rodents (Coomber et al., 2021), whilst large-scale citizen science programmes inspired by the NDMP have been launched to provide information on other dormouse species (Büchner et al., 2022).

In **Chapter 4** I used the extensive NDMP data to update the current trend in dormouse abundance in Great Britain and provide evidence for increased threatened status; an analysis which would not have been possible without volunteer generated data. Furthermore, I was able to use active NDMP sites as a positive control when selecting sites for hedge and scrub surveys in **Chapter 3**. Surveying close to known dormouse populations increased the robustness of the inferences from this chapter. This demonstrates the importance of the NDMP for selecting sites for more detailed research into dormouse ecology. An NDMP site also provided the basis for the collection of British individual-level data used in **Chapter 6**, demonstrating the high resolution data which volunteers are able to collect through the NDMP system. Through using NDMP data, my thesis highlights the importance of citizen science programmes for studying multiple aspects of species' ecology. Both large and fine scale studies benefit from having the NDMP as a resource, which is lacking for many British mammals.

The NDMP data also provided the nest box occupancy and population abundance information used in **Chapter 5**, facilitating detailed investigation into the habitat and climate drivers of local extinction and recolonization, and an estimation of the prebreeding adult population size in Britain. Although previous work has investigated possible biases in the NDMP and validated the data (Goodwin et al., 2017), I found considerable preferential sampling biases in this chapter (**Chapter 5**). I was able to control for these biases through my modelling approach, highlighting the importance of advanced modelling techniques for producing robust analysis from imperfect citizen science data. However, controlling for this bias altered the allocation of variation in the model, preventing it from identifying drivers of extinction that had already been detected. This demonstrates the continued concerns about the NDMP and its robustness, reflected in many conversations about citizen science data as a whole (Bayraktarov et al., 2019; McClure and Rolek, 2023). In **Chapter 5** I highlight some of the ways the NDMP could be improved by encouraging volunteers to continue to survey sites after dormice have disappeared. This would reduce preferential sampling biases, as site extinction would no longer by so closely correlated to the cessation of sampling, and would provide the opportunity to detect more colonisation events, which were often omitted in the data. Ideally, some NDMP sites would be established in areas where dormice are not known to occur, perhaps in marginal habitat, and so detect colonisation events, rather than relying of colonisation after local extinction. These positive changes could help create a more robust monitoring programme for British dormice, and could be applied to other schemes.

Dormouse population trends in Great Britain

Conservationists have been aware of dormouse population decline in Britain throughout the 19^{th} and 20^{th} centuries (Bright and Morris, 1996). More recent estimates of the trend (Goodwin et al., 2017) suggest extensive losses even since the beginning of monitoring in the 1990s. Despite recent work on dormouse population change (Goodwin et al., 2017), it is important to continue to monitor and update the trend as I did in **Chapter 4**. As I found in this chapter, population declines can worsen and provide evidence for up-listing at future Red List assessments. Continuing declines also have implications for conservation planning, indicating that current conservation measures are insufficient and new, more proactive actions may need to be implemented. There is also a pervasive misconception that Red Lists are conservation prioritisation schemes though they in fact only assess extinction risk (Collen et al., 2016). This means that increasing the threatened status of a species can mean automatic legislative protection and increases in available funding (Farrier et al., 2007), which could be of benefit to dormouse conservation. Beyond Red Listing, which as I discuss in **Chapter 4** can have extensive issues for chronically declining species, my analysis reveals the extent of the population increases which will be required to return dormice to 'Favourable Conservation Status' (FCS), an aspect of UK legislation. My findings indicate dormouse population recovery would require doubling the population in the next 10 years, and again the following 10 years, which would require significantly expanding conservation activities.

I also explore further aspects of the dormouse decline in **Chapter 5** by considering the decline in nest box occupancy and pre-breeding adult population size. This chapter gives a more complete understanding of population changes through the use of different methods and population focuses. I highlight some of the issues with the NDMP due to the use of volunteers, as explained above, which has implications for our confidence in population trends derived from this data. I also have competing decline trends in **Chapter 4** and **Chapter 5** for the same period of time because of the different methods used. Although there may still be biases in the NDMP data I could not account for, it is the most extensive, and frequently the only, data available for dormice in Britain (Coomber et al., 2021). It is therefore the only way we can understand population declines, as long as the data is modelled appropriately as I have demonstrated. With regards to the different trends I have produced, one of the most important applications will be future Red List assessment, where the central estimate will be measured against precise thresholds. Here, the International Union for Conservation of Nature (IUCN) provides guidelines to implement the precautionary principle and use the evidence of the greatest population decline for assessment (IUCN Standards and Petitions Committee 2019, Section 3.2). This would be the larger decline presented in **Chapter 4** with evidence that dormice could be considered Endangered in the next Red List assessment.

Dormice and environmental change

With a comprehensive understanding of the decline in British dormice, my thesis can also shed some light on the possible drivers of these changes and emerging threats from climate change. My findings both support the existing understanding of dormouse habitat and climate requirements, whilst also providing some new insights.

Habitat loss

Traditionally, hazel dormice have been considered specialist of early-successional woodland (Fedyń et al., 2021). Focusing on this habitat, research has suggested dormice require a considerable area, at least 20ha, to survive (Bright et al., 1994) which has become a benchmark in forestry guidelines providing there are hedges or woodland within 500m (Forestry Commission, 2019). Below this threshold, forestry practice does not require practitioners to act as though dormice, a protected species, are present (Forestry Commission, 2019) which could put individuals and potentially populations at risk. However, my work in **Chapter 5** substantiates more recent discoveries of dormice thriving in smaller patches of woodland (Büchner, 2008). As the smallest amount of woodland within 1km of a site was 12ha and produced a high probability of persistence (**Chapter 5**), it suggests that a wider range of small isolated woodlands could support dormice. This contributes important knowledge to our understanding of dormouse habitat requirements for conservation planning, and for altering forestry and development guidelines to ensure dormice are appropriately protected. As I focus on the area of woodland within 1km of the NDMP site, I combine the effects of patch size and connectivity. My findings, therefore, support the established island biogeography theory of the importance of both of these factors (MacArthur and Wilson, 2001). My work also supports dormouse-focused studies that have highlighted role connectivity via woodland plays in increasing dormouse abundance (Goodwin et al., 2018b) and patch colonisation (Iannarilli et al., 2017).

I have also explored dormouse habitat use beyond the traditional focus on woodland. There is growing evidence that dormice extensively use hedges and scrub for both connecting (Phillips et al., 2022) and residential habitat (Ehlers, 2012; Schulz and Büchner, 2018). Some studies have investigated the habitat associations of dormice in hedges, indicating the importance of structural complexity, width and species diversity (Ehlers, 2012; Dondina et al., 2016). However, these surveys have relied on natural nests and nest tubes to ascertain presence, and there has been little research into the habitat associations in scrub habitat (Phillips et al., 2022). I extend our understanding of dormouse hedge and scrub use in **Chapter 3** by surveying these habitats with footprint tunnels. This technique is faster (Mills et al., 2016; Bullion et al., 2018) and more effective for detecting dormice (Melcore et al., 2020), generating greater information from which to draw inferences and possibly emphasising habitat features used in dispersing or foraging rather than just nesting. My findings in **Chapter 3** show dormice extensively use these understudied habitats, substantiating their importance for dormice.

Dormice habitat requirements include woodland (**Chapter 5**), hedges and scrub (**Chapter 3**), which indicates a possible cause for their ongoing decline. In the UK, woodland area decreased until the beginning of the 20th century when legislation started to encourage afforestation to meet timber demand (Raum, 2020). On the surface, the resulting increases in woodland cover could be positive for dormouse populations. However, this forestry practice frequently results in homogeneous mono-specific and even-aged conifer stands (Raum, 2020), which are less suitable for dormice (Bright and Morris, 1996). The ongoing decline may therefore result from a legacy of forestry practice reducing the availability of suitable woodland in the landscape, contributing to local extinction rates (**Chapter 5**). Dormice can thrive in conifer plantations converted to broadleaf woodland (Trout et al., 2012), however there too few of these sites in the NDMP to be able to shed light on potential differing habitats requirements of individuals in these recovering woodlands.

There has also been a shift in forest management practices away from traditional methods such as coppicing towards high forest management or neglect, creating woodland less vertical structure and heterogeneity (Kirby et al., 2017). This has been implicated in the dormouse decline (Bright and Morris, 1996) but I was unable to test whether under-storey structure impacted dormouse occupancy as I focused on data available through remote sensing. The combined loss of woodland area and reduction in woodland management greatly reduces the availability of suitable woodland in the wider landscape.

Furthermore, there has been reduction in the number of hedgerows in Britain, with a 50% loss of farmland hedges since 1945 (Robinson and Sutherland, 2002). It is unclear how the amount of scrub has changed in Britain, however the increased intensification of agricultural land use (Robinson and Sutherland, 2002) suggests it has likely decreased. This has greatly reduced the amount of connecting and residential habitat available to dormice. Hibernation may also reduce the amount of time available for dispersal (**Chapter 2**) further limiting the capacity for dormice move through the landscape. Local extinctions are therefore more likely to be permanent as dormice cannot reach woodlands to recolonise. Overall, a reduction in the quantity and quality of habitat available in the British landscape is likely a key contributor to dormouse decline.

Climate change

There have been limited studies of hazel dormouse hibernation as it relates to ecology and conservation, with previous studies primarily focusing on hibernation mechanisms (Juškaitis, 2014) or hibernation locations (Gubert et al., 2021, 2023). I therefore conducted a literature review to investigate what could be learned from the previous work across hibernating taxa that might be applied to dormice (**Chapter 2**). In relation to climate change, this review reveals climate change could have significant impacts on hibernator conservation, through changes in phenology and demographic rates. However, this chapter also highlights the difficulty in generalising climate responses across species, especially for temperature changes where responses can be dependent on the location and age, as well as species. I therefore cannot suggest how dormice may respond to climate change based on this chapter, but show it important to consider responses at multiple scales and for multiple ages of individuals, which I am able to do in later chapters.

Previous work has indicated that dormice are sensitive to climate (Bright and Morris, 1996), preferring consistent cold winters and warm dry summers (Goodwin et al., 2018b). My thesis adds considerable detail to this understanding. In **Chapter 6**

I show strong correlations between multiple British demographic rates and climate variables, where the direction of correlations sometimes change seasonally, and different stage classes respond to different aspects of climate. All of these correlations could have implications for dormouse population growth under climate change, however in this chapter I discuss the two which have the greatest contribution to population growth; early-born juvenile recruitment, which is negatively correlated with early winter precipitation, and late-born juvenile hibernation survival, which is negatively correlated with autumn temperature range. The expected climate changes in Britain (Watts et al., 2015) will create declining conditions for early-juvenile recruitment as adults emerge from hibernation with less energy following increasingly wet winters. I also show that greater late winter temperature range increases the local extinction rate for dormice at NDMP sites (**Chapter 5**). More variable temperatures decrease the efficiency of hibernation and increase energy use (**Chapter 2**), which may mean more individuals either starve during hibernation or emerge in very poor condition. Late winter temperature range was not a correlate for any British demographic parameters in **Chapter 6**, so does not indicate that a particular parameter, such a hibernation survival, is key in local extinction. Late winter temperature range could decrease multiple demographic parameters by small amounts which were not detected in combination.

