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Research Article

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

Leonardo Gubert[1,*], Robbie McDonald[2], Jonathan Bennie[3], Fiona Mathews[4]

[1] *Centre for Ecology and Conservation, University of Exeter, Penryn Campus, Penryn, TR10 9FE, UK*
[2] *Environment and Sustainability Institute, University of Exeter, Penryn, TR10 9FE, UK*
[3] *Centre for Geography and Environmental Science, University of Exeter, Penryn Campus, Penryn TR10 9FE, UK*
[4] *School of Life Sciences, University of Sussex, Brighton, BN1 9QG, UK*

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Abstract

The hazel dormouse is mainly an arboreal species with nocturnal habits that, in northern European countries, moves down to the ground to hibernate in the autumn where they stay until spring at locations not well understood. To prepare for hibernation, dormice accumulate fat reserves necessary to maintain vital bodily functions when food supply is lower and the energy cost of staying active exceeds the amount of energy that can be harvested in their habitat. Little is known about the hibernation ecology of hazel dormice or where they go in the winter. In this study, different methods to identify dormouse hibernacula were used: telemetry, systematic searches, and wildlife detection dogs. The movements of 31 individuals prior to and during hibernation were observed using radiotelemetry. Weight measurements of eight wild hazel dormice were recorded during the hibernation period and the rate of weight loss of each individual calculated as proportion of body mass per day. A total of 44 hazel dormouse hibernacula were identified: 24 by telemetry, 20 by systematic searches and none by wildlife detection dogs. Telemetry results indicated that dormice selected sites for their hibernaculum within 43 m (SD=30) from the place where they were captured while active, suggesting that hibernation normally takes place within their home range. The timing of hibernation varied amongst individuals, with some dormice remaining active and feeding throughout the month of December. On average dormice lost 0.47 % of their body mass per day during hibernation bouts. Despite dormice hibernating largely in leaf litter on the woodland floor, often at conspicuous locations, detecting hibernacula without the use of radiotelemetry proved labour intensive but possible through systematic searches. The fact that hazel dormice lose a relatively high proportion of their body mass during the winter highlights the challenges wild animals face to survive hibernation.

Introduction

The hazel dormouse is known for its ability to hibernate for long periods of time in temperate climates, but hibernation is still one of the least known aspects of the species' ecology. As primarily arboreal rodents, adult hazel dormice are relatively sedentary and have home ranges of around 0.5–1.0 ha during the active season (Goodwin et al., 2018; Juškaitis, 1997; Bright and Morris, 1991). Juveniles generally settle in their permanent home ranges in the autumn of the year in which they are born. Most research on the species' movements and dispersal in temperate climates is focused on the active season between spring and autumn (Juškaitis, 1997; Bright and Morris, 1991). During this period, individuals, particularly juveniles, have been recorded travelling distances of hundreds of metres, particularly by juveniles that are born earlier in the year (see summary in Juškaitis, 2014). Hazel dormice typically build natural nests in thick scrub, hollows and crevices in shrubs and trees and along hedgerows feeding on different foods varying with their availability throughout the year (Juškaitis and Baltrūnaitė, 2013; Bright and Morris, 1993).

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

Once on the ground, hazel dormice generally build nests for individual use (Vogel and Frey, 1995) although communal nests have been reported at least once (see Juškaitis, 2014). These nests are constructed in a similar way to the ones built in the canopy earlier in the year, using locally sourced materials (Gubert et al., 2022; Verbeylen et al., 2017) and can be occupied for several months at a time (Juškaitis, 2014).

Most previous research has focused on the physiology of hibernation in captive animals (Pretzlaff et al., 2021; Walhovd, 1976; Walhovd and Jensen, 1976). Others describe where winter nests have been found

*Corresponding author
Email address: leogubert@yahoo.com (Leonardo Gubert)

(Gubert et al., 2023; Verbeylen et al., 2017; Bright, 1992) as well as the size of winter nests (Vogel and Frey, 1995; Kahmann and von Frisch, 1950). But little is known about the winter behaviour of wild hazel dormice. In particular, dormouse movements and dispersal between the autumn and spring is largely unknown and, apart from Lemmers et al. (2022), there is virtually no published information about the distance between summer nest sites and hibernaculum. Similarly, there is no evidence on whether hazel dormice are able to forage and increase body weight during the hibernation season to boost survival chances.

