

Hibernation nest site selection but not overwinter activity is associated with microclimatic conditions in a hibernating mammal

Rachel Findlay-Robinson^{a,1,*}, Davina L. Hill^{b,c}

^a Institute of Science and Environment, University of Cumbria, Ambleside, Cumbria, LA22 9BB, UK

^b School of Biodiversity, One Health and Veterinary Medicine, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow, G12 8QQ, UK

^c School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, Private Bag 3, Wits 2050, South Africa

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ABSTRACT

Fine-scale variation in microclimates between habitats may impact energy consumption for the organisms that inhabit them. This may be particularly important for sedentary species or those unable to change habitats for long periods, such as hibernators. Low ambient temperatures were traditionally thought key to microclimatic selection for hibernation locations, but recent research suggests that other factors may contribute or exceed ambient temperature in importance. We aimed to characterise microclimates at hibernacula of wild hibernating hazel dormice *Muscardinus avellanarius*, and test how these microclimates differ to those at locations without hibernacula using a microclimatic modelling approach. Dormice hibernated in areas with warmer soil temperatures and lower variability in humidity and relative shortwave radiation. These results add to the growing body of evidence that low ambient temperatures may not be the primary driver of hibernation microclimate selection, although temperature is still likely to play an important role. We also found that ambient temperatures measured at the microclimatic level were substantially buffered compared to point samples taken at the nearest weather station (~1.6 km away), highlighting the importance of considering microclimates in wildlife conservation in the face of future environmental change.

1. Introduction

Owing to the crucial influence of energy availability on a range of behaviours and life-history traits, understanding relationships between energy expenditure and environmental variables such as temperature is vital to predict species' responses to climate change (Anderson and Jetz, 2005; Kronfeld-Schor and Dayan, 2013). For example, high ambient temperatures may cause individuals to spend less time foraging, therefore reducing energy intake as they seek to avoid heat stress and evaporative water loss (Levy et al., 2016). High ambient temperatures can negatively affect milk energy output in small rodents, with consequences for offspring energy gain and growth (Zhao et al., 2020), with consequences for offspring energy gain and growth (Zhao et al., 2020). Reductions of water availability in the environment due to high ambient temperatures may force organisms to catabolize fat for hydration (Rutkowska et al., 2016). Temperatures at either extreme may force endothermic organisms to use energetic reserves to maintain their core body temperature at euthermic levels (Anderson and Jetz, 2005), and may

also coincide with periods of low food availability, restricting access to energetic resources.

Hibernation and torpor are widely used thermoregulatory strategies among mammals for decreasing energy expenditure during sub-optimal environmental conditions (Geiser and Ruf, 1995). Such conditions can include wildfire (Nowack et al., 2016), water scarcity (Geiser, 2004a) and cold (Geiser, 2013), and are often associated with resource scarcity (Vuarin and Henry, 2014). Many organisms spend extended periods during such unfavourable conditions showing highly depressed metabolic rates and body temperatures (generally <10 °C, Geiser and Ruf, 1995). This is known as prolonged torpor, or hibernation (Geiser and Ruf, 1995). Energy expenditure and metabolic rates during hibernation, including frequency of periodic returns to euthermia (known as inter-bout arousals or IBAs; Nowack et al., 2019), are positively correlated with torpid body temperature (Geiser, 2004b), which in turn may be influenced by ambient temperatures (Pretzlaff and Dausmann, 2012). Ambient temperatures may therefore influence energy expenditure during hibernation (Pretzlaff and Dausmann, 2012). For fat-storing

* Corresponding author.

E-mail addresses: rachel.findlay-robinson@glasgow.ac.uk (R. Findlay-Robinson), davina.hill@glasgow.ac.uk (D.L. Hill).

¹ present address Graduate School, College of Medical, Veterinary and Life Sciences, University of Glasgow, G12 8QQ.

hibernators, which often cannot replenish resources during hibernation (although exceptions to this exist, as described below), excess energy expenditure induced by environmental conditions may have detrimental effects on overwinter survival (Rézouki et al., 2016) or reproductive success the following year (Bieber et al., 2012).

During IBAs, energy expenditure is also influenced by the level of activity that individuals engage in. Under laboratory conditions, where *ad libitum* food is generally available for ethical reasons, fat-storing hibernators will feed during arousals (e.g. Kauffman et al., 2004; Pretzlaff et al., 2021), which may offset the energetic costs of IBAs (Pretzlaff et al., 2021). However, for fossorial species not known to cache food, it is unlikely that during-hibernation feeding opportunities are available in the wild. Surface-level or above-ground hibernators tend to exhibit more activity than fossorial hibernators, including foraging if temperatures allow (e.g. *Myotis* bats in southern England, Hope and Jones, 2013; *Myotis lucifugus* little brown bats in central Canada, Czenze and Willis, 2015), and non-foraging movement such as mating (Thomas et al., 1979) or changing hibernacula (Vogel and Frey, 1995).

Although declines in body temperature and metabolism experienced by hibernators allow energy retention during a fasting period lasting several months, hibernation may also induce costs, such as oxidative damage (Carey, 2000), reduced immune function (Prendergast et al., 2002) and vulnerability to predation (Estók et al., 2010; Haarsma and Kaal, 2016). Even within species, hibernation at different ambient temperatures may induce different costs, e.g. greater telomere damage when hibernating at cooler temperatures (Nowack et al., 2019). Microclimatic conditions (i.e. climatic conditions in the immediate vicinity of the hibernator, on a scale of centimetres to metres depending on the species; Potter et al., 2013) in hibernation habitats may therefore impact hibernators both during hibernation, and in the following active season(s).