Temperature variation has negative impacts on both late-born juvenile hibernation and site persistence probability. However, the effects of climate change on temperature variation are difficult to predict. Short-term (i.e. daily) temperature ranges may decrease, whilst longer-term (i.e. seasonal or annual) ranges may increase (Guo et al., 2021), and these trends will have different impacts on dormouse ecology. There is asymmetry in the expected minimum and maximum temperature increases for the UK in winter (Murphy et al., 2009), which would reduce temperature ranges and could lower site extinction probability and increase hibernation survival. This contradicts the expected reduction in early-born juvenile recruitment from increased precipitation. As early-born juvenile recruitment has the biggest contribution to population growth (**Chapter 6**), the effects of reducing this parameter might not be compensated for by increases in the others. Similar to my findings in **Chapter 2**, it is difficult to predict how dormice will respond to temperature and precipitation changes from climate change, due to uncertainty in weather predictions and opposing effects in different parts of the population.

I found climate effects for British demographic rates but not Lithuanian ones (**Chapter 6**). This may be because Britain is on the north-western edge of the dormouse range in Europe (Juškaitis, 2014), as such individuals may be more sensitive to the climate to which they are less well adapted. Small changes in climate variables at the range margins can elicit large and non-linear effects at the population level (Westerbom et al., 2019). This might contribute to the ‘centre–periphery hypothesis’ in which genetic variation and demographic performance is reduced at range peripheries compared to the centre (Pironon et al., 2017). My findings support this hypothesis for dormice, as I show average growth rate is lower in Britain than that in Lithuania. It is possible that climate change will make Britain more suitable for dormice, as I would expect the northern edge of the species range to increase latitude (Estrada et al., 2018).

However, I found that hibernation as a life history strategy does not appear to aid individuals in filling their suitable ranges, and may impede range filling by reducing the time available for dispersal (**Chapter 2**). Dormice are thought to have low dispersal capacity, only travelling a few hundred metres (Bright and Morris, 1996) though some longer dispersal events have been recorded (Juškaitis, 2014). This may limit their capacity to track climate changed induced alterations to their suitable range. This highlights the importance of connecting habitat such as hedges (**Chapter 3**), though as discussed there has been a significant loss of hedges in Britain (Robinson and Sutherland, 2002) which could limit range shifting. Targeting environmental factors influencing colonisation probability could be useful for promoting range shifting, however I was unable to identify any habitat or climate variables associated with colonisation in **Chapter 5**. This may partly be because there are few observed colonisation events in the NDMP data, which could reflect the limited ability of dormice to move through current landscapes, but is also confounded by preferential sampling where absent sites are not surveyed and may miss colonisation events.

Conservation implications and future directions

My results in **Chapter 4** have implications for the definition of ’Favourable Conservation Status’ (FCS) for Britain. The definition requires a reversal of the population decline and a return to the population size in 1993 (Morris, 2021), which given the estimates in this chapter means returning the population to around 3.5 million. This would entail at least doubling the current population in the next 10 years, then doubling the population again in the subsequent 10 years. In this chapter, I also emphasise that the focus should be on FCS for dormice, as focusing on the IUCN Red List for conservation priorities would mean waiting for this chronically decline species to dwindle further. However, **Chapter 4** also provides sufficient evidence to for hazel dormice to be listed as Endangered at the next Red List assessment for British mammals. The extent of population recovery required in FCS and the up-listing on the Red List should both encourage further conservation actions for dormice beyond the current practice.

Currently, broad-scale conservation actions for dormice focus on population monitoring, through the NDMP, and reintroduction. I have demonstrated the value of the NDMP data in this thesis, however, it is important not to monitor species to extinction without implementing conservation strategies (Lindenmayer et al., 2013). The British reintroduction project started in 1993 and has reintroduced dormice to 24 sites in the north of England, aiming to restore distribution to counties where they were once found (Cartledge et al., 2021). Sites tend to be initially successful in establishing a population, but only around half have maintained this population beyond 10 years (Cartledge et al., 2021). Reintroducing dormice along their leading range edge could be a useful strategy for promoting range shifting under climate change (**Chapter 2**). However, reintroduction sites can be quite isolated, and the focus on establishing sites at a county scale means there does not appear to be a long term plan for an interconnected population. Beyond these broad-scale actions, local conservation strategies by landowners might focus on habitat management and creation to bolster their populations. My findings indicate these and other actions could be beneficial to dormouse recovery if implemented on a broader scale.

Planting trees to expand existing woodlands, or creating new woodland patches in close proximity to others, may decrease the local extinction probability at NDMP sites (**Chapter 5**) and therefore other dormouse sites as well. This has been consistently highlighted as a conservation strategy (Bright and Morris, 1996), however the implementation of the recent Environment Act (2021), which allows the creation of 'Species Conservation Strategies', could help move the focus of conservation actions to the landscape scale. Restoring large areas of woodland could be difficult, especially in landscapes with heavy agricultural usage as this could mean taking prime land out of production. My findings that hedges and scrub are readily used by dormice (**Chapter 3**) indicates that increasing the abundance of these habitats could be a viable method for increasing landscape connectivity and carrying capacity while using significantly smaller areas. Scrub in particular could be created by allowing marginal land to succeed naturally (Phillips et al., 2022). My findings also indicate some planting strategies which could increase dormouse presence in these habitats (**Chapter 3**). Hedges could be planted with abundant hazel (*Corylus avellana*) and honeysuckle (*Lonicera periclymenum*), without hedge banks, and prioritising creating numerous interconnections where possible. Meanwhile, scrub creation could focus on reducing bracken (*Pteridium aquilinum*) dominance in favour of flowering and fruiting shrubs. Given the possibility of natural succession as a conservation action, bracken control could be implemented, though it would have to be carefully timed to avoid disturbing individuals. Alternatively, planting woody species into the area might be sufficient to shift away from bracken dominance. There are multiple methods for increasing dormouse habitat at a landscape scale, which allows strategies to be tailored to the precise area involved.

In **Chapter 6** I found that recruitment had the largest contribution to population growth rate in both Britain and Lithuania, suggesting conservation actions which targeted this rate would be the most efficient for increasing growth. Recruitment might be increased by creating habitats with ample food sources, such as hazel and willow (*Salix spp.*) which are associated with more breeding events (Goodwin et al., 2018b). Greater fruiting and flowering of understorey plants can be encouraged by creating more light within woodlands (Kirby et al., 2017), which can also create the complex understorey structure preferred by dormice. This highlights the importance of woodland management, and dormice have often been associated with traditional techniques such as coppicing (Bright and Morris, 1996; Goodwin et al., 2018b).

Improving hibernation conditions may also increase recruitment, especially of early-born juveniles, by allowing adults to emerge from hibernation in good condition with sufficient resources for breeding. Hibernation survival could be improved by applying some of the techniques used for other hibernating species (**Chapter 2**). Hazel dormice hibernate on the ground in an unprotected nests (Gubert et al., 2021), specifically avoiding the nest boxes used in the active season (Juškaitis, 2014). It is therefore unlikely that practitioners could create artificial hibernacula or alter the microclimate of existing hibernacula to make hibernation more efficient, and besides, these had mixed results for other species. Similarly supplementary feeding shortly before or during hibernation, especially in years with poor autumn fruiting, should increase hibernation survival but had some mixed results on other species (**Chapter 2**).

Disturbing individuals during hibernation can rapidly exhaust their stored resources, causing them to starve or emerge from hibernation in poor condition (**Chapter 2**). Dormice hibernate in woven nests on the ground (Gubert et al., 2021) making them especially vulnerable to disturbance, or even destruction, through trampling or management activities. Tree thinning has been shown to damage the most artificial dormouse hibernation nests out of the management activities tested (Trout et al., 2012), but the effects of human or animal trampling have not been studied. Protecting species from disturbance through physical and legislative restrictions on human activities has been mostly successful, especially for bats roosting in caves (**Chapter 2**), but has yet to be tested for less clustered hibernators. For dormice, protections would have to reduce activity in woodlands during winter, confining humans to paths as much as possible and stopping conservation grazing by domestic cows, a significant portion of which occurs in the winter (Armstrong et al., 2003). Further, large herds of deer could also disturb or trample hibernating dormice, especially given the overabundance of deer in Britain currently (Spake et al., 2020). Restricted access rules or even fences could prevent disturbance and increase hibernation survival for dormice, but have yet to be tested.

Although woodland management is thought to be beneficial for dormice (Bright and Morris, 1996; Goodwin et al., 2018b), the timing of such practices can be difficult, as practitioners must avoid disturbing dormice in their nests to comply with their legal protection (Conservation of Habitats and Species Regulations 2017, Wildlife and Countryside Act 1981, as amended). This can restrict conservation woodland management, and broader forestry activities, to between the breeding and hibernation seasons (Forestry Commission, 2019). Limited windows for management can make it difficult for practitioners to complete vital tasks, which would likely benefit dormouse populations in the long run. The seasonal contributions of survival to population growth rate (**Chapter 6**) suggests that disturbance early in the season (April to June) would have minimal impacts on population growth. However, recruitment has the largest contribution, and the production of early-born juveniles could be effected by disturbance in this period. My findings also suggest that woodland management might be timed differently in Lithuania, due to differences in contributions to growth. Here, management might take place in the late season (August to October) to avoid reducing early-born juvenile survival or hibernation survival which have the largest contributions. Resolving optimal timings for woodland management requires a clearer understanding of how forestry practices at different times of year affects individuals. Some work suggests felling reduces dormouse dispersal (Goodwin et al., 2018a), however there is no information on survival or reproduction. Disturbing a few individuals to create better habitat for the population may be a worthwhile conservation action, but would require strong evidence to oppose current species protection legislation.

Future work could also investigate the impacts of woodland management actions on demographic rates by implementing my integrated population model (**Chapter 6**) within an adaptive management framework. More broadly, the effects of management could also be modelled within an occupancy model framework to explore its impacts on local colonisation and extinction (**Chapter 5**). I was not able to do so in this chapter as there is a current lack of broad-scale management data for Britain and I did not use surveys of landowners, as used in previous work (Goodwin et al., 2018b), to collect fine-scale information. As well as the effects of woodland management, I would also be interested for future work to consider the effects of deer abundances on dormice, as they may disturb hibernating individuals and can severely damage trees through browsing and bark damage (Spake et al., 2020), reducing understorey structure and resources availability.

