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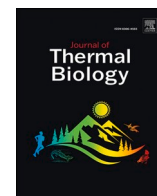
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Variation in hibernation patterns of a temperate zone mammal

Katie Crawford^{*} , Ruby Orsman, Laura Parry, Thomas O'Hagan, Julia Nowack 

School of Biological and Environmental Sciences, Liverpool John Moores University, Liverpool, UK

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ABSTRACT

Temperate-zone species frequently employ hibernation as a winter energy-saving strategy to overcome periods with unfavourable ambient conditions and low food availability. With winters becoming warmer and seasons becoming less predictable, one question is whether species will show flexibility in the use of hibernation and whether this will be sufficient to keep pace with rapid anthropogenic alteration of the environment. We examined the hibernation pattern of a wild hedgehog population (*Erinaceus europaeus*) in a semi-rural habitat in the north-west of England that is subject to a mild winter climate. We conducted night surveys across a 1-year study period, collecting population-level activity data on a total of 26 individuals as well as detailed data on hibernation timing and pattern in five individuals tagged with temperature-sensitive VHF tags through the hibernation period. While all five tagged individuals employed hibernation, we found a variation of up to 93 days in the hibernation start date and 47 days in end date between individuals, although the general pattern of hibernation such as average torpor bout duration was similar. Some individuals used shorter torpor bouts over an extended period in combination with extended activity of several days prior to the onset and after termination of hibernation, presumably allowing them to save energy during the colder nights while being able to forage during warmer days when invertebrates were active. This flexibility in hibernation timing suggests that hedgehogs may be able to adapt to changing environmental conditions.

1. Introduction

Endothermic mammals and birds have high energetic requirements in order to maintain a relatively high and stable body temperature (T_b). When ambient temperature (T_a) falls and food is limited, they typically encounter periods of energetic bottleneck in their environment. Some heterothermic mammals and birds can lower their threshold of T_b regulation and employ torpor as a physiological strategy to reduce energy expenditure during these periods (Geiser and Ruf, 2023). Torpor use allows animals to conserve energy during periods of low resource availability, such as seasonal changes in food and water. The most energy efficient strategy for saving energy is hibernation (Geiser and Ruf, 2023). During hibernation, an animal enters multiday torpor bouts in which metabolic rate is decreased and T_b lowered to a range closely following T_a (Ruf and Geiser, 2014). In hibernation, torpor bouts are typically interspersed with frequent periods of short arousals in which animals rewarm to normothermic values (Ruf and Geiser, 2014). This pattern occurs in most hibernators, although cases of extended torpor without interbout arousal have been documented (Dausmann et al.,

2004; Lovegrove et al., 2014). Arousals