Historically, research on optimal hibernation conditions for prolonged hibernators has focussed largely on parameters describing ambient temperature (McGuire et al., 2021). Low temperatures were widely assumed to be preferable due to their positive relationship with energy conservation (Humphries et al., 2002), but recent work suggests that other environmental variables are also important (reviewed by Findlay-Robinson et al., 2023). For example, IBA frequency increased with rates of evaporative water loss in Kuhl's pipistrelle bats *Pipistrellus kuhlii* (Ben-Hamo et al., 2013) and with decreasing barometric pressure in little brown bats (Czenze and Willis, 2015). Extremely low ambient temperatures may even be detrimental to hibernators, as below a particular minimum body temperature (e.g. 5 °C in alpine marmots *Marmota marmota*, Arnold et al., 1991), individuals expend energy to prevent physiological damage from freezing. "Optimal" hibernation strategies and locations should therefore seek to minimise these costs compared to the energetic benefits of hibernation (Boyles et al., 2020).

Hibernators may mitigate the effects of climatic variation on energy expenditure during hibernation through selecting hibernation locations with appropriate microclimates. Models of climatic suitability for species are often determined at large scales (Lembrechts and Lenoir, 2020), such as mesoclimatic (i.e. > 100m) or macroclimatic (i.e. > 1 km, Maclean et al., 2017) resolutions. Currently, macroclimatic datasets such as WorldClim (Fick and Hijmans, 2017), or data interpolated from local weather stations (e.g. HadUK; Hollis et al., 2019) are commonly used as inputs for these types of models. Such data are typically interpolated down to scales of ~1 km². For small-bodied organisms with home ranges <1 km², data at these scales may not accurately capture the climatic variation these organisms experience (Varner and Dearing, 2014). In particular, species or individuals selecting a habitat where they are likely to remain in situ for prolonged periods, such as a breeding nest or hibernaculum, are likely to be strongly affected by its microclimate. Conditions within this microclimate may be dramatically different to those calculated at larger scales, due to (for example) local albedo effects, evaporative cooling or surface roughness effects of vegetation cover (D'Odorico et al., 2013).

Hibernating species inhabit a wide range of hibernacula, including underground burrows, tree hollows and caves, so may experience a wide variety of conditions. Many of the most commonly studied rodent hibernators (e.g. yellow-bellied marmots *Marmota flaviventris*, Columbian ground squirrels *Urocitellus columbianus*, arctic ground squirrels *Urocitellus parryi* and edible dormice *Glis glis*) hibernate in underground burrows, so hibernation microclimates are often measured via proxies such as soil temperature (Sheriff et al., 2011). However, any activities performed during IBAs remain difficult to measure. Owing to this, most work conducted on hibernation microclimates in the wild has been conducted on species using hibernacula which are more accessible to researchers, such as lemurs (e.g. Schmid, 1998) and, to a greater extent, bats (Boyles et al., 2007, 2017; Boyles and McKechnie, 2010). However, the caves where the majority of bat hibernation studies have occurred provide largely stable climates for hibernation that are mostly buffered from external conditions (although microclimates may also exist within these; Boyles et al., 2017), suggesting that there is likely lower variation in hibernation microclimate suitability for cave-dwelling bats than some other hibernators. Additionally, many bat species hibernate in clusters or colonies, so microclimates may also be influenced by the tightness and number of individuals in a cluster (e.g. Boyles et al., 2007).

Hazel dormice *Muscardinus avellanarius* are small, arboreal rodents present throughout much of Europe and Asia Minor. Hazel dormice hibernate during the winter across the majority of their range (Juskaitis and Büchner, 2013); in the UK, this is usually between October and May (Bright and Morris, 1996). Unlike many other rodent hibernators, hazel dormice do not hibernate underground; instead, they build a hibernation nest on the woodland floor, often within root stocks or under leaf litter (Juskaitis and Büchner, 2013), and are often dug at least partially (up to approximately 5 cm deep) into the soil (pers. obs). Materials used in nest construction depend on local availability, but typically consist of a tightly woven core of grasses, bracken and/or moss, surrounded by an outer layer of leaves (Gubert et al., 2022, Fig. 1). Although anecdotal records of hazel dormice hibernating in pairs do exist, they are mostly thought to hibernate individually. Other mammal species known to hibernate on the forest floor include Eastern red bats *Lasiurus borealis* (Mormann and Robbins, 2007) and European hedgehogs *Erinaceus europaeus* (Morris, 2018). As hazel dormice hibernate at the soil surface, choice of hibernation locations is likely to be influenced by a wide range of microclimatic conditions, such as sun exposure, making hazel dormice an ideal model for examining the effects of microclimate on hibernation location selection and hibernation patterns.

Wild hazel dormice have been reported to change hibernacula during the hibernation season (Gubert et al., 2023a; Vogel and Frey, 1995), and are occasionally observed foraging (Gubert et al., 2023b), although they also show IBAs without leaving the hibernaculum (Vogel and Frey, 1995; Walhovd, 1976). Regular overwinter foraging has been recorded in captive hazel dormice (Pretzlaff et al., 2021), although the *ad libitum* food provided for captive dormice is unlikely to reflect winter food availability in the wild.



Fig. 1. Examples of hazel dormouse hibernacula located during the study. (a) A hibernaculum with a mossy outer layer located under leaf litter and partially protruding from the soil, (b) a hibernaculum with the woven inner core visible, located under a cushion of moss (replaced following photo).

In this study, we aimed to assess climatic conditions experienced by hazel dormice at their hibernacula and determine (1) if hibernation locations are characterised by particular microclimatic conditions, and (2) if dormice are more likely to be active during the hibernation season under certain weather conditions. To achieve this, we used a combination of fieldwork and microclimatic modelling to (a) locate wild dormouse hibernacula and record winter activity of the dormice at these locations, (b) measure microclimatic differences between hibernacula and randomly-selected non-hibernacula locations, and (c) assess the relationships between microclimatic variables and dormouse winter activity. We also (d) analysed the level of climatic buffering occurring at the local microclimatic level compared to measurements taken from a local weather station (as a proxy for mesoclimate). We predicted that hibernation locations would experience lower microclimatic variability, particularly with regards to ambient and soil temperature and humidity, than non-hibernation locations and that winter activity would be positively correlated with increased temperatures. We also predicted that we would find differences in the climatic variables measured at the local microclimatic level and the weather station, indicative of climatic buffering.