Concluding remarks

Conservation science requires an understanding of species' population trends, responses to environmental change and habitat requirements to be effective. It is important to continue to develop knowledge of species ecology, identifying emerging threats and evaluating current conservation measures, even for species which have been considerably studied. The continued decline of hazel dormice in Britain is concerning given its extensive monitoring programme, existing legal protections, and high public awareness of this charismatic species. In this thesis, I reviewed the literature to understand how hibernation as a life history strategy intersects with conservation threat and practice, and use the Discussion to explore how this applies to British dormice. I have also updated our understanding of the dormice decline and provided evidence for future Red List assessments. I used field observations to explore how dormice use understudied habitats, whilst increasing our knowledge of how traditional woodland habitats affect dormouse occupancy using Bayesian model approaches. This later model also explores climate influences, which I investigated in more detail by using an integrated population model to estimate vital rates and explore their contributions to population growth. My findings provide recommendations for future conservation actions to restore dormouse populations, whilst indicating possible emerging threats from climate change. Continuing dormouse declines are indicative of deteriorating quality of woodland and other structurally complex habitats. Conservation efforts can therefore leverage the appeal of this charismatic species to conserve additional biodiversity.

Appendices

Appendix 1: Methodological details of literature search (Chapter 2)

To conduct the literature search, we used Google Scholar as the search engine. We used a variety of search terms to investigate the how hibernation and conservation might be linked. Given the breadth of subjects that falls under conservation threats and actions, a large number of search terms were used, often in conjunction with hibernation, to explore the subject. Some examples of search terms are given below. We also used references from within articles found via the literature search to explore further.

We were very broad in our inclusion of literature, and only rejected papers that focused solely on other aspects of heterothermy other than hibernation. To limit the number of references included in the article, we included references that included unique case studies, or could be used at more than one point in the text.

Example search terms:

- Hibernation conservation
- Hibernation ‘climate change’
- Hibernation disease
- Mammal forestry timing
- Hibernation range filling
- ‘White nose syndrome’ management
- Dormice hibernation predation
- Tropical hibernation

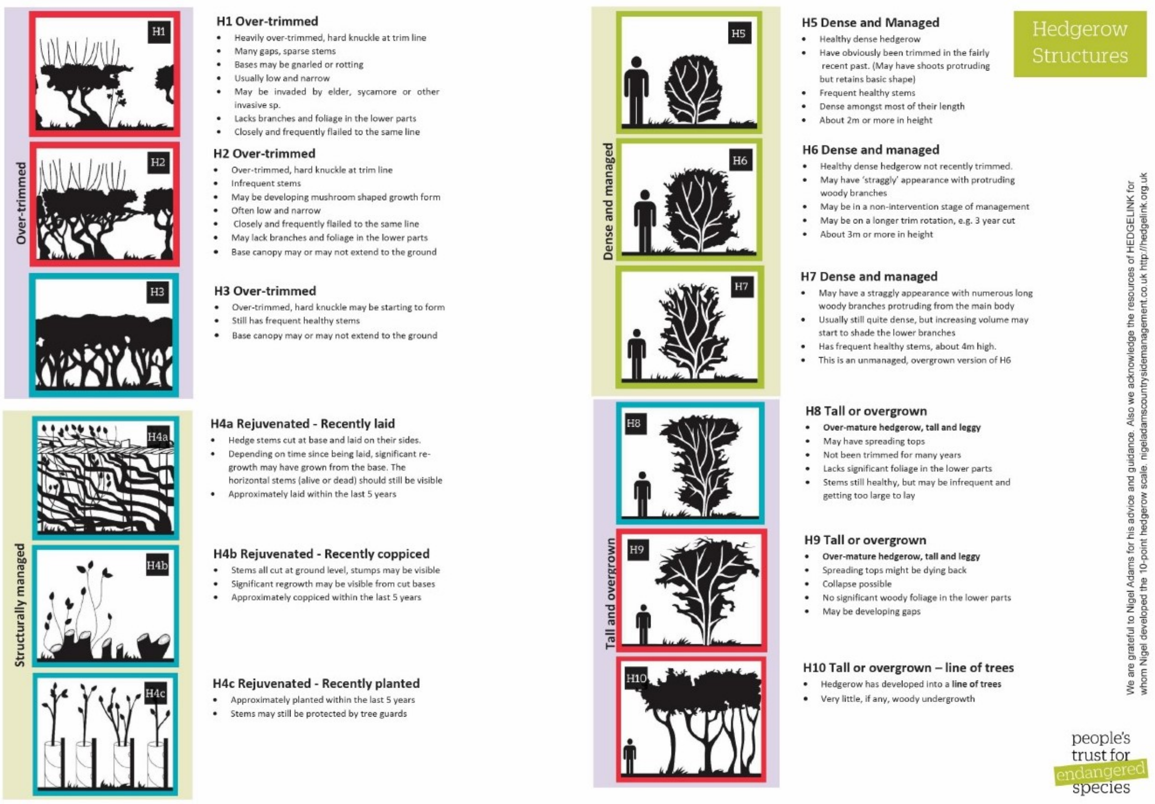
Appendix 2: List of habitat data collected (Chapter 3)

A list of habitat data collected in the field that was used in the analysis. Some further data was collected but did not offer sufficient variation (e.g. no hedges had evidence that gaps had been replanted) for analysis.

Data collected in the field for hedges

- **Number of access gates/openings greater than 2m wide**
- **Estimate of the percentage of the hedge that is vegetative gaps**
- **Number of vegetative gaps that are wider than 5m**
- **Average height of the woody component of the hedge** (<5m, 5-10m, 10-15m, >15m)
- **Average width (m) at the widest point of the woody component of the hedge**
- **The most applicable cross-section illustration and description (Figure S 2.1)** grouped to ”Laid” (H4a), ”Over-trimmed” (H1, H2, H3), ”Well-managed” (H5, H6, H7), and ”Overgrown” (H8, H9, H10)
- **Whether the hedge shows evidence of a hard ‘knuckle’** where it has been frequently trimmed to the same point
- **Number of emergent trees**
- **The presence/absence of a bank or wall** along at least half the hedge length. A hedge bank is a ridge of earth which the hedge sits on
- **The height of the bank, if applicable**
- **Estimation of abundance of certain plant species based on the DAFOR scale** Dominant >75%, Abundant 51–75%, Frequent 26–50%, Occasional 11–25%, Rare 1–10%, plus Absent. This was converted to ordinal continuous data, e.g.

Absent =0, Dominant =5. Species selected reflect previous research on plant species associated with dormice abundance population trend (Goodwin et al., 2018b): Hazel (*Corylus avellana*), willow spp. (*Salix* spp.), sycamore (*Acer pseudoplatanus*), honeysuckle (*Lonicera periclymenum*) and bramble (*Rubus fruticosus*)



H1 Over-trimmed

- Heavily over-trimmed, hard knuckle at trim line
- Many gaps, sparse stems
- Bases may be gnarled or rotting
- Usually low and narrow
- May be invaded by elder, sycamore or other invasive sp.
- Lacks branches and foliage in the lower parts
- Closely and frequently flailed to the same line

H2 Over-trimmed

- Over-trimmed, hard knuckle at trim line
- Infrequent stems
- May be developing mushroom shaped growth form
- Often low and narrow
- Closely and frequently flailed to the same line
- May lack branches and foliage in the lower parts
- Base canopy may or may not extend to the ground

H3 Over-trimmed

- Over-trimmed, hard knuckle may be starting to form
- Still has frequent healthy stems
- Base canopy may or may not extend to the ground

H4a Rejuvenated - Recently laid

- Hedge stems cut at base and laid on their sides.
- Depending on time since being laid, significant re-growth may have grown from the base. The horizontal stems (alive or dead) should still be visible
- Approximately laid within the last 5 years

H4b Rejuvenated - Recently coppiced

- Stems all cut at ground level, stumps may be visible
- Significant regrowth may be visible from cut bases
- Approximately coppiced within the last 5 years

H4c Rejuvenated - Recently planted

- Approximately planted within the last 5 years
- Stems may still be protected by tree guards

H5 Dense and Managed

- Healthy dense hedgerow
- Have obviously been trimmed in the fairly recent past. (May have shoots protruding but retains basic shape)
- Frequent healthy stems
- Dense amongst most of their length
- About 2m or more in height

H6 Dense and managed

- Healthy dense hedgerow not recently trimmed.
- May have 'straggly' appearance with protruding woody branches
- May be in a non-intervention stage of management
- May be on a longer trim rotation, e.g. 3 year cut
- About 3m or more in height

H7 Dense and managed

- May have a straggly appearance with numerous long woody branches protruding from the main body
- Usually still quite dense, but increasing volume may start to shade the lower branches
- Has frequent healthy stems, about 4m high.
- This is an unmanaged, overgrown version of H6

H8 Tall or overgrown

- **Over-mature hedgerow, tall and leggy**
- May have spreading tops
- Not been trimmed for many years
- Lacks significant foliage in the lower parts
- Stems still healthy, but may be infrequent and getting too large to lay

H9 Tall or overgrown

- **Over-mature hedgerow, tall and leggy**
- Spreading tops might be dying back
- Collapse possible
- No significant woody foliage in the lower parts
- May be developing gaps

H10 Tall or overgrown – line of trees

- Hedgerow has developed into a **line of trees**
- Very little, if any, woody undergrowth

We are grateful to Nigel Adams for his advice and guidance. Also we acknowledge the resources of HEDGELINK for whom Nigel developed the 10-point hedgerow scale. nigeladamscountrysidemanagement.co.uk http://hedgelink.org.uk

Figure S2.1. *Hedgerow cross-section illustration and description used to assign hedge structure categories (PTES, 2019b)*

Data collected in the field for scrub patches

- **Number of paths wider than 1m**
- **Average height of the shrub portion of the scrub** (1m, 1.5m, 2 m, 2.5m, 3m)
- **The ground coverage of scrub** on the scale Dominant (>75%), Medium (25-75%) and Encroaching (<25%)
- **Any evidence of management on the edges of the scrub** (Y/N)
- **Any evidence of management in the interior of the scrub** (Y/N)
- **Number of emergent trees**
- **Are there connections between mid-storey shrubs/trees or are individual shrubs/trees isolated**
- **The percentage of adjacent land use around the scrub which is in the following categories** Arable, Water, Road/Route, Pasture/Grass and Woodland
- **Dominant vegetative species in the ground cover layer (<0.5m)**
- **Dominant vegetative species in the mid-storey layer (0.5-2m)**
- **Dominant vegetative species in the upper storey layer (>2m)**
- **Estimation of abundance of certain plant species based on the DAFOR scale** Dominant >75%, Abundant 51–75%, Frequent 26–50%, Occasional 11–25%, Rare 1–10%, plus Absent. Species selected reflect previous research on plant species associated with dormice abundance population trend (Goodwin et al., 2018b). Hazel (*Corylus avellana*), willow spp. (*Salix* spp.), birch spp. (*Betula* spp.), honeysuckle (*Lonicera periclymenum*) and bramble (*Rubus fruticosus*)