A key challenge in studying wild hibernating dormice is the difficulty of finding their hibernacula in the wild. Because of their low density and the inconspicuous nature of their hibernation nests, it is not an easy task and has historically been recorded through incidental finds by people involved in woodland management or recreation. There have also been many anecdotal reports of hibernating animals being found in garden sheds, flowerpots, compost heaps, and other unusual locations (Juškaitis, 2014). Identifying hazel dormouse hibernacula in the wild is not only useful for understanding the species' ecology, but also has crucial implications for conservation. With hibernation being one of the key stages of the hazel dormouse life cycle, habitat disturbance during this period can greatly affect overwinter survival rates (Trout et al., 2012). Whilst in hibernation, hazel dormice are vulnerable to predators and to trampling by domestic animals or human activities, such as recreation, development and woodland management (Bright and Morris, 1996).

Many studies on hazel dormice ecology during the active season have successfully employed telemetry (see summary in Juškaitis, 2014 and, to a lesser extent, used this method to locate hibernacula (Gubert et al., 2023; Lemmers et al., 2022; Verbeylen et al., 2017; Bright and Morris, 1996). This technique might be helpful in addressing gaps in behaviour during the period prior to hibernation, particularly with respect to the use of resting places and ranging.

Systematically searching for hibernacula is another method that has recently become more widely used in Britain at development sites. This involves ground "fingertip" searches of suitable habitats during the hibernation season prior to habitat clearance and is often a condition of project specific derogation licences to minimise the risk of death or injury to a species protected under the Habitats Directive.

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

The aim of this paper is to: (1) establish whether hazel dormice hibernate within their home range by investigating Euclidean distances from rest sites in the autumn to hibernaculum, (2) measure weight loss during hibernation and (3) detail aspects of behaviour prior to and during the hibernation period.

Methods

Study areas

The study was conducted at 18 sites in southwest England (Fig. 1), in areas of broad-leaved and coniferous woodland, roadside habitats, and hedgerows in different central and southern areas of England where dormice had previously been recorded (Tab. S1). These locations represent the main habitat types used by the hazel dormouse in Great Britain. Apart from hedgerows, the study areas included other vegetation types that formed a mosaic of habitats, comprising scrub, grasslands, marginal vegetation, and woodland edge.

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

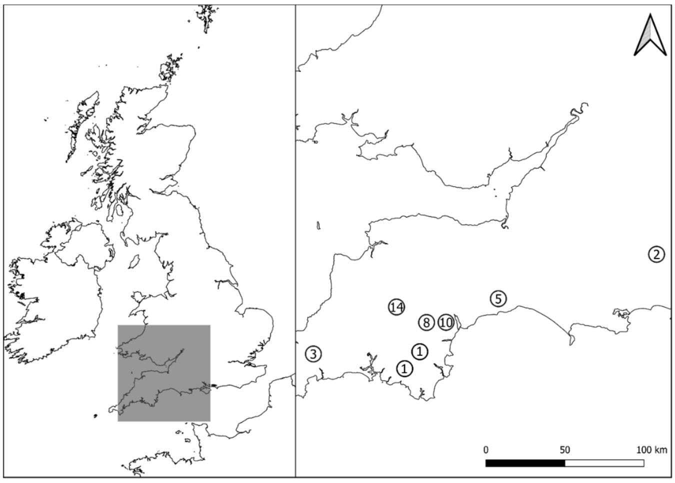

Figure 1 – Location of the study areas in southern England. Numbers in circles indicate number of hibernacula identified in the area.

Methods used to identify hazel dormouse hibernacula

Radio tracking (telemetry)

Thirty-two wild dormice were captured from nest boxes at eight different sites in Devon, southwest England, between 28 October and 24 November 2016. The animals captured were 14 males (11 adults and three juveniles) and 18 females (nine adults and nine juveniles). The captures were timed just before the arrival of the first cold weather front in autumn whilst dormice were still active in the canopy and using nest boxes. Each captured dormouse was weighed, sexed, scanned for Passive Integrated Transponder (PIT) tags at sites where this method was being used as part of a parallel investigation, fitted with a radio-transmitter collar (Type PIP3 mounted on a Teflon ribbon collar (tag size 13 mm × 7 mm × 4 mm and total weight of 0.89 gram), Biotrack Ltd, Wareham, Dorset, UK, Fig. 2) and released back into the same nest box immediately after. Initially, all animals were fitted with a lighter version of the radio-transmitter collar with a battery life of four to five weeks and at the end of this period, nine animals had their collars replaced by a slightly heavier collar with a bigger battery with expected life of 12 weeks (tag size 13 mm × 8 mm × 9 mm and total weight of 1.4 gram). The new Teflon ribbon collar design was trialled using dummy tags on three bank voles *Myodes glareolus* in the lab and on a captive dormouse at Paignton Zoo in Devon, UK, over a three-week period to test and practice collar fitting methodology and assess any impacts on animal welfare.