2. Methods

2.1. Study sites

Two study sites were chosen based on the presence of long-term and ongoing dormouse PIT (passive integrated transponder) tagging programmes. Coed Fron y Wylt (latitude 52.109365 N; longitude -3.370318 W, altitude 130m) in Denbighshire, North Wales, is a 0.74 km² planted ancient woodland, managed by Cyfoeth Naturiol Cymru (Natural Resources Wales) to restore native species. The woodland contains a mixture of broad-leaf and coniferous species, including oak *Quercus* spp., holly *Ilex aquifolium*, hazel *Corylus avellana*, Norway spruce *Picea abies* and honeysuckle *Loniceria periclymenum*. The site is almost entirely on a north-west facing slope of varying steepness.

Bradfield Woods (latitude 52.187036 N; longitude, altitude 96m) in Suffolk, south-east England, is a 0.81 km² ancient broadleaf woodland that has been under continuous coppice-management since 1252. Tree species in the woodland include hazel *Corylus avellana*, ash *Fraxinus excelsior*, oak *Quercus* spp. and honeysuckle *Loniceria periclymenum*. These woods are largely flat, differing in only ~8m of elevation across the site. Hazel dormouse monitoring is carried out at both study sites by volunteers under the UK National Dormouse Monitoring Programme (White, 2012). The two sites exemplify different UK climate zones, as described by Blenkinsop et al. (2008). Briefly, Coed Fron y Wylt experiences a “modified upland temperate climate”, which is generally cooler and wetter than the “temperate maritime climate” experienced at Bradfield Woods. In particular, Coed Fron y Wylt has higher mean winter (October–March inclusive) precipitation rates (835.2 mm) than Bradfield Woods (368.3 mm; Blenkinsop et al., 2008). Due to the relatively warm maritime climate of the UK, neither site experiences significant snowfall; Coed Fron y Wylt experiences on average < 10 days of lying snow annually, whilst Bradfield woods experiences <5 days, and this is decreasing over time due to climate change (Perry, 2008).

2.2. PIT tagging

PIT tags are electronic microchips encased in a biocompatible glass capsule. They are commonly used to identify individual animals, as they can be encoded with a unique ID that can be detected and read by a scanning device. PIT tags can be detected from a short distance away, and systematic searches with PIT tag scanners have previously been used to locate species in cryptic habitats, such as toads in long grass (Salazar et al., 2016) and subterranean-hibernating hatchling turtles (Duncan, 2013).

All PIT tagging of dormice was performed by experienced dormouse

monitors working under licences granted by Natural England and Cyfoeth Naturiol Cymru prior to the commencement of the study.

2.3. Locating hibernating dormice and recording overwinter activity

We undertook systematic searches for six consecutive days at each site during February 2020 and for five consecutive days at each site in November 2020. Searches were carried out for approximately 5–6h per day. Specific search protocols are described in the associated Research Elements article. Briefly, we divided each study site into 5000 m² grids (approximate dormouse home range size, Juskaitis and Büchner, 2013) using QGIS (QGIS Development Team, 2021) and assigned each grid an abundance category of “high”, “medium”, “low” or “none” based on approximate counts of dormice found in nestboxes within each grid during previous active season monitoring visits. We focussed searches on grids with “high” or “medium” abundances. Grids were systematically searched using a HPR Plus PIT tag reader with a BP Plus Portable Antenna (Biomark Inc., Idaho, USA), hereafter referred to as “the scanner”. The scanner could detect a PIT tag from up to 20 cm distance, depending on the orientation of the scanner. When the scanner detected a PIT tag, the leaf litter surrounding the detection area was gently cleared by hand to confirm the presence of a hibernaculum. Following confirmation, the leaf litter was replaced and the location marked on a GPS unit (Garmin Etrex 10, Garmin Corp., Olathe, USA).

When we located a hibernaculum, dataloggers (LogTag Haxo-8, LogTag Recorders Ltd, Auckland, New Zealand; accurate to within 0.1 °C and 0.1% relative humidity) were deployed next to the nest to measure ambient temperature and relative humidity at 30 min intervals. Prior to deployment, we tested dataloggers to ensure they recorded the expected values using a temperature and humidity-controlled incubator set to 5 °C and 85% relative humidity. Only dataloggers recording expected values were deployed in the field. Agreement of recorded values with microclimatic models was also tested by correlation (see section 2.4). Dataloggers were housed within plastic tubes, open at both ends to allow recording of ambient temperature and humidity whilst protecting them from rainfall. One or two camera traps (Bushnell Essential E3, Bushnell Corp., Overland Park, USA) were deployed at each hibernaculum to detect dormouse overwinter activity (i.e., where a dormouse left the nest during the hibernation season). Camera traps were set to record 10s videos with a 5s gap between recordings based on 24h triggering available through infra-red capabilities.

For the purpose of the study, we defined the hibernation season for each hibernaculum as the period between the start of the day (midnight) when the nest was located and May 5th (the dormouse hibernation season is considered to end in early May; (Bright and Morris, 1996; Pretzlaff and Dausmann, 2012). If a dormouse was recorded leaving and not re-entering a hibernaculum, the end of hibernation date for that dormouse was set as the date of dormouse departure from the hibernaculum. All hibernacula were confirmed not to contain loose microchips or dead dormice at the end of the season.