Appendix 3: Tunnel-level model selection (Chapter 3)

Table S3.1. Model selection for variables to include in hedge and scrub tunnel-level models. *The table shows the parameters included in each model, the model degrees of freedom (DF) and Akaike information criterion (AIC). The models are arranged in order of lowest AIC values, and the AIC difference indicates the difference from the next lowest model. The asterisk indicates the model was selected for further analysis, based on AIC and variable significance.*

Habitat	Model parameters	DF	AIC	AIC difference
Hedge	patch + check day + tunnel height + gaps within 1m *	41	1072.04	0
	patch + check day + tunnel height	40	1077.99	5.95
	patch + check day	39	1088.61	10.62
	patch + check day + tunnel height + rank 1 dominant species	64	1093.1	4.49
Scrub	patch + check day + tunnel height + edge *	26	852.84	0
	patch + check day + tunnel height	23	855.58	2.74
	patch + check day + tunnel height + rank 1 dominant species	47	871.91	16.33
	patch + check day	22	889	17.09

Table S3.2. Model selection for the shape of the relationship between check day and detection, in hedge and scrub tunnel-level models, based on k-fold cross validation (k=10). *The table shows the polynomial degree of the relationship in each model, and the mean squared error (MSE) from the cross validation analysis. The models are arranged in order of lowest MSE. The asterisk indicates the model was selected for further analysis, based on the lowest MSE.*

Habitat	**Polynomial degree**	**MSE**
Hedge	2*	165.64
	3	166.56
	1	166.78
	4	174.52
	5	183.54
Scrub	1*	159.59
	2	165.6
	3	171.08
	5	172.63
	4	181.69

Appendix 4: Detection Frequencies (Chapter 3)

Table S4.1. Frequency of hazel dormouse detection for each plot in all hedges and scrub patches. *The table shows the detection probability and standard error derived from the final tunnel-level model for each habitat respectively.*

County	Site	Habitat	Hedge	Detection Probability	Standard Error
Cornwall	Darlington	Hedge	1	0	1
	Goss Moor	Scrub	1	0	1
			2	0	1
	Henwood	Scrub	1	0	1
			2	0	1
	Keveral	Scrub	1	0	1
	Kilkhampton	Hedge	1	0.123	0.244
			2	0.156	0.203
			3	0.217	0.356
			4	0	1
			5	0	1
		Scrub	1	0.081	0.171

	Red Moor	Hedge	1	0	1
			2	0	1
			3	0	1
			4	0	1
		Scrub	1	0.106	0.217
			2	0.275	0.434
Devon	Andrews wood	Hedge	1	0.8	0.105
			2	0.605	0.186
			3	0.438	0.176
			4	0.181	0.316
			5	0.482	0.186
		Scrub	1	0.794	0.181
			2	0.764	0.256
			3	0.952	0.063
	Barn Owl Trust	Hedge	1	0	1
	Bovey	Hedge	1	0.743	0.273
	Drogo	Hedge	1	0.129	0.245

		2	0.444	0.174
		3	0.388	0.244
		4	0.118	0.228
	Scrub	1	0.643	0.168
East Wray	Hedge	1	0	1
		2	0	1
		3	0.435	0.366
		4	0	1
	Scrub	1	0	1
Fingle	Hedge	1	0.372	0.238
		2	0.238	0.256
		3	0.655	0.143
		4	0.297	0.179
	Scrub	1	0.858	0.107
		2	0.937	0.045
Fingle Teign Weir	Scrub	1	0.475	0.399
Heddon	Hedge	1	0	1

		2	0	1
	Scrub	1	0	1
Hembury	Scrub	1	0	1
		2	0	1
Slapton	Hedge	1	0	1
		2	0	1
		3	0	1
		4	0.044	0.097
		5	0	1
		6	0.362	0.205
Southweek	Hedge	1	0.274	0.303
	Scrub	1	0.702	0.202
Stover	Scrub	1	0	1

Appendix 5: Detection model selection for occupancy analysis (Chapter 5)

Table S5.1. A comparison of possible year and site effects to model detection probability in the occupancy models. *Chi-squared values refer to posterior predictive goodness-of-fit tests between the observed data and data generated by the proposed model for the open (ecological) and closed (detection) parts of the model. The effects chosen are indicated with an asterisk based on the lowest DIC and closed chi-squared value closest to 0.5.*

Model	Open model Chi-sq	Closed model Chi-sq	DIC
Random year and annual varying random site *	0.65	0.56	28113
Random year and random site	0.47	0	28784
Random year only	0.56	0	30496

Table S5.2. A comparison of possible shapes for the relationship between detection probability and the number of boxes at a site and the week of the year the survey occurred respectively*. Chi-squared values refer to posterior predictive goodness-of-fit tests between the observed data and data generated by the proposed model for the open (ecological) and closed (detection) parts of the model. The shape chosen is indicated with an asterisk based on the lowest DIC and closed chi-squared value closest to 0.5.*

Variable	**Shape**	**Open model Chi-sq**	**Closed model Chi-sq**	**DIC**
Number of boxes	linear*	0.7	0.53	28075
Number of boxes	quadratic	0.68	0.53	28127
Number of boxes	cubic	0.71	0.55	28289
Week of the year	quartic polynomial*	0.62	0.52	25861
Week of the year	quintic polynomial	0.61	0.54	25877
Week of the year	sextic polynomial	0.62	0.53	25913
Week of the year	cubic	0.66	0.56	27232
Week of the year	quadratic	0.68	0.55	27433
Week of the year	linear	0.63	0.56	27864

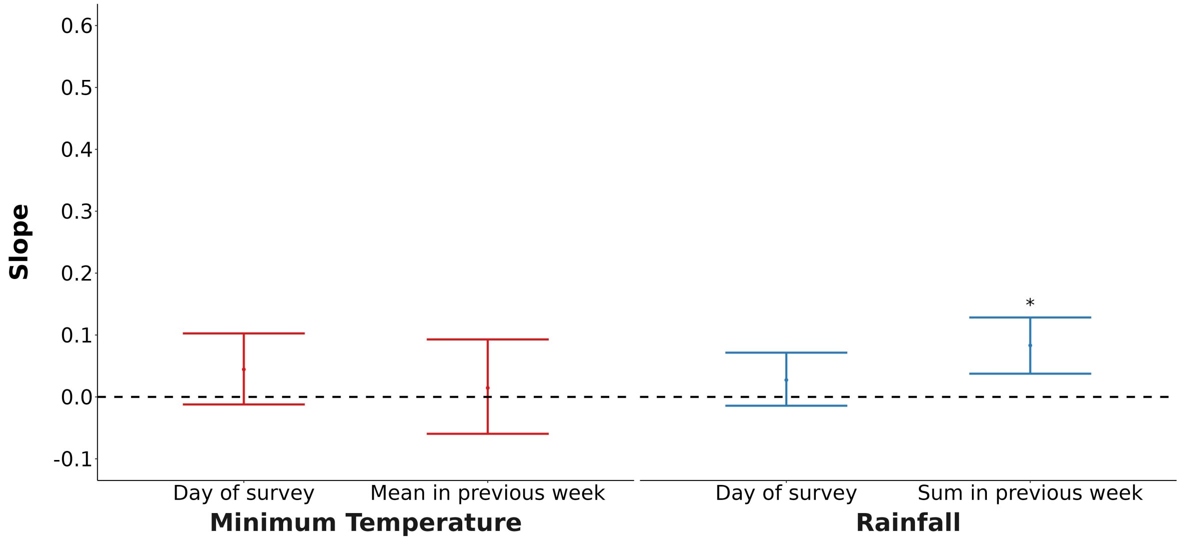


***Figure S5.1. The estimated linear effect slopes of each climate variable tested against probability of dormouse detection at a monthly survey**. Each variable was included in its own model. The points show the mean of the posterior distribution, and the error bars show the 95% confidence interval, with significance indicated by an asterisk if the error bar does not cross zero.*

Appendix 6: Single variable models for occupancy analysis (Chapter 5)

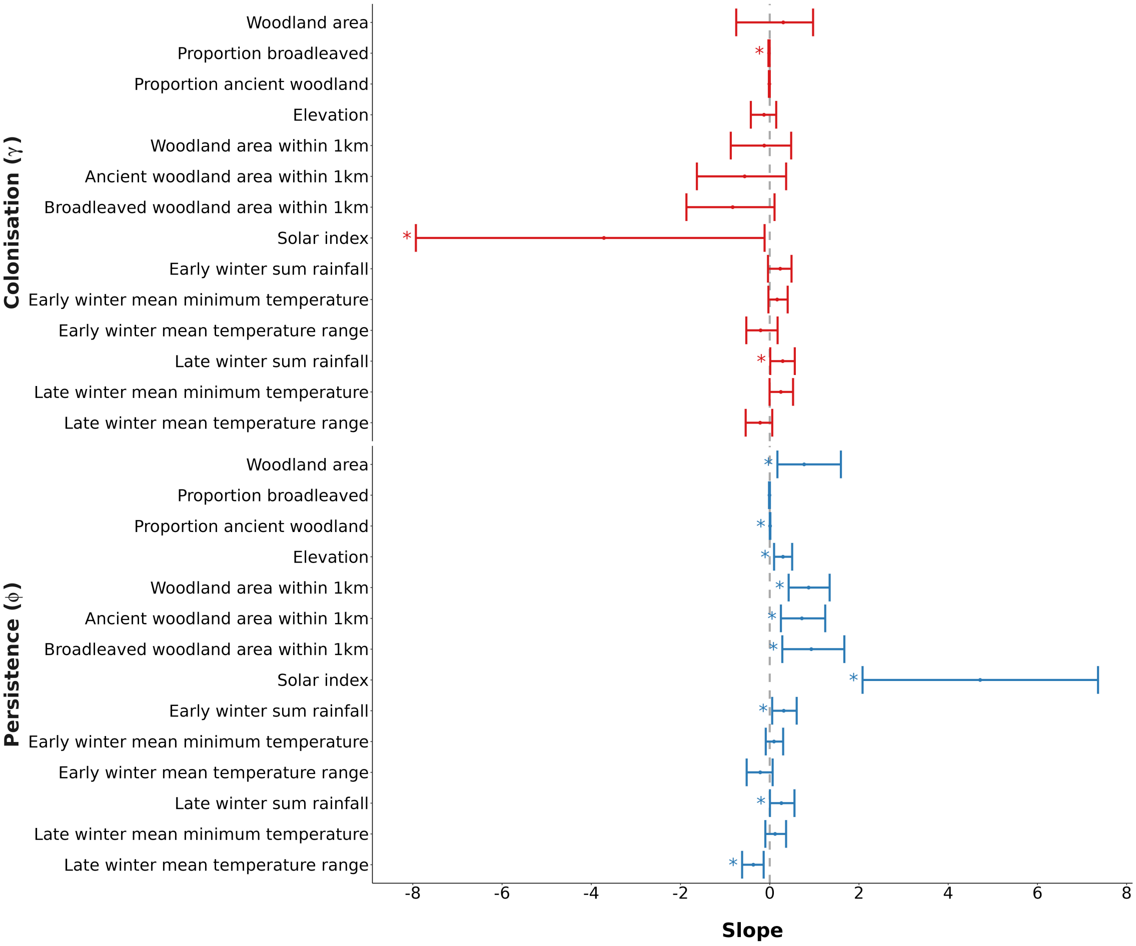


***Figure S6.1. The estimated linear effect slopes of each variable tested through the exploratory analysis of covariate drivers of local colonisation and persistence**. Each variable was included in its own model, though effecting both colonisation and persistence. The points show the mean of the posterior distribution, and the error bars show the 95% confidence interval, with significance indicated by an asterisk if the error bar does not cross zero.*

Appendix 7: Integrated population model equations

This appendix includes the population state-space equations and the Cormack-Jolly-Seber (CJS) model transition tables for the integrated population model. The two sites share the same state-space model, so this is only detailed for Lithuania. The CJS model differs between the two sites as the months of observation are different. Time effects were included by matching corresponding months and years in the between the site models. Details on demographic parameter notation can be found in Table 6.1 and below. Note t refers to year and m month.