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

Field and lab work in this study was conducted under licence from Natural England 2015-11955-SCI-SCI, Home Office PPL 3003431 and PIL I69D694C7, and with the approval of the University of Exeter College of Life and Environmental Sciences animal ethics committee.

Systematic searches

Details of hibernation nests have been collected from systematic searches, often carried out as part of protected species licensing conditions, by the research team and a wider community of ecologists. This method involved searching the woodland floor for dormouse hi-

Figure 2 – Photographs detailing methodologies used in dormouse searches and examples of 'summer' natural nests. a) dormouse fitted with radio collar, b) example of pre-hibernation nest location in tree crevice, c) example of low "summer" nest in bramble, d) dormouse "summer" nest at the base of a hazel shrub, e) dormouse "summer" nest in grass tussock just above ground level, f) nest in gorse being used late in autumn when deciduous trees are dropping their leaves, and g) wildlife search dog in action.

bernation nests by hand. This 'fingertip method' is often used to locate hibernating dormice for development purposes, although no clear protocol yet exists. For this study, the woodland floor was thoroughly searched through leaf litter, moss and ivy *Hedera helix* covered ground, root systems, tree bases, crevices, burrows (as far as practicable), under moveable stones, fallen tree branches and brash, and ground vegetation.

Wildlife detection (search) dog

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

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

Data analysis

The Euclidean distances between paired points of 32 hazel dormice, classified as place of capture, canopy nest(s) and hibernation nest(s), were calculated on QGIS and rounded up to the nearest metre. Linear mixed-effects models were then run separately, including/excluding points obtained from nest box locations since these locations are not randomised. Using the distance between paired points as a response variable, the models were used to test whether the classification of the paired points (fixed response variable), predicted the distance between the points using individual animal id as random effect. This model assumes that if hibernation nests tend to be outside, or at the margins of animal's home range, distances containing hibernation nests are expected to be further than other nest types. The significance of results was tested using Analysis of Variance (ANOVA).

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

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

Results

The locations of 44 hazel dormouse hibernacula were identified as part of this study: 24 by telemetry and 20 by systematic searches. The wildlife detection dog found no nests. The location of hibernacula varied but the majority were found in the leaf litter on the woodland floor (n=33), the remaining under or anchored in ferns (n=3), in hazel stools (n=3), open ground adjacent to woodland or hedge (n=3), on a hedge bank (n=1) and surprisingly, on highway concrete structure under moss and grass (n=1) (Tab. S2). Despite the arrival of cold weather fronts and the leaf fall within their habitat, most dormice were still active at the beginning of November often using inconspicuous natural nests (Fig. 2).

Identifying location of hazel dormouse hibernacula

Radio tracking

Thirty-two hazel dormice were fitted with radio collars from late October to mid-November resulting in 1241 tracking days and an average of 44 days per collared dormouse (Tab. S3). A maximum of 28 individuals were tracked simultaneously during a period of two weeks at the beginning of November. Within one month from the beginning of the radio tracking exercise, five active individuals could not be located within 1 km radius of the study areas; three were recaptured in nest boxes wearing damaged/chewed tag casings (with the electronic components exposed) that were removed; one collar was found on the ground and another individual, recognised by its subcutaneous microchip, was found without the collar in a nest box near to where it was originally captured. Contact with four other dormice was lost once they had left their hibernaculum later in the winter, possibly due to malfunction, predation, or collar damage by other dormice.

By mid-November nearly half of the tracked dormice were hibernating (Fig. 3). At the end of November, the collars fitted with a battery life of four weeks were being removed or replaced. Dormice that had collars replaced whilst they were in hibernation, moved their hibernaculum location in every instance from as soon as the following night following collar removal to up to two weeks later, except for one adult male that remained in the same nest for a further eight weeks until emerging from hibernation by the beginning of April.