The occurrence of dormouse activity at a given hibernaculum was recorded from camera-trap videos based on whether dormice were seen active at the hibernaculum during the hibernation period or not. Hazel dormice can be differentiated from other small mammals based on their furred tails and lighter fur colour. We recorded the times and dates of activity from videos where dormice were identified. We assigned a binary value to each hourly time step from camera deployment to collection: 0 for “no dormouse activity” and 1 for “dormouse activity”. This was carried out for all hourly time steps until a dormouse was recorded leaving the hibernaculum and not returning. Activity times from each hibernaculum were rounded to the nearest hour and matched with hourly point samples of microclimatic predictions for the same nest (see section 2.5).

2.4. Determining microclimatic differences between hibernacula and random points

We used QGIS (QGIS Development Team, 2021) to compare hibernaculum locations with non-hibernaculum locations, whereby we selected random points within the search grids that did not contain hibernacula (hereafter referred to as “random points”). We selected an equal number of random points to the number of hibernacula found to allow a balanced design. We also simulated a larger number of random points ($n = 59$) from within the search areas, and compared these with the selected random points via a principal component analysis (Figs. S1 and S2) to ensure the selected random points were representative of the wider habitat.

We used the *microclimc* package (Maclean and Klings, 2021) in the R statistical environment (R Core Team, 2019) to calculate hourly point sample predictions for microclimatic variables for each hibernaculum location and random point for the full length of the hibernation season. The *microclimc* package uses interpolated global weather datasets from the US National Oceanic and Atmospheric Administration’s National Centers for Environmental Prediction (NOAA-NCEP) reanalysis programme (Kanamitsu et al., 2002) to run mechanistic models for user-defined locations from which hourly predictions for a range of microclimatic variables are calculated. The model was set to account for the habitat type as deciduous broadleaf forest with a soil type of clay loam. These settings applied to both sites.

Predicted hourly location ambient temperature and location relative humidity values generated by the *microclimc* package were respectively plotted against hourly ambient temperature and relative humidity data recorded in situ by dataloggers to check for agreement between *microclimc* predictions and in situ data. Dataloggers and *microclimc* predictions showed strong correlations (i.e., correlation coefficient >0.7) in 45% of cases and good correlations (i.e., correlation coefficients ≥ 0.4 but ≤ 0.7) in a further 45% of cases. Where agreement was poor (i.e., correlation coefficients <0.4), dataloggers were generally found to be returning improbable measurements (e.g., 22.1 °C on 4th March). A possible cause of this was the disturbance of vegetation covering dataloggers in several cases, exposing dataloggers to direct sunlight, which may lead to inflated ambient temperature values (Maclean, 2019). Due to the generally broad agreement between datalogger measurements and *microclimc* predictions, we used *microclimc* predictions in all subsequent analyses.

As *microclimc* returns predictions for a large number of microclimatic variables, we selected variables for analysis via a two-step process. Firstly, variables that affect hibernation energetics directly or indirectly (based on previous studies in other species) were identified (Table 1). These “potential effect” variables were then tested for collinearity. We constructed a global model containing all “potential effect” variables, and we sequentially eliminated the variables with the highest Variance Inflation Factors (VIFs), calculated using the “vif” function from the *car* package (Fox and Weisberg, 2019), until all potential-effect variables showed VIFs of <5 (Zuur et al., 2007).

We fitted a generalised linear mixed-effects model (GLMM) with a binomial error structure to test for differences in microclimate between hibernacula and random locations (described above) using the *MCMCglmm* package (Hadfield, 2021). A binary response variable where 1 represented the presence of a nest and 0 represented “absence” (i.e. random locations) was used.

Microclimatic variables (Table 1), expressed as daily mean and standard deviation for each location, were included in the model as fixed effects, in addition to “season” (a two-level factor representing the two field seasons) and “site” (a two-level factor representing the study site). We included location ID as a random effect to account for the repeated-measures nature of the data, which were expressed at a daily scale for each hibernacula and random point. A parameter-expanded prior was used, as recommended for binary responses by Hadfield (2021). Models were run for 1×10^9 iterations, with a burn-in of 5×10^5 and thinning of

Table 1

Variables returned by the *microclimc* package that have been found to be associated with hibernation energetics in previous studies. Means and standard deviations of each variable were tested for collinearity, and retained variables are highlighted in bold.

Variable		Reason and source for including variable
Ambient temperature at 1.5m above ground - derived from NCEP ^a data	Mean Standard deviation	Air temperature is associated with many aspects of hibernation (reviewed in Findlay-Robinson et al., 2023). For example, hibernation emergence dates have become earlier with increasing air temperature in most species studied.
Ambient temperature 1 cm above the ground	Mean Standard deviation	
Relative humidity at 1.5m above ground derived from NCEP ^a data	Mean Standard deviation	Hibernating bats avoid dry air conditions (Boyles et al., 2022).
Relative humidity at 0 cm depth	Mean Standard deviation	
Relative humidity at 2.5 cm depth	Mean Standard deviation	
Relative humidity at 5 cm depth	Mean Standard deviation	
Soil temperature at 0 cm depth	Mean Standard deviation	Soil temperature may influence temperature of hibernacula; heterothermy may be associated with soil temperature (Sheriff et al., 2013)
Soil temperature at 2.5 cm depth	Mean Standard deviation	
Soil temperature at 5 cm depth	Mean Standard deviation	
Soil water content at 0 cm depth	Mean Standard deviation	Soil water content influences soil temperature and likelihood of soil freezing (Mo et al., 2022).
Soil water content at 2.5 cm depth	Mean Standard deviation	
Soil water content at 5 cm depth	Mean Standard deviation	

^a National Centers for Environmental Prediction.

500 to reduce autocorrelation. Fixed effects with 95% confidence intervals that crossed zero were sequentially removed to reach the final model for all GLMMs. Model convergence was checked using visual assessment of trace plots and examination of autocorrelation values.