Mathematical notation:

- $Nad_{t,m}$ Estimated population size, Adult
- $Nej_{t,m}$ Estimated population size, Early-born juvenile
- $Nlj_{t,m}$ Estimated population size, Late-born juvenile
- $\phi ad_{t,m}$ Active season survival, Adult
- $\phi ej_{t,m}$ Active season survival, Early-born juvenile
- $\phi lj_{t,m}$ Active season survival, Late-born juvenile
- θad_t Hibernation survival, Adult
- θej_t Hibernation survival, Early-born juvenile
- θlj_t Hibernation survival, Late-born juvenile
- γej_t Recruitment (all productivity and immigration), Early-born juveniles
- γlj_t Recruitment (all productivity and immigration), Late-born juveniles
- ρad_m Recapture, Adult
- ρej_m Recapture, Early-born juvenile
- ρlj_m Recapture, Late-born juvenile

Lithuania data model

***April**, month 1, transition from October previous year*

State-space model - population model:

$$Nad_{t,1} = \theta ad_t \times Nad_{t-1,7} + \theta ej_t \times Nej_{t-1,7} + \theta lj_t \times Nlj_{t-1,7} \tag{7.1}$$

$$Nej_{t,1} = 0 \tag{7.2}$$

$$Nlj_{t,1} = 0 \tag{7.3}$$

CJS model - transition table:

		State in April			
		Early juvenile	Late juvenile	Adult	Dead
State in October	Early Juvenile	0	0	θej_t	$1 - \theta ej_t$
	Late Juvenile	0	0	θlj_t	$1 - \theta lj_t$
	Adult	0	0	θad_t	$1 - \theta ad_t$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in April			
		Early juvenile	Late juvenile	Adult	Not seen
State in April	Early Juvenile	0	0	0	1
	Late Juvenile	0	0	0	1
	Adult	0	0	ρad_1	$1 - \rho ad_1$
	Dead	0	0	0	1

***May**, month 2, transition from April*

State-space model - population model:

$$Nad_{t,2} = \phi ad_{t,1} \times Nad_{t,1} \tag{7.4}$$

$$Nej_{t,2} = \gamma ej_{t} \times Nad_{t,1} \tag{7.5}$$

$$Nlj_{t,2} = 0 \tag{7.6}$$

CJS model - transition table:

		State in May			
		Early juvenile	Late juvenile	Adult	Dead
State in April	Early Juvenile	0	0	0	0
	Late Juvenile	0	0	0	0
	Adult	0	0	$\phi ad_{t,1}$	$1 - \phi ad_{t,1}$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in May			
		Early juvenile	Late juvenile	Adult	Not seen
State in May	Early Juvenile	ρej_1	0	0	$1 - \rho ej_1$
	Late Juvenile	0	0	0	1
	Adult	0	0	ρad_2	$1 - \rho ad_2$
	Dead	0	0	0	1

***June**, month 3, transition from May*

State-space model - population model:

$$Nad_{t,3} = \phi ad_{t,2} \times Nad_{t,2} \tag{7.7}$$

$$Nej_{t,3} = \gamma ej_t \times Nad_{t,2} + \phi ej_{t,1} \times Nej_{t,2} \tag{7.8}$$

$$Nlj_{t,3} = 0 \tag{7.9}$$

CJS model - transition table:

		State in June			
		Early juvenile	Late juvenile	Adult	Dead
State in May	Early Juvenile	$\phi ej_{t,1}$	0	0	$1 - \phi ej_{t,1}$
	Late Juvenile	0	0	0	0
	Adult	0	0	$\phi ad_{t,2}$	$1 - \phi ad_{t,2}$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in June			
		Early juvenile	Late juvenile	Adult	Not seen
State in June	Early Juvenile	ρej_2	0	0	$1 - \rho ej_2$
	Late Juvenile	0	0	0	1
	Adult	0	0	ρad_3	$1 - \rho ad_3$
	Dead	0	0	0	1

***July**, month 4, transition from June*

State-space model - population model:

$$Nad_{t,4} = \phi ad_{t,3} \times Nad_{t,3} \tag{7.10}$$

$$Nej_{t,4} = \gamma ej_t \times Nad_{t,3} + \phi ej_{t,2} \times Nej_{t,3} \tag{7.11}$$

$$Nlj_{t,4} = 0 \tag{7.12}$$

CJS model - transition table:

		State in July			
		Early juvenile	Late juvenile	Adult	Dead
State in June	Early Juvenile	$\phi ej_{t,2}$	0	0	$1 - \phi ej_{t,2}$
	Late Juvenile	0	0	0	0
	Adult	0	0	$\phi ad_{t,3}$	$1 - \phi ad_{t,3}$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in July			
		Early juvenile	Late juvenile	Adult	Not seen
State in June	Early Juvenile	ρej_3	0	0	$1 - \rho ej_3$
	Late Juvenile	0	0	0	1
	Adult	0	0	ρad_4	$1 - \rho ad_4$
	Dead	0	0	0	1

***August**, month 5, transition from July*

State-space model - population model:

$$Nad_{t,5} = \phi ad_{t,4} \times Nad_{t,4} \tag{7.13}$$

$$Nej_{t,5} = \phi ej_{t,3} \times Nej_{t,4} \tag{7.14}$$

$$Nlj_{t,5} = \gamma lj_t \times (Nad_{t,4} + Nej_{t,4}) \tag{7.15}$$

CJS model - transition table:

		State in August			
		Early juvenile	Late juvenile	Adult	Dead
State in July	Early Juvenile	$\phi ej_{t,3}$	0	0	$1 - \phi ej_{t,3}$
	Late Juvenile	0	0	0	0
	Adult	0	0	$\phi ad_{t,4}$	$1 - \phi ad_{t,4}$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in August			
		Early juvenile	Late juvenile	Adult	Not seen
State in August	Early Juvenile	ρej_4	0	0	$1 - \rho ej_4$
	Late Juvenile	0	ρlj_1	0	$1 - \rho lj_1$
	Adult	0	0	ρad_5	$1 - \rho ad_5$
	Dead	0	0	0	1

***September**, month 6, transition from August*

State-space model - population model:

$$Nad_{t,6} = \phi ad_{t,5} \times Nad_{t,5} \tag{7.16}$$

$$Nej_{t,6} = \phi ej_{t,4} \times Nej_{t,5} \tag{7.17}$$

$$Nlj_{t,6} = \gamma lj_t \times (Nad_{t,5} + Nej_{t,5}) + \phi lj_{t,1} \times Nlj_{t,5} \tag{7.18}$$

CJS model - transition table:

		State in September			
		Early juvenile	Late juvenile	Adult	Dead
State in August	Early Juvenile	$\phi ej_{t,4}$	0	0	$1 - \phi ej_{t,4}$
	Late Juvenile	0	$\phi lj_{t,1}$	0	$1 - \phi lj_{t,1}$
	Adult	0	0	$\phi ad_{t,5}$	$1 - \phi ad_{t,5}$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in September			
		Early juvenile	Late juvenile	Adult	Not seen
State in September	Early Juvenile	ρej_5	0	0	$1 - \rho ej_5$
	Late Juvenile	0	ρlj_2	0	$1 - \rho lj_2$
	Adult	0	0	ρad_6	$1 - \rho ad_6$
	Dead	0	0	0	1

***October**, month 7, transition from September*

State-space model - population model:

$$Nad_{t,7} = \phi ad_{t,6} \times Nad_{t,6} \tag{7.19}$$

$$Nej_{t,7} = \phi ej_{t,5} \times Nej_{t,6} \tag{7.20}$$

$$Nlj_{t,7} = \gamma lj_t \times (Nad_{t,6} + Nej_{t,6}) + \phi lj_{t,2} \times Nlj_{t,6} \tag{7.21}$$

CJS model - transition table:

		State in October			
		Early juvenile	Late juvenile	Adult	Dead
State in September	Early Juvenile	$\phi ej_{t,5}$	0	0	$1 - \phi ej_{t,5}$
	Late Juvenile	0	$\phi lj_{t,2}$	0	$1 - \phi lj_{t,2}$
	Adult	0	0	$\phi ad_{t,6}$	$1 - \phi ad_{t,6}$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in October			
		Early juvenile	Late juvenile	Adult	Not seen
State in October	Early Juvenile	ρej_6	0	0	$1 - \rho ej_6$
	Late Juvenile	0	ρlj_3	0	$1 - \rho lj_3$
	Adult	0	0	ρad_7	$1 - \rho ad_7$
	Dead	0	0	0	1

British data model

The state-space model is the same as that described above, so only the CJS model is detailed here.