In total, fifteen dormice were tracked to their hibernaculum (see Fig. 4 for examples). Some animals moved to new hibernaculum loc-

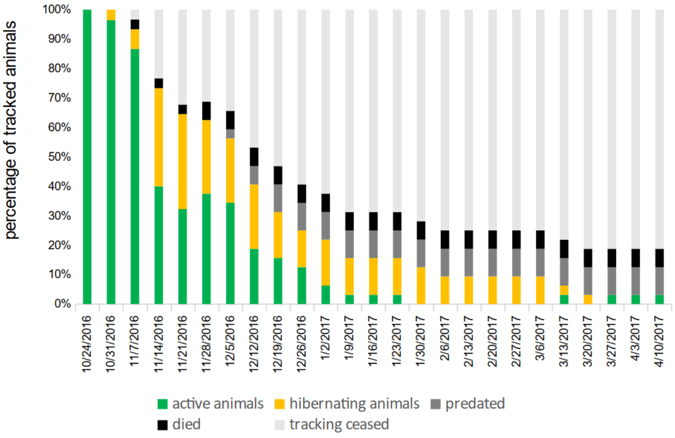

Figure 3 – Weekly summary of dormouse activity during radio tracking between October 2016 and April 2017 at eight different sites in Devon, southwest England.

ations hence tracking resulted in the discovery of 24 different hibernacula (Tab. 1). Four individuals moved once to new hibernacula, one moved twice, and another built four different hibernacula moving three times over its hibernation period.

Systematic searches

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

Wildlife detection (search) dog

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

Mortality during radio tracking period

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

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

Pre hibernation movements

Results of the linear mixed-effects models indicated that there were no significant differences in the distances from places of capture to canopy nests or hibernacula including (p=0.221) or excluding (p=0.113) capture events in nest boxes, suggesting that dormice largely remain within their home range. We found that the mean distance from place of capture to hibernaculum location was 43 m (SD=30). Juveniles were found to move further away from place of capture to other canopy nests than adults while active (=73 m (SD=53) and 44 m (SD=35) respectively) and chose to hibernate at further locations than adults (=48 m (SD=29) and 42 m (SD=32) respectively). Our findings indicate that 10 of the 32 radio tracked dormice, adults and juveniles of both sexes, moved to canopy nests beyond distances of >100 metres prior to hibernation, which is likely to be beyond their expected home range (Fig. 5). During this period of pre-hibernation activity, dormice were tracked to natural nests in mature trees such as oak *Quercus robur*, willows *Salix spp*, and alder *Alnus glutinosa*, often with thick ivy cover (n=10), grey squirrel *Sciurus carolinensis* dreys (n=3), concealed wild nests in low growing scrub such as gorse and bramble (n= 8), purple moor grass *Molinia caerulea* tussocks (n=2), and low nests at the base of hazel *Corylus avellana* shrubs (n=2, Fig. 2). Except for one adult female that moved 141 m from its place of capture to hibernaculum location, most animals chose to hibernate within their expected home range. One male juvenile did not move nests during the six weeks tracking period and was consistently tracked back to the same nest box where it was captured. The animal was found both active and in torpor, it was also noted that the body weight varied between monitoring visits, indicating that it must have been actively feeding at night.

Weight loss during hibernation

Results of the linear mixed-effect models indicate that on average dormice lost 0.47 % of their body mass per day during hibernation bouts (Fig. 6). During the radio tracking period, an adult female started hibernating on 1 November at a mass of 28 g, and at the last capture occasion in mid-March, 131 days later, it had a mass of 14 g. This individual moved hibernaculum location three times and, between the last two weighing events taken on two consecutive days (15.5 g and 14 g respectively), revealed a loss 10 % of its body weight over night after full arousal and leaving hibernaculum for a nest at the base of a hazel shrub over 50 metres away. Another tracked juvenile male weighing 13 g in late October remained active and feeding through November and was recorded weighing 18 g in early December, moving to a hibernation nest on 2 January at 15.5 g. It remained in the hibernaculum for two weeks before moving to a nearby nest box where it stayed between bouts of torpor and activity. The final weight, recorded at the end of January when the radio collar was removed, was 13 g, the same as when radio tracking started.