2.5. Assessing relationships between microclimate and dormouse winter activity

To test for associations between microclimatic variables and dormouse winter activity, we generated point values of potential effect variables (Table 1) at an hourly scale for hibernacula where dormouse activity was recorded, and matched these with hourly records of dormouse activity (section 2.3). We then fitted a GLMM with a binomial error structure and a parameter-expanded prior using the *MCMCglmm* package as described in the previous section. In this analysis, the binary response variable indicated dormouse activity (1) or no dormouse activity (0) observed outside the nest in a given hour. Only data from hibernacula where activity was recorded were used in this analysis. All hibernacula in this analysis were from the same site (Bradfield Woods) and season, hence these variables were not included as fixed effects in this model. Location ID was included as a random effect. Microclimatic

variables (Table 1) were included as fixed effects. Models were run for 1×10^7 iterations with a burn-in of 4×10^5 and thinning of 2500 to reduce autocorrelation. Model convergence was checked as above.

2.6. Analysing climatic buffering between local microclimate and weather station data

We extracted data from the UK Meteorological Office's Integrated Data Archive System (MIDAS) dataset (Met Office, 2012) for the weather station at Felsham, approximately 1.6 km from Bradfield Woods. There was no weather station collecting ambient temperature data within 35 km of Coed Fron y Wyllt for the time period of the study; we therefore excluded this site from this part of the analysis. Point samples of ambient temperature ($^{\circ}\text{C}$) and relative humidity (%) were taken daily at 0900 at the weather station, and daily minimum and maximum ambient temperature were also recorded. Data were only available between the 1st and 20th of each month of the study. We calculated the daily maximum temperature, daily minimum temperature and daily 9am temperature (all 1 cm above the ground) for each hibernaculum and random point using the *microclimc* package as described above. Correlations between *microclimc* values and those recorded at the weather station were calculated using the *cor.test* function from the *stats* package (R Core Team, 2019).

2.7. Ethics statement

All research in dormouse habitats was carried out under project licences granted to R Findlay-Robinson (Natural England Science Education and Conservation Schedule 5, licence number 2020-44498-SCI-SCI; Natural Resources Wales licence number S087420/1) and with the permission of the landowners. Ethical approval was granted by the University of Cumbria's Research Ethics Panel (Reference 19/05).

3. Results

3.1. Characterising microclimatic conditions of hibernacula

During the study, we located nine hibernacula. In the first season, two were found at Bradfield Woods and three at Coed Fron y Wyllt; in the second season, four were found at Bradfield Woods and none were

found at Coed Fron y Wyllt.

Daily mean ambient temperature 1 cm above the ground, as determined by *microclimc*, was 3.54 ± 2.80 $^{\circ}\text{C}$ (mean \pm SD, $n = 9$ hibernacula; Fig. 2). The highest mean daily temperature recorded was 10.39 $^{\circ}\text{C}$, and the lowest mean daily temperature recorded was -3.47 $^{\circ}\text{C}$. The average mean daily soil temperatures at 0 cm (2.95 ± 2.86 $^{\circ}\text{C}$) and 5 cm below the surface (3.19 ± 2.29 $^{\circ}\text{C}$) were both lower than daily mean temperature 1 cm above the ground (paired t-tests, $t_{1163} = 22.08$, $p < 0.001$; $t_{1163} = 9.38$, $p < 0.001$ respectively; Fig. 2). There were strong positive correlations between daily mean ambient temperature 1 cm above the ground and daily mean soil temperature at both 0 cm and at 5 cm below the soil surface (Table 2a). Mean relative ambient humidity at hibernacula was very high ($99.98 \pm 0.37\%$). Relative soil humidity was also very high at both 0 cm ($99.98 \pm <0.01\%$) and 5 cm depths ($99.99 \pm 0.02\%$). As with temperature, strong positive correlations were found between relative humidity at 1 cm above the ground and soil humidity at 0 cm, and between soil humidities at 0 cm and 5 cm depth (Table 2b). However, relative humidity at 1 cm above ground and soil humidity at 5 cm depth were not correlated (Table 2b). Average daily mean relative shortwave radiation 1 cm above the ground at hibernacula was 8.56 ± 6.01 W/m^2 .

We detected dormouse overwinter activity on twelve occasions from four hibernacula at Bradfield Woods in season 2. The mean ambient temperature 1 cm above ground level at hibernacula where activity occurred during the study period was 2.95 ± 2.74 $^{\circ}\text{C}$. At these hibernacula, mean ambient temperature was strongly positively correlated with mean soil temperature at 5 cm depth (2.15 ± 1.95 $^{\circ}\text{C}$; $r_p = 0.862$, $t_{11152} = 116.2$, $p < 0.001$). Mean daily ambient relative humidity at nests where overwinter activity was detected was $99.73 \pm 0.73\%$, which was weakly positively correlated with relative humidity at the soil surface ($99.99 \pm 0.002\%$; $r_p = 0.329$, $t_{11152} = 36.73$, $p < 0.001$).