***May**, transition from October previous year, and April this year*

CJS model - transition table:

		State in May			
		Early juvenile	Late juvenile	Adult	Dead
State in October	Early Juvenile	0	0	θej_t	$1 - \theta ej_t$
	Late Juvenile	0	0	θlj_t	$1 - \theta lj_t$
	Adult	0	0	$\theta ad_t + \phi ad_{t,1}$	$1 - (\theta ad_t + \phi ad_{t,1})$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in May			
		Early juvenile	Late juvenile	Adult	Not seen
State in May	Early Juvenile	ρej_1	0	0	$1 - \rho ej_1$
	Late Juvenile	0	0	0	1
	Adult	0	0	ρad_1	$1 - \rho ad_1$
	Dead	0	0	0	1

June, *transition from May*

CJS model - transition table:

		State in June			
		Early juvenile	Late juvenile	Adult	Dead
State in May	Early Juvenile	$\phi ej_{t,1}$	0	0	$1-\phi ej_{t,1}$
	Late Juvenile	0	0	0	0
	Adult	0	0	$\phi ad_{t,2}$	$1-\phi ad_{t,2}$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in June			
		Early juvenile	Late juvenile	Adult	Not seen
State in June	Early Juvenile	ρej_2	0	0	$1-\rho ej_2$
	Late Juvenile	0	0	0	1
	Adult	0	0	ρad_2	$1-\rho ad_2$
	Dead	0	0	0	1

***September**, transition from June/July/August*

CJS model - transition table:

		State in September			
		Early juvenile	Late juvenile	Adult	Dead
State in August	Early Juvenile	$(\phi ej_{t,2} \times \phi ej_{t,3} \times \phi ej_{t,4})$	0	0	$1 - (\phi ej_{t,2} \times \phi ej_{t,3} \times \phi ej_{t,4})$
	Late Juvenile	0	$\phi lj_{t,1}$	0	$1 - \phi lj_{t,1}$
	Adult	0	0	$(\phi ad_{t,3} \times \phi ad_{t,4} \times \phi ad_{t,5})$	$1 - (\phi ad_{t,3} \times \phi ad_{t,4} \times \phi ad_{t,5})$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in September			
		Early juvenile	Late juvenile	Adult	Not seen
State in September	Early Juvenile	ρej_3	0	0	$1 - \rho ej_3$
	Late Juvenile	0	ρlj_1	0	$1 - \rho lj_1$
	Adult	0	0	ρad_3	$1 - \rho ad_3$
	Dead	0	0	0	1

October, *transition from September*

CJS model - transition table:

		State in October			
		Early juvenile	Late juvenile	Adult	Dead
State in September	Early Juvenile	$\phi ej_{t,5}$	0	0	$1 - \phi ej_{t,5}$
	Late Juvenile	0	$\phi lj_{t,2}$	0	$1 - \phi lj_{t,2}$
	Adult	0	0	$\phi ad_{t,6}$	$1 - \phi ad_{t,6}$
	Dead	0	0	0	1

CJS model - observation table:

		Observation in October			
		Early juvenile	Late juvenile	Adult	Not seen
State in October	Early Juvenile	ρej_4	0	0	$1 - \rho ej_4$
	Late Juvenile	0	ρlj_2	0	$1 - \rho lj_2$
	Adult	0	0	ρad_4	$1 - \rho ad_4$
	Dead	0	0	0	1

Appendix 8: Integrated population model priors

- Initial population sizes for Lithuania:
  - Adults - **uniform prior 1-10**
  - Early-born Juveniles - **zero**
  - Late-born Juveniles - **zero**
- Initial population sizes for Britain:
  - Adults - **uniform prior 1-20**
  - Early-born Juveniles - **zero**
  - Late-born Juveniles - **zero**
- The global means for hibernation survival, active season survival, and recapture for all three age classes - **uniform prior 0-1**
- The global mean for recruitment - **uniform prior 0-3**
- The standard deviation of all time random effects (normal distribution around global mean) for all demographic parameters and age classes - **uniform prior 0-1**
- The standard deviation of all site random effects (normal distribution around global mean) for all demographic parameters and age classes - **uniform prior 0-1**

Appendix 9: Integrated population model goodness-of-fit

This appendix shows the goodness-of-fit (GOF) posterior predictive checks for each sub-model of the IPM. For the state-space models, GOF was calculated for each population (adults, early- and late-born juveniles) whilst a single check was completed for the capture-mark-recapture (CMR) model. For both sub-models measures, GOF is assessed by the proximity of the discrepancy value estimates from each iteration to the 1:1 line.

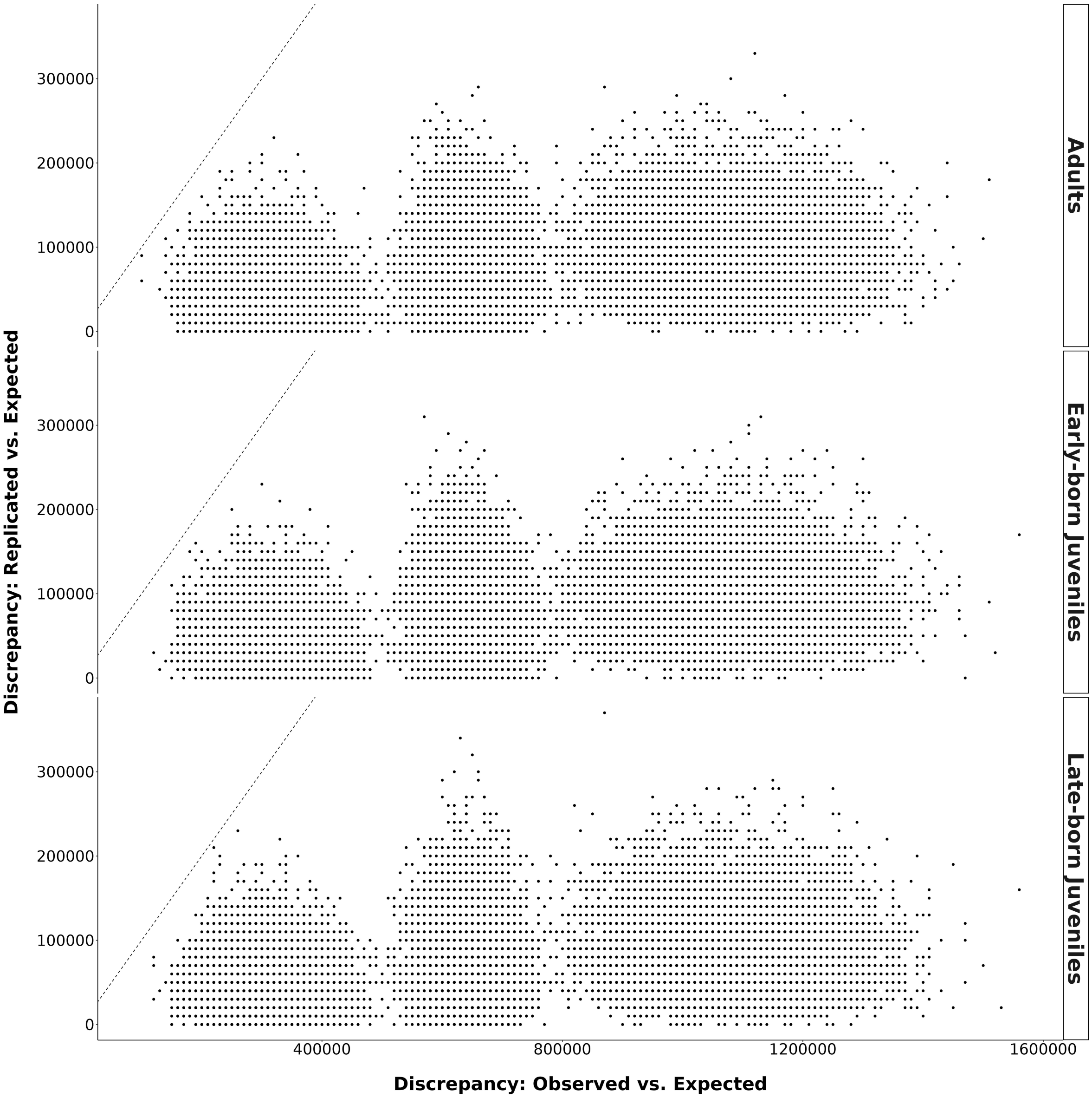


Figure S9.1. The posterior predictive check for the state-space model and Lithuanian data for each stage class: adults, early- and late-born juveniles. *The points show the discrepancy statistic for each iteration. The dashed line is a 1:1, with fit indicated by the point cloud sitting along this line.*

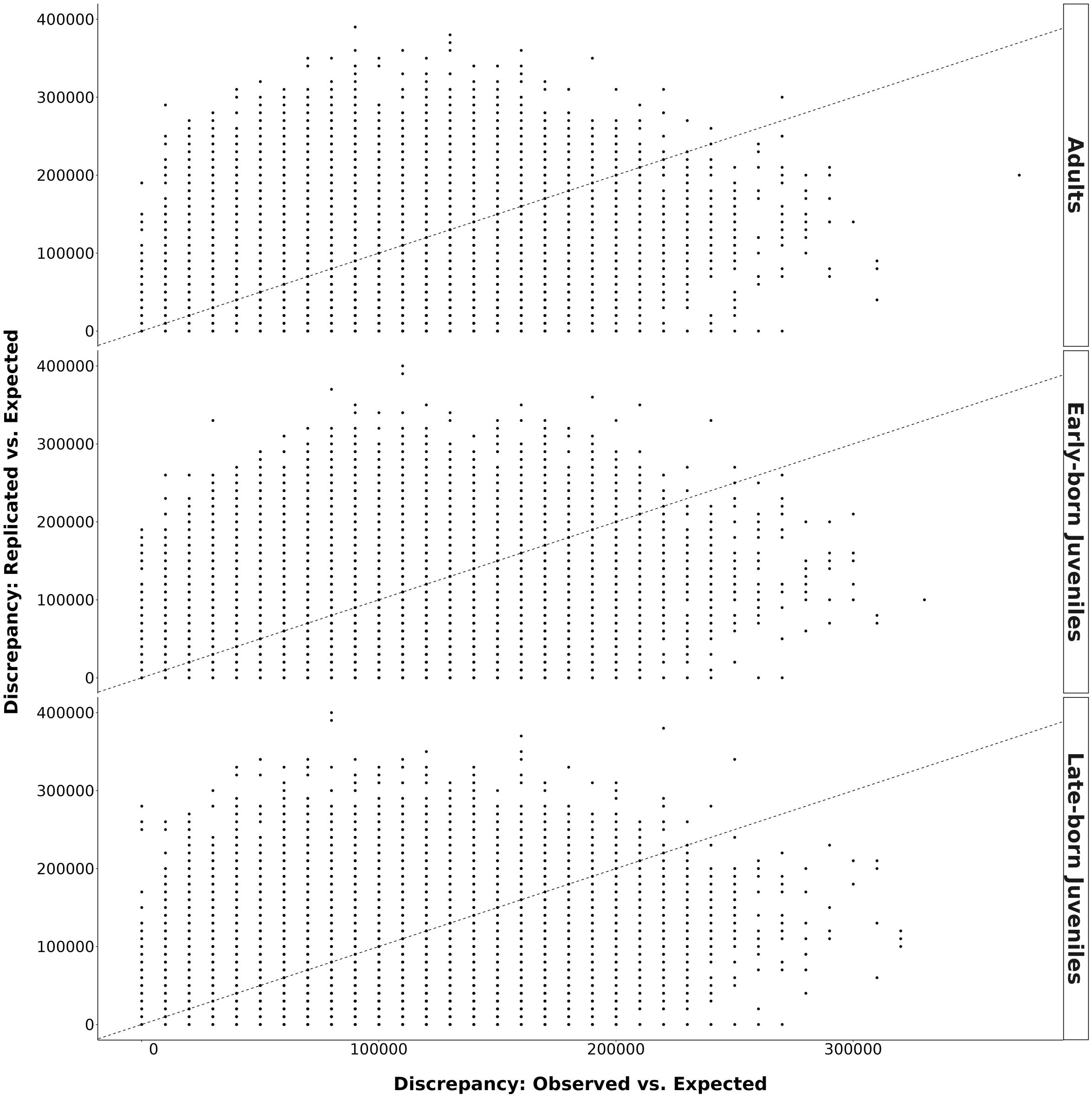


Figure S9.2. The posterior predictive check for the state-space model and British data for each stage class: adults, early- and late-born juveniles. *The points show the discrepancy statistic for each iteration. The dashed line is a 1:1, with fit indicated by the point cloud sitting along this line.*