Discussion

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

Telemetry proved an effective method to identify hibernaculum locations whilst providing opportunities to investigate aspects of the species ecology such behaviour and habitat use, timing of hibernation, movements, selection of resting sites and weight gain/loss prior and during hibernation period. However, equipment is costly (each radio collar £150, telemetry receiver and antenna approximately £1500 in August 2016), liable to faults, requires training, while permits and licenses that can be expensive and time consuming to obtain are also required. Systematic searches, on the other hand, are a relatively simple method for locating hazel hibernacula, but can be difficult to conduct over large areas, it is intrusive by causing disturbance to woodland floor cover, its accuracy is associated with survey effort, habitat characteristics, surveyor thoroughness, and it is inevitably prone to bias (Juškaitis, 2014).

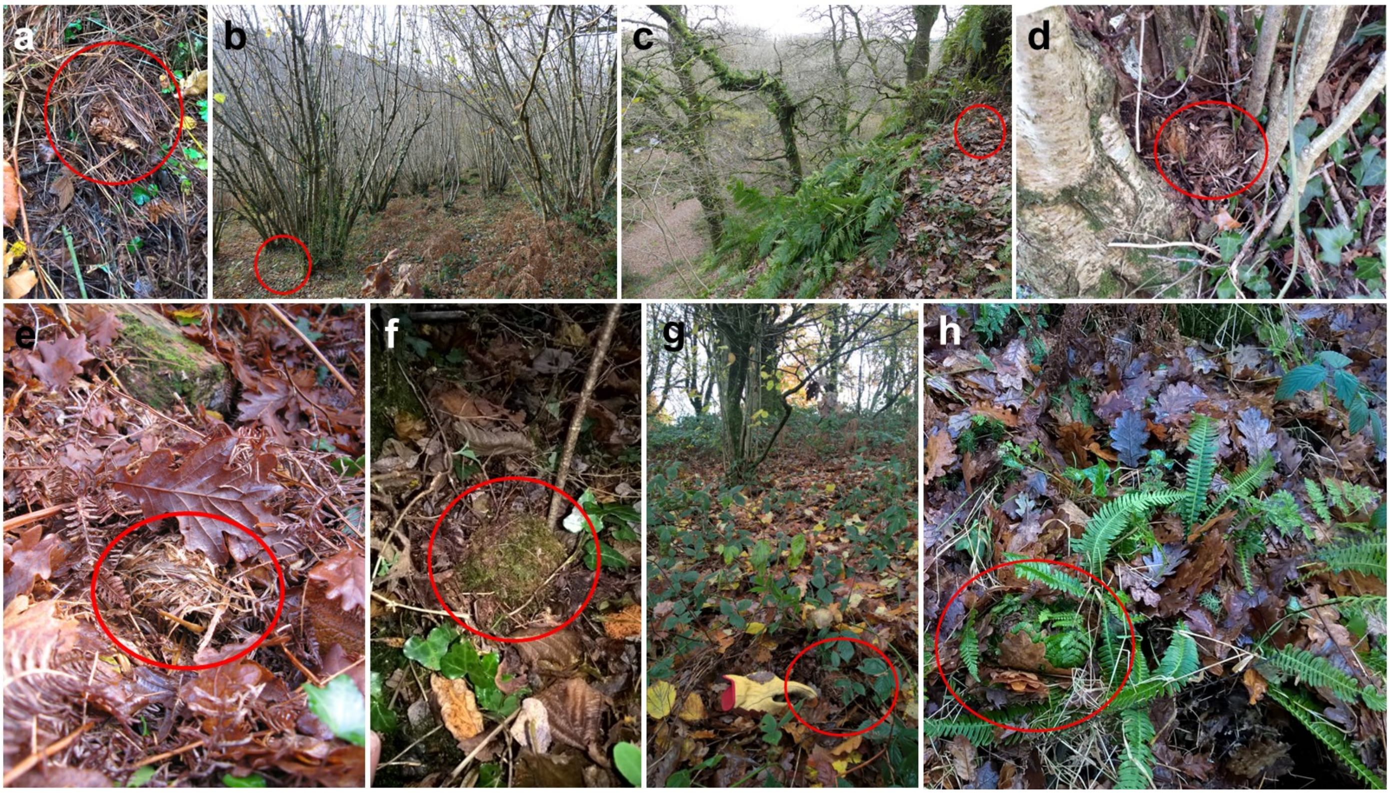

Figure 4 – Examples of hibernation nests and hibernaculum locations. a) nest constructed with bracken and pine needles next to Scots pine *Pinus sylvestris*, b) hibernaculum location in hazel coppice, c) hibernaculum location anchored in leaf litter on steep slope, d) hibernaculum located in hazel stool in hedgerow, e) inconspicuous hibernaculum constructed with bracken bark in south facing exposed clearing by woodland edge, f) hibernaculum in woodland floor by hazel stool, g) well-hidden hibernation nest in leaf litter under sparse bramble and, h) hibernaculum constructed at the base of hard fern Blechnum spicant next to footpath..