3.2. Determining microclimatic differences between hibernacula and random points

The likelihood of a hazel dormouse hibernaculum being present at a location was negatively related to the variability in both the ambient relative humidity 1 cm above the ground and in the amount of shortwave radiation (i.e., sunlight) reaching the location (Fig. 3). A positive relationship was found between the mean soil temperature 5 cm below

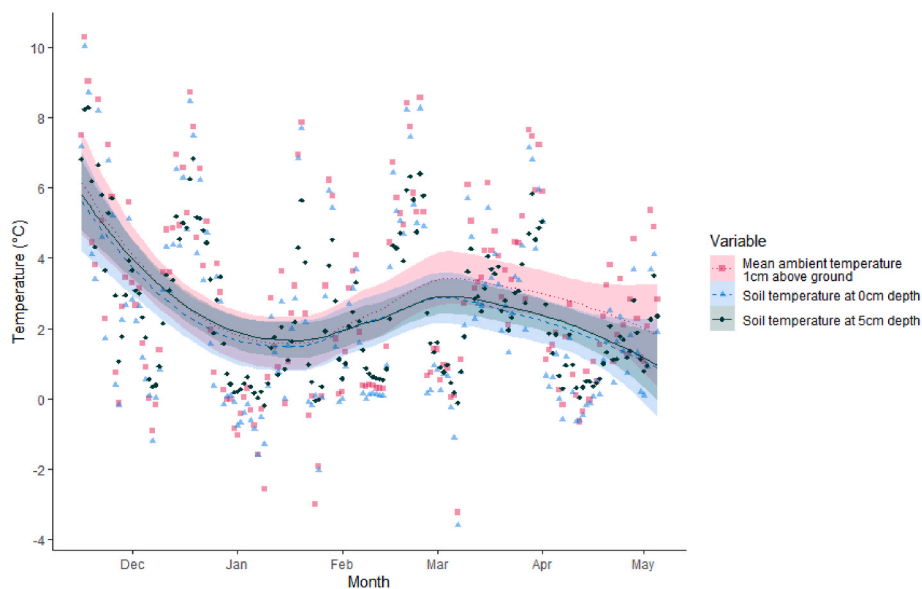


Fig. 2. Mean and 95% confidence intervals of daily mean ambient temperature 1 cm above the ground, soil at 0 cm depth and soil at 5 cm depth between November 2020 and May 2021. Data were collected at two woodland sites – Coed Fron y Wyllt (Denbighshire, N. Wales) and Bradfield Woods (Suffolk, SE England).

Table 2

Pearson’s correlation coefficients of (a) the mean and standard deviation (SD) of daily ambient temperature at 1 cm above ground, 0 cm soil depth and 5 cm soil depth, and (b) the mean and SD of daily relative humidity (RH) recordings at 1 cm above ground, 0 cm soil depth and 5 cm soil depth. Values for microclimatic variables were calculated using the *microclimc* R package for nine hazel dormouse hibernacula monitored between February and May 2020 and November 2020 to May 2021 at two study sites in NE Wales and SE England. Values in bold are statistically significant ($p < 0.05$). Sample size (n) = 1164. \pm represents 95% confidence intervals.

(a)		Soil temperature at 0 cm depth (°C)		Soil temperature at 5 cm depth (°C)	
		Mean	SD	Mean	SD
Ambient temperature 1 cm above the ground (°C)	Mean	0.949 \pm 0.006		0.895 \pm 0.011	
	SD		0.832 \pm 0.017	0.699 \pm 0.028	
Soil temperature at 0 cm depth (°C)	Mean			0.936 \pm 0.007	
	SD			0.823 \pm 0.017	
(b)		Soil RH at 0 cm depth (%)		Soil RH at 5 cm depth (%)	
		Mean	SD	Mean	SD
Ambient RH 1 cm above ground (%)	Mean	0.074 \pm 0.057		0.011 \pm 0.058	
	SD		-0.016 \pm 0.026	-0.012 \pm 0.036	
Soil RH at 0 cm depth (%)	Mean			0.885 \pm 0.012	
	SD			0.842 \pm 0.016	

the surface and the likelihood of a dormouse hibernaculum being present at the location (Fig. 3). Mean soil relative humidity 5 cm below the surface and at the soil surface, variability in location temperature, location and season were not associated with the probability of a

Table 3

Results of a Generalised Linear Mixed Effects Model with a binomial error structure testing for effects of microclimatic variables on hazel dormouse winter activity at four hazel dormouse hibernacula. Microclimatic variables were chosen for inclusion following VIF analysis of variables generated by microclimatic modelling using the *microclimc* package. All data were collected from 4 hibernacula at Bradfield Woods (SE England) between November 2021 and May 2022.

Fixed effects	β	pMCMC
Intercept	-4.023 (-5.750 to -2.469)	0.015
Ambient temperature 1 cm above ground (°C)	-0.392 (-1.033 to 0.205)	0.213
Relative ambient humidity 1 cm above ground (%)	0.277 (-0.483 to 1.049)	0.532
Soil temperature at 5 cm depth (°C)	0.577 (-0.069 to 1.227)	0.071
Relative humidity at soil surface (%)	0.411 (-0.073 to 0.894)	0.088

hibernaculum being present.

3.3. Assessing relationships between microclimate and dormouse winter activity

Hazel dormouse overwinter activity was not associated with ambient temperature at 1 cm above the ground nor ambient relative humidity 1 cm above the ground (Table 3). There was a trend towards an increased probability of overwinter activity with increasing soil temperature at 5 cm depth and relative humidity at the soil surface, but these associations were not statistically significant.

3.4. Analysing climatic buffering between local microclimate and weather station data

Ambient air temperature recorded daily at 9am at the closest weather station to the study site showed a strong positive correlation with ambient surface temperature at hibernaculum and random