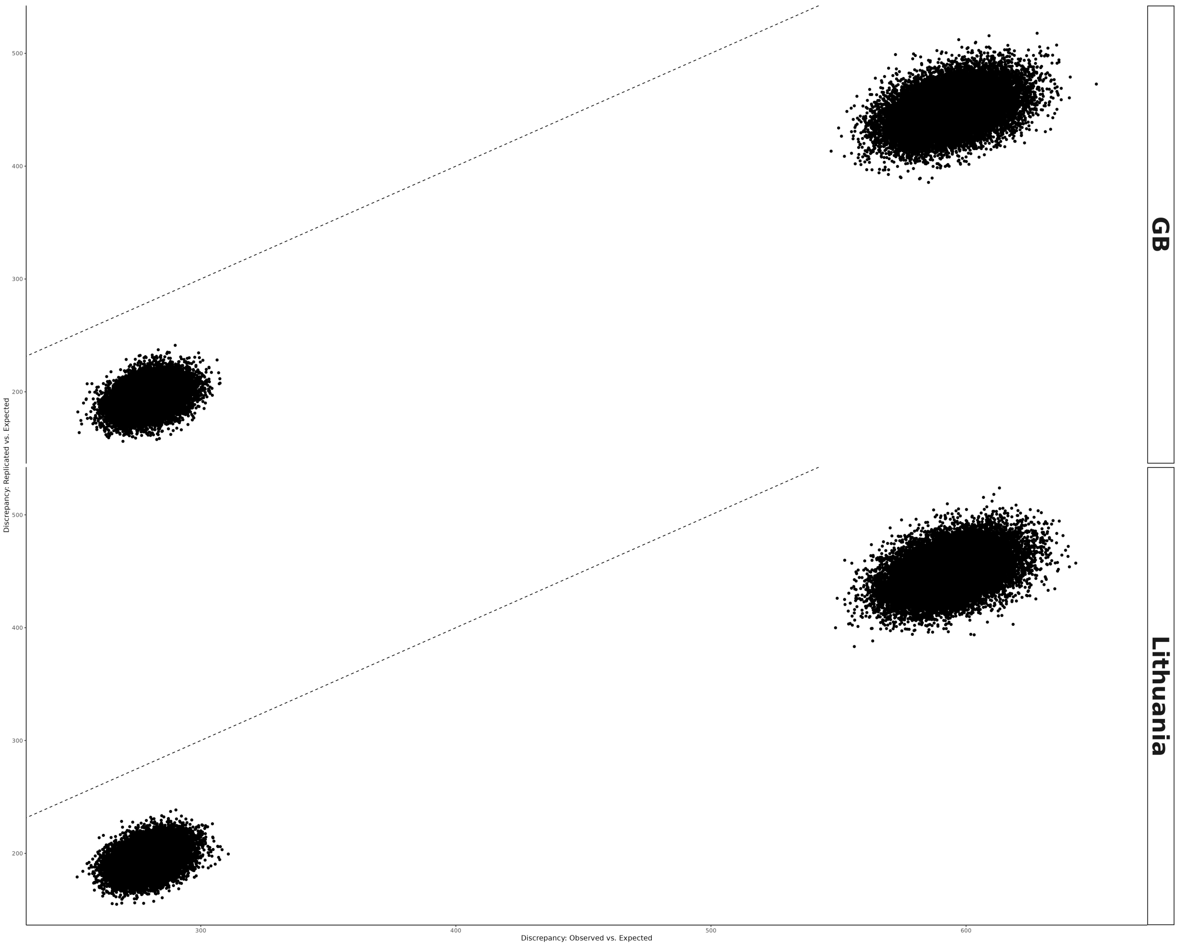


Figure S9.3. The posterior predictive check for the capture-mark-recapture model for each country. *The points show the discrepancy statistic for each iteration. The dashed line is a 1:1, with fit indicated by the point cloud sitting along this line.*

Appendix 10: Comparison of hibernation and active season survival on a monthly scale

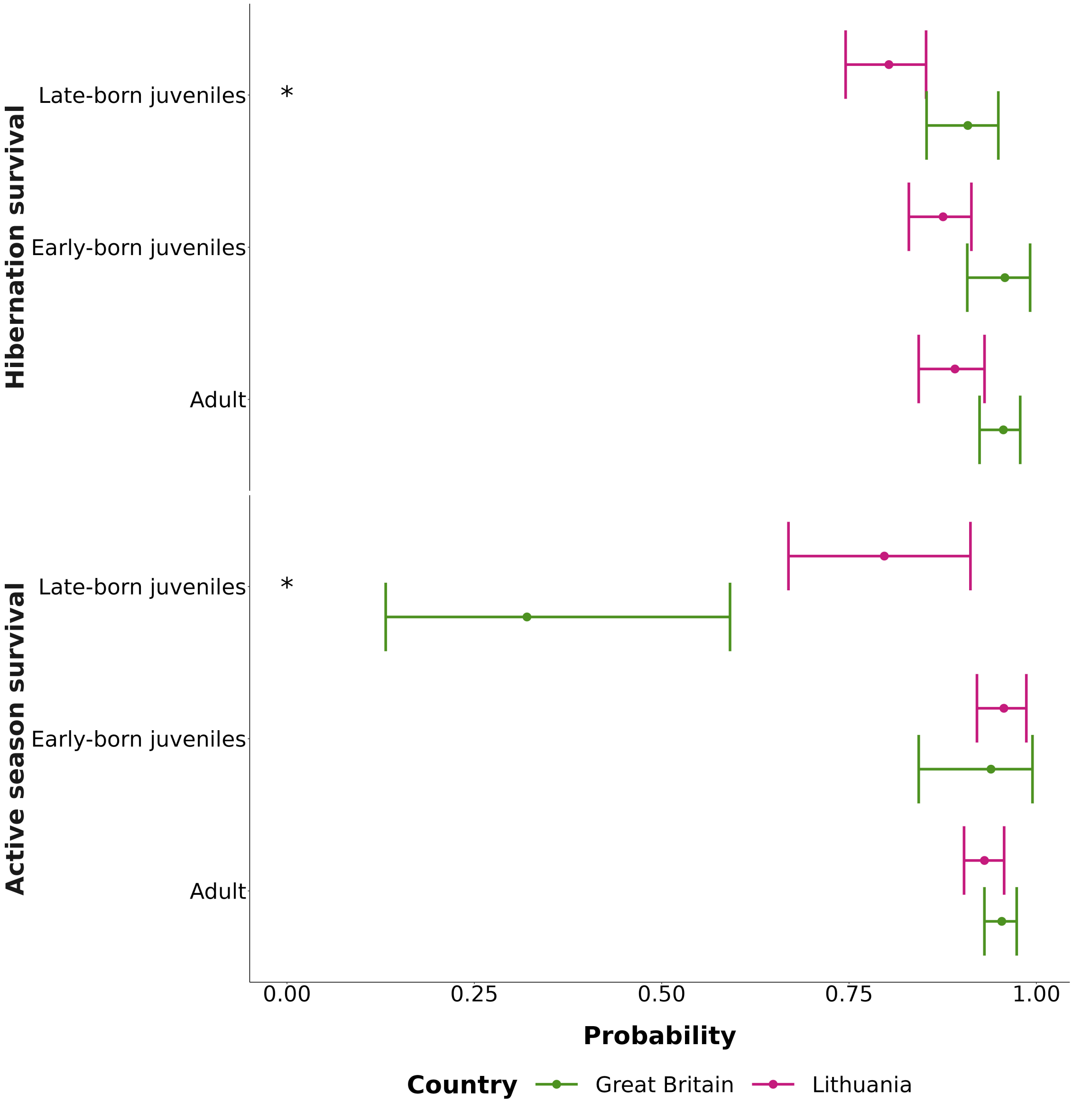


Figure S10.1. The mean hibernation and active season survival, on a monthly scale, for each stage class and both countries, Britain (green) and Lithuania (pink), around which there is temporal variation. *The mean (points) and 95% confidence interval (error bars) of the posterior distribution is shown. An asterisk indicates a significant difference between sites, when the confidence intervals do not overlap.*

Appendix 11: All tested correlations between climate variables and demographic parameters

Table S11.1. All tested correlations between demographic parameters and climate variables in the previous month or season. *The time period refers to the period over which the climate variables are calculated, and are previous to the respective demographic parameter. The table is arranged according to absolute correlation size. The line break indicates the correlation greater than 0.5 that are presented in the main text.*

Site	Parameter	Age class	Time period	Climate variable	Correlation
Britain	Active season survival	Adult	September	Temp. range	-0.62
Britain	Hibernation survival	Early-born juv.	Autumn	Mean min. temp.	0.58
Britain	Hibernation survival	Late-born juv.	Autumn	Mean temp. range	-0.57
Britain	Active season survival	Adult	June	Temp. range	0.55
Britain	Recruitment	Early-born juv.	Early winter	Total precipitation	-0.55
Britain	Hibernation survival	Early-born juv.	Autumn	Mean max. temp.	0.54
Britain	Active season survival	Early-born juv.	September	Precipitation	-0.53
Britain	Active season survival	Adult	August	Precipitation	-0.51

Lithuania	Recruitment	Early-born juv.	Early winter	Total precipitation	-0.48
Britain	Active season survival	Adult	September	Min. temp.	0.45
Britain	Active season survival	Adult	May	Precipitation	0.44
Britain	Active season survival	Early-born juv.	August	Precipitation	-0.44
Britain	Hibernation survival	Early-born juv.	Autumn	Total precipitation	-0.44
Lithuania	Active season survival	Adult	July	Max. temp.	0.43
Britain	Recruitment	Early-born juv.	Early winter	Mean max. temp.	-0.43
Britain	Active season survival	Adult	May	Min. temp.	0.42
Britain	Active season survival	Adult	August	Min. temp.	-0.42
Lithuania	Recruitment	Early-born juv.	Late winter	Mean max. temp.	-0.42
Britain	Active season survival	Early-born juv.	July	Min. temp.	-0.4
Lithuania	Active season survival	Late-born juv.	August	Min. temp.	0.39
Lithuania	Active season survival	Adult	July	Min. temp.	0.38