Table 1 – Number of hibernacula constructed by radio tracked hazel dormice and their behaviour after handling events associated with collar replacement or removal..

Animal id	Sex	Age	Number of hibernacula built	Notes
J776	Male	Adult	4	Three handling events in total: moved hibernacula after 2nd and 3rd times
J807	Male	Adult	2	Moved hibernaculum after handling
J790	Male	Adult	1	Stayed in hibernaculum after handling
J778	Female	Juvenile	1	Stayed in hibernaculum after handling
J772	Female	Juvenile	1	Stayed in hibernaculum after handling
J775	Male	Adult	2	Stayed in hibernaculum after handling
J782	Female	Juvenile	1	Stayed in hibernaculum after handling
J870	Male	Adult	1	Stayed in hibernaculum after handling
J788	Female	Adult	1	Left hibernaculum and became active after handling
J774	Male	Adult	2	Stayed in hibernaculum after handling
J797	Male	Adult	2	Moved hibernaculum after handling both occasions
J806	Female	Adult	1	Moved hibernaculum after handling
J785	Male	Juvenile	1	Moved hibernaculum after handling
J792	Female	Adult	3	Moved hibernaculum after all three handling events
J799	Male	Adult	1	Stayed in hibernaculum after handling

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

Despite reports of at least two previous cases of dogs finding hibernating hazel dormice on the forest floor in the literature (see summary in Juškaitis, 2014) and the effective use of search dog in many wildlife species' surveys where success rate has been much greater than human surveyors (del Valle et al., 2020; Mathews et al., 2013; Long et al., 2007; Harrison, 2006), this approach did not prove viable as a survey method

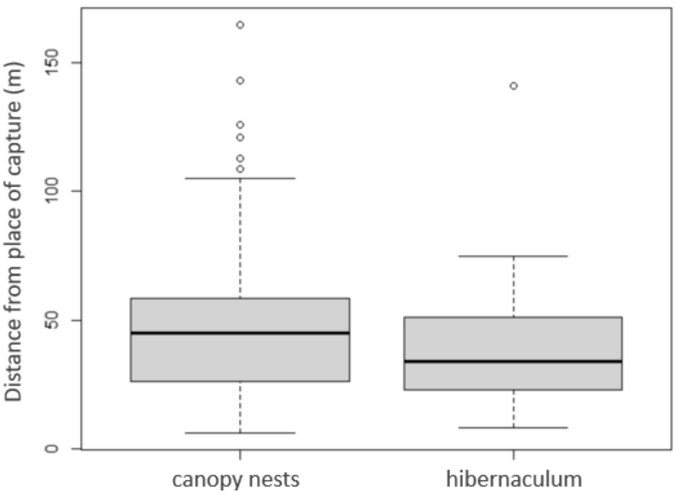

Figure 5 – Euclidean distance from dormouse place of capture to natural nests (places of rest) in the canopy and to hibernaculum. Boxes represent the range of distances recorded, black lines inside the boxes are the median markers whilst error bars extend upward from the third quartile to the maximum and the other extends downward from the first quartile to the minimum. Dots (outliers) represent the Euclidean distances by individuals above the upper quartile.

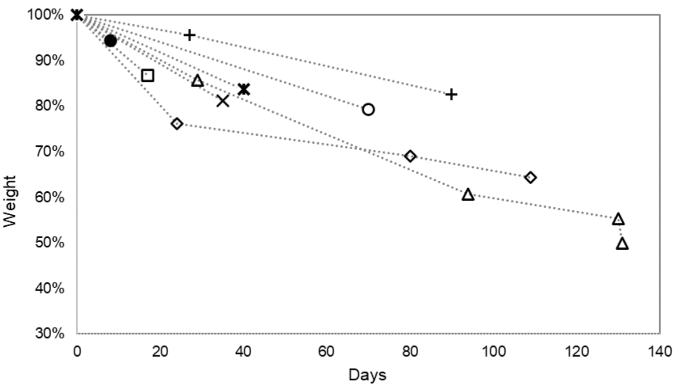

Figure 6 – Percentage of body weight loss during hibernation period of eight individual wild dormice in southwest England.