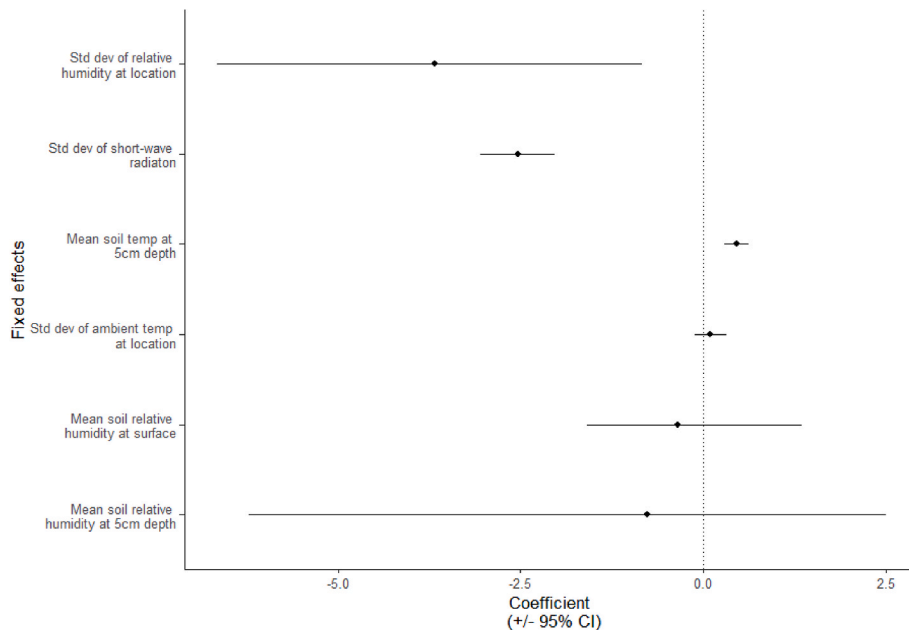


Fig. 3. Results of a Generalised Linear Mixed Effects Model with a binomial error structure testing for differences in microclimatic variables at hazel dormouse hibernacula and paired randomly selected non-hibernacula locations ($N = 9$). Fixed effects were chosen following variance inflation factor analysis of microclimatic variables generated from a microclimatic model using the *microclimc* package. Individual ID was included as a random effect. Parameter estimates (β) are modes from the posterior distribution, with upper and lower 95% confidence shown. Coefficients not overlapping zero are significant. Location and season were included as fixed rather than random effects due to the low number of levels for each (Bolker et al., 2009). These fixed effects are not shown on the figure because of their wide confidence intervals. Location: 53.1 (-56.1 to 195.1); Season: -54.6 (-187.4 to 53.8).

locations sampled using *microclimc* at the same time point ($r_p = 0.87$, $t_{973} = 55.83$, $p < 0.001$), although weather station values were higher (mean \pm SD; 4.73 ± 3.39 °C) than surface temperature values (3.04 ± 3.36 °C; $t_{974} = 31.04$, $p < 0.001$). The difference between 9am ambient temperature predicted at hibernacula by *microclimc* and recorded at the weather station ranged from -2.14 °C to 7.03 °C (1.69 ± 1.7 °C). There were also strong positive correlations between daily maximum air temperatures measured at the weather station and hibernacula and random locations ($r_p = 0.73$, $t_{1092} = 34.86$, $p < 0.001$), although maximum temperatures at weather stations were on average 3.8 °C higher than at hibernacula and random locations ($t_{1093} = 38.61$, $p < 0.001$). A similar pattern was seen between minimum air temperatures as measured at the weather station and at hibernacula and random locations ($r_p = 0.726$, $t_{1070} = 34.55$, $p < 0.001$), with minimum air temperatures being on average 1.9 °C higher at the weather station than at nest and random locations ($t_{1071} = 25.83$, $p < 0.001$).

4. Discussion

We used microclimatic modelling to test if hibernacula locations of hazel dormice were associated with microclimatic conditions, and if these conditions influence overwinter activity. As meso- and macroclimatic data are widely used in ecological studies (Zellweger et al., 2019), we also analysed the amount of climatic buffering that occurs at the microclimatic level compared to local weather station data (as a proxy for the mesoclimate).

The results of our correlative study provide evidence that soil temperature, variability in ambient relative humidity and relative shortwave radiation may influence where dormice choose to hibernate, although our small sample size means that our results should be interpreted with caution. Mean soil temperature 5 cm below ground level was positively related to the likelihood of hibernaculum presence, whilst the standard deviation of ambient relative humidity and shortwave radiation were negatively related to hibernaculum presence. However, none of the microclimatic variables that we examined influenced dormouse winter activity. We found differences were found between ambient temperature measurements taken at forest floor level and at a nearby weather station, indicative of climatic buffering. Surface temperatures showed strong positive correlations with ambient air temperature data recorded by a weather station ~ 1.6 km from the study site (Bradfield Woods), suggesting that weather station data are an appropriate proxy for forest floor sites if appropriate ground-truthing is carried out to calculate the level of buffering occurring.

Mean soil temperature at 5 cm depth was positively associated with the probability of a hibernaculum being present. Although low hibernaculum temperatures minimise energy expenditure during hibernation (Geiser, 2004b), there are also costs associated with prolonged exposure to these temperatures, such as telomere shortening (Nowack et al., 2019) and metabolic imbalances (Humphries et al., 2003). Selection of hibernation microclimate may depend on the strength of selective pressures for energy conservation compared to other needs (Boyles et al., 2022). Hence, hibernators that are able to periodically forage during the hibernation season, such as *Myotis* bats in warmer climates (e.g. Hope and Jones, 2013), Eastern red bats (Dunbar et al., 2007) and hazel dormice (Pretzlaff et al., 2021) may select warmer hibernation temperatures to minimise metabolic and molecular costs (Lovegrove et al., 2014; Nowack et al., 2019).