Lithuania	Recruitment	Early-born juv.	Early winter	Mean max. temp.	-0.38
Lithuania	Recruitment	Early-born juv.	Late winter	Mean min. temp.	-0.38
Lithuania	Recruitment	Early-born juv.	Early winter	Mean min. temp.	-0.37
Britain	Recruitment	Early-born juv.	Late winter	Mean temp. range	-0.37
Lithuania	Hibernation survival	Adult	Autumn	Mean max. temp.	-0.37
Lithuania	Active season survival	Early-born juv.	June	Precipitation	0.35
Britain	Active season survival	Early-born juv.	June	Max. temp.	-0.35
Britain	Hibernation survival	Adult	Autumn	Mean temp. range	-0.35
Lithuania	Active season survival	Late-born juv.	August	Max. temp.	0.34
Britain	Active season survival	Early-born juv.	May	Max. temp.	0.34
Britain	Active season survival	Early-born juv.	June	Precipitation	0.34

Britain	Active season survival	Late-born juv.	August	Precipitation	-0.34
Britain	Recruitment	Early-born juv.	Early winter	Mean min. temp.	-0.34
Lithuania	Active season survival	Early-born juv.	May	Min. temp.	-0.33
Britain	Active season survival	Adult	June	Max. temp.	0.33
Britain	Active season survival	Early-born juv.	May	Min. temp.	0.33
Lithuania	Recruitment	Late-born juv.	Spring	Total precipitation	0.32
Lithuania	Active season survival	Early-born juv.	July	Max. temp.	0.31
Britain	Active season survival	Adult	July	Precipitation	-0.31
Britain	Active season survival	Adult	August	Temp. range	0.31
Lithuania	Active season survival	Early-born juv.	September	Temp. range	-0.3
Lithuania	Active season survival	Adult	July	Temp. range	0.29
Lithuania	Recruitment	Early-born juv.	Late winter	Total precipitation	-0.29

Lithuania	Active season survival	Early-born juv.	July	Min. temp.	0.27
Britain	Active season survival	Adult	May	Temp. range	-0.27
Britain	Active season survival	Early-born juv.	June	Min. temp.	-0.27
Britain	Recruitment	Late-born juv.	Spring	Total precipitation	0.27
Lithuania	Hibernation survival	Adult	Autumn	Mean min. temp.	-0.27
Britain	Active season survival	Adult	June	Precipitation	-0.26
Lithuania	Recruitment	Late-born juv.	Spring	Mean min. temp.	0.26
Lithuania	Active season survival	Adult	May	Min. temp.	0.25
Britain	Active season survival	Late-born juv.	September	Temp. range	0.25
Britain	Recruitment	Late-born juv.	Spring	Mean max. temp.	-0.25
Britain	Hibernation survival	Early-born juv.	Autumn	Mean temp. range	-0.25
Britain	Active season survival	Adult	July	Min. temp.	0.24
Lithuania	Active season survival	Adult	April	Precipitation	-0.23
Lithuania	Active season survival	Adult	May	Precipitation	-0.23

Lithuania	Active season survival	Adult	May	Max. temp.	0.23
Britain	Active season survival	Early-born juv.	July	Max. temp.	-0.23
Britain	Active season survival	Early-born juv.	August	Max. temp.	-0.23
Britain	Recruitment	Late-born juv.	Spring	Mean min. temp.	-0.23
Lithuania	Hibernation survival	Adult	Autumn	Mean temp. range	-0.23
Lithuania	Active season survival	Early-born juv.	July	Temp. range	0.22
Lithuania	Active season survival	Late-born juv.	September	Min. temp.	0.22
Britain	Active season survival	Late-born juv.	August	Min. temp.	-0.22
Britain	Active season survival	Late-born juv.	September	Precipitation	-0.22
Lithuania	Hibernation survival	Late-born juv.	Autumn	Mean max. temp.	-0.22
Britain	Hibernation survival	Adult	Autumn	Mean min. temp.	0.22

Britain	Recruitment	Early-born juv.	Early winter	Mean temp. range	-0.21
Britain	Recruitment	Early-born juv.	Late winter	Mean max. temp.	-0.21
Britain	Hibernation survival	Adult	Autumn	Total precipitation	-0.21
Lithuania	Active season survival	Early-born juv.	August	Precipitation	0.2
Britain	Active season survival	Early-born juv.	May	Precipitation	-0.2
Lithuania	Recruitment	Early-born juv.	Early winter	Mean temp. range	0.2
Lithuania	Active season survival	Early-born juv.	May	Max. temp.	-0.19
Lithuania	Active season survival	Late-born juv.	September	Max. temp.	0.19
Britain	Active season survival	Adult	July	Max. temp.	0.19
Britain	Active season survival	Early-born juv.	June	Temp. range	-0.19
Britain	Active season survival	Early-born juv.	August	Temp. range	-0.19

Lithuania	Hibernation survival	Adult	Autumn	Total precipitation	0.19
Lithuania	Hibernation survival	Early-born juv.	Autumn	Mean min. temp.	-0.19
Lithuania	Hibernation survival	Late-born juv.	Autumn	Mean min. temp.	-0.19
Lithuania	Active season survival	Adult	August	Temp. range	0.18
Britain	Active season survival	Adult	April	Precipitation	0.18
Britain	Active season survival	Early-born juv.	July	Precipitation	0.18
Britain	Active season survival	Early-born juv.	September	Temp. range	-0.18
Britain	Active season survival	Late-born juv.	September	Max. temp.	0.18
Lithuania	Active season survival	Early-born juv.	September	Min. temp.	0.17
Britain	Active season survival	Adult	June	Min. temp.	-0.17
Britain	Active season survival	Early-born juv.	May	Temp. range	0.17
Britain	Hibernation survival	Late-born juv.	Autumn	Mean min. temp.	0.17

Lithuania	Active season survival	Early-born juv.	June	Temp. range	-0.16
Britain	Active season survival	Late-born juv.	August	Temp. range	0.16
Britain	Active season survival	Adult	September	Precipitation	-0.15
Lithuania	Recruitment	Late-born juv.	Spring	Mean max. temp.	0.15
Lithuania	Hibernation survival	Early-born juv.	Autumn	Mean max. temp.	-0.15
Lithuania	Active season survival	Adult	April	Min. temp.	-0.14
Lithuania	Active season survival	Early-born juv.	July	Precipitation	0.14
Britain	Active season survival	Early-born juv.	September	Max. temp.	-0.14
Lithuania	Active season survival	Adult	June	Min. temp.	-0.13
Lithuania	Active season survival	Adult	August	Max. temp.	0.13
Britain	Active season survival	Adult	August	Max. temp.	-0.13
Britain	Recruitment	Early-born juv.	Late winter	Total precipitation	-0.13
Britain	Hibernation survival	Adult	Autumn	Mean max. temp.	0.13

Lithuania	Active season survival	Late-born juv.	August	Temp. range	0.12
Britain	Recruitment	Late-born juv.	Spring	Mean temp. range	-0.12
Lithuania	Active season survival	Adult	August	Precipitation	-0.11
Lithuania	Active season survival	Early-born juv.	September	Precipitation	0.11
Britain	Active season survival	Adult	July	Temp. range	0.11
Lithuania	Active season survival	Adult	May	Temp. range	0.1
Lithuania	Active season survival	Adult	June	Max. temp.	-0.1
Lithuania	Active season survival	Adult	September	Precipitation	0.1
Lithuania	Active season survival	Adult	September	Max. temp.	0.1
Lithuania	Active season survival	Early-born juv.	June	Max. temp.	-0.1
Lithuania	Active season survival	Early-born juv.	September	Max. temp.	-0.1
Britain	Active season survival	Adult	April	Min. temp.	0.1
Lithuania	Hibernation survival	Early-born juv.	Autumn	Total precipitation	0.1
Britain	Hibernation survival	Late-born juv.	Autumn	Total precipitation	0.1

Lithuania	Active season survival	Adult	September	Temp. range	0.09
Lithuania	Active season survival	Early-born juv.	May	Temp. range	0.08
Britain	Active season survival	Adult	April	Temp. range	-0.08
Britain	Active season survival	Late-born juv.	August	Max. temp.	-0.08
Lithuania	Hibernation survival	Late-born juv.	Autumn	Mean temp. range	-0.08
Lithuania	Active season survival	Adult	April	Max. temp.	-0.07
Lithuania	Active season survival	Adult	June	Precipitation	0.07
Lithuania	Active season survival	Adult	July	Precipitation	-0.07
Lithuania	Active season survival	Early-born juv.	May	Precipitation	-0.07
Lithuania	Active season survival	Early-born juv.	August	Min. temp.	0.06
Britain	Active season survival	Adult	May	Max. temp.	0.06
Britain	Active season survival	Adult	September	Max. temp.	0.06
Britain	Active season survival	Early-born juv.	July	Temp. range	-0.06
Britain	Recruitment	Early-born juv.	Late winter	Mean min. temp.	-0.06

Lithuania Active season survival	Late-born juv.	September	Precipitation	0.05
Lithuania Active season survival	Adult	August	Min. temp.	-0.04
Lithuania Active season survival	Adult	September	Min. temp.	0.04
Lithuania Active season survival	Early-born juv.	June	Min. temp.	-0.04
Lithuania Active season survival	Late-born juv.	August	Precipitation	0.04
Lithuania Active season survival	Late-born juv.	September	Temp. range	0.04
Lithuania Recruitment	Late-born juv.	Spring	Mean temp. range	-0.04
Lithuania Active season survival	Adult	April	Temp. range	0.03
Lithuania Active season survival	Early-born juv.	August	Temp. range	-0.03
Lithuania Recruitment	Early-born juv.	Late winter	Mean temp. range	0.03
Lithuania Hibernation survival	Early-born juv.	Autumn	Mean temp. range	0.03

Lithuania	Hibernation survival	Late-born juv.	Autumn	Total precipitation	-0.03
Britain	Active season survival	Adult	April	Max. temp.	0.02
Britain	Active season survival	Early-born juv.	August	Min. temp.	-0.02
Lithuania	Active season survival	Adult	June	Temp. range	-0.01
Lithuania	Active season survival	Early-born juv.	August	Max. temp.	0.01
Britain	Active season survival	Late-born juv.	September	Min. temp.	-0.01
Britain	Hibernation survival	Late-born juv.	Autumn	Mean max. temp.	0.01
Britain	Active season survival	Early-born juv.	September	Min. temp.	0

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