on this occasion. However, it is important to point out a limiting factor that only one dog was used in this study. We conclude that the scent originating from hibernating dormice was not conspicuous enough, even for a trained and experienced animal. A similar conclusion was drawn by a team of researchers in Germany where two search dogs were used but unable to detect dormouse hibernacula (B. Schulz, *pers. comm.*). With the reduction in metabolic functions during hibernation, dormice are likely to have evolved to avoid disturbance and detection by potential predators. The diversity of the habitat around their hibernacula (Gubert et al., 2023) and the use of different materials to build hibernation nests (Gubert et al., 2022; Verbeylen et al., 2017), may mean that a predator cannot develop a 'search image' which would lead to systematic finding and predation, as suggested by Bright and Morris (1996). Also, there is likely to be strong evolutionary pressure for being inconspicuous during hibernation to avoid predation (Ruf and Bieber, 2023)

The verified mortality of radio tracked individuals during field observations was 16 % (n=5), but the actual figure could be as high as 47 % if equipment failure is discarded (e.g. battery/tag failures). High overwinter mortality of wild hazel dormice is reported in the literature (Bird et al., 2012; Csorba, 2003; Juškaitis, 2014) and has been described as being around two thirds of the population based on mark-recapture techniques (Juskaitis, 1999) but without distinguishing the numbers lost to predation and natural causes. Overwinter mortality under controlled conditions with predation excluded has been reported as being 44 % (n=18; Csorba, 2003).

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

The results of the radio tracking exercise suggest that dormice largely remained within their autumnal home range during the onset of hibernation choosing hibernaculum locations close to their places of rest during the late stages of their active period in autumn. As suggested by Juškaitis (1997), at this time most juveniles have already dispersed and those that stayed have become sedentary. In this study, however, juveniles moved further away from the place of capture than adults, but this may be associated with searches for better foraging areas as they prepare to enter hibernation which is normally later than in heavier adults (Juškaitis, 2014). During the pre-hibernation period, hazel dormice were found to nest in a range of concealed locations, notably mature trees, squirrel dreys and in low growing scrub, highlighting the importance of habitat structural diversity, especially in the autumn when broadleaved trees and shrubs are dropping their leaves making natural nests in the understorey more conspicuous. We found that the longest Euclidean distance from place of capture to hibernaculum was 160m which is an intermediate value between the maximum distance of 81m reported by Verbeylen et al. (2017) in Belgium and 250m reported by Lemmers et al. (2022) in the Netherlands.

As animals entered hibernation, we found that the rate of weight loss was 0.47 % bodyweight/day, which is relatively high when compared to mean estimates of 0.17 % bodyweight/day (n=18, including animals that died during the study) reported in a study in a controlled environment where animals fed *ad libitum* (Csorba, 2003). However, the highest rate of weight loss was recorded by Csorba (2003) was 0.64 % bodyweight/day by a juvenile that died during the experiment after 96 days in hibernation. The highest rate recorded amongst those that survived hibernation was 0.41 % bodyweight/day. Difference is also evident with a capture-mark-capture study (Juškaitis, 2001), where a mean of 33 % body weight decrease was observed from the first half of October until the recapture of marked individuals in the spring (males in April and for females in April – early May). For example, marked males weighed an average of 30 g in the first half of October and 20 g in the spring; using our data, the same individual would be weighing close to 13.5 g during similar period of 170 days, representing a loss of 55% of pre hibernation body weight. It is important to bear in mind that in mark recapture studies using nest boxes, the real duration of the dormouse activity season may be a little longer than the period of nest box use, both in spring and in autumn (Juškaitis, 2014) so that the actual weight immediately before and after hibernation is not considered nor is the possibility of extended foraging periods in the autumn that may result in further weight gain. On the other hand, negative impacts of radio collars on individual dormice cannot be ruled out as it has been observed in similar radio tracking exercise (Verbeylen et al., 2017) and may exacerbate weight loss before and during hibernation.

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

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Location and habitat description of study areas in England.

Table S2 Description of the location where dormouse hibernacula were found and associated search method.

Table S3 Details of individual hazel dormice fitted with radio collars.