We found a strong positive correlation between soil temperature at 5 cm depth and ambient air temperature 1 cm above the soil surface, despite the latter not being associated with hibernaculum presence. The insulative properties of soil allows soil temperatures to remain elevated at very low air temperatures (Morecroft et al., 1998); for instance, soil temperatures below 0 °C were rarely recorded in our study (Fig. 2), despite ambient air temperatures falling below this on several occasions. Hibernators that overwinter in underground burrows might therefore benefit from the thermal insulation of soil to maintain a stable

temperature, and avoid temperature extremes at the surface (e.g. alpine marmots, Arnold et al., 1991; arctic ground squirrels, Buck and Barnes, 1999). Such avoidance of temperature extremes is hypothesised to drive subterranean hibernation in Eastern dwarf lemurs *Cheirogaleus sibreei*, *C. crossleyi* and *C. major* (Blanco et al., 2013). Surface hibernators may also be able to take advantage of this insulative property of soil, by digging their hibernacula at least partially into the soil (observed in hazel dormice in this study and by Vogel and Frey, 1995), or by being in contact with the soil (e.g. hibernating under the leaf litter as observed in Eastern red bats; Mormann and Robbins, 2007). In future work, it would be useful to examine if dormice and other surface or underground hibernators adjust the depth of their hibernacula and/or extent of leaf litter coverage depending on ambient and soil temperatures to take further advantage of this buffering.

Variability in ambient relative humidity was negatively associated with the probability of a hibernaculum being present. Few studies to date have examined the role of variability in ambient relative humidity on hibernation site selection, although there is some evidence that a constant level of humidity is favoured by some bat species (Hall, 1982). Experimental research suggests that high humidity levels minimise energy expenditure during hibernation in tri-coloured bats *Perimyotis subflavus*, likely due to lower evaporative water loss (McGuire et al., 2021); it can be assumed that fluctuations in humidity at a given ambient temperature may therefore increase evaporative water loss, increasing energy expenditure. It is worth noting that the variability in relative humidity in our study was very low (0.01%), suggesting that dormice may be highly sensitive to even small changes in relative humidity, although our sample size was also small. Further research experimentally manipulating mean humidity could help to further explain the importance of humidity in hibernation microclimate selection. Previous research using remotely-sensed variables suggests that dormice prefer to build hibernacula on sloping areas rather than flat areas (Gubert et al., 2023b), with the suggestion that this prevents hibernacula from flooding. There was little variation in slope and elevation in our sample, so this was not tested in the present study.

There were some limitations to our searching method that may have influenced our results. For ethical and licencing reasons, areas with thick undergrowth were avoided during searches, as being unable to see the ground increased the risk of stepping on a hibernaculum. This means that the majority of hibernacula included in the study were in relatively easy-to-access areas with low undergrowth. Nevertheless, the ability of the scanner to detect PIT tags through several natural materials (e.g. leaves, wood, moss and soil) potentially increases the chances of locating hibernacula compared to hand-searching (i.e. moving leaves and grasses by hand to search for hibernacula), which is the primary method used in locating hibernacula of this species. Hand-searching may also increase the risk of disturbance to hibernating animals.

Contrary to expectations, our results suggest that microclimate does not influence the frequency or timing of dormouse overwinter activity, in contrast to other studies on this species (Pretzlaff et al., 2021; Pretzlaff and Dausmann, 2012). Overwinter activity may also be influenced by factors such as circadian rhythms (Körtner and Geiser, 2000); as dormice are primarily nocturnal, they may be more likely to experience IBAs at night, and no may be more influenced by nighttime temperatures than daytime maxima. However, the camera trap method used in our study can only record activity that occurs when the dormouse leaves the nest, and not the euthermic intervals occurring within the nest that have been measured in captive studies.

It was not possible to monitor IBAs that occurred without external activity in our study, but this would be an avenue for future work in wild hibernators. Studies in other species also suggest that overwinter activity may be more strongly or additionally influenced by individual factors. Edible dormice show differences in hibernation patterns based on body condition, with fatter individuals arousing from hibernation more often than leaner individuals (Bieber et al., 2014). Similar patterns are seen in yellow-bellied marmots (French, 1990), woodchucks

Marmota monax (Zervanos et al., 2014), Eastern chipmunks *Tamias striatus* (Munro et al., 2005) and little brown bats (Czenze et al., 2017), in addition to age-specific differences in the length of torpor bouts in the latter species. We were unable to measure individual body mass or age in this study, so cannot discount the potential role of these factors.

Although we found differences between ambient temperatures at forest floor locations and those recorded at weather stations, these values were also strongly correlated. This suggests that, although climatic buffering is occurring at the forest floor, local weather station data are useful proxies for near-ground temperatures at a coarse scale, despite the effects of habitat, topography and distance of the weather station from the location. However, the differences seen between weather station data and microclimatic measurements indicate that understanding the scale of an organism's thermal tolerance (e.g. threshold temperatures for activity/metabolism; Pörtner, 2002) may help to evaluate the appropriateness of using weather-station data as a proxy for microclimatic data. It is also worth noting that the majority of this study took place at times of the year where the woodland canopy is open (i.e. winter in deciduous woodlands), and that greater differences in microclimatic compared to mesoclimatic values (i.e. buffering) might be found beneath a closed canopy.

In summary, our results suggest that microclimatic characteristics may influence the selection of hibernation locations in above-ground or surface-level hibernators. The finding that presence of dormouse hibernacula was positively associated with soil temperature supports recent work in other species suggesting that hibernators may not select the lowest available environmental temperatures for hibernation (Boyles et al., 2022), although this may also depend on body condition (Boyles et al., 2007). This association with warmer temperatures may be encouraging as to the fate of hibernators in warming winters, although the roles of other variables may outweigh this. The effects of variability in climatic variables apart from temperature are rarely considered in studies of hibernation microclimates, but here were shown to be more strongly associated with the presence of hibernation sites than were mean values for some variables. Further research is needed to understand preferences of above-ground hibernators in hibernation microclimates, particularly of the role of microclimatic variability, and how habitats of declining species can be managed to promote their over-winter survival.

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CRediT authorship contribution statement

Rachel Findlay-Robinson: Writing – review & editing, Writing – original draft, Validation, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Davina L. Hill:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare no conflicts of interest.

Data availability

Data are available at <http://dx.doi.org/10.5525/gla.researchdata.1539>.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2024.103909>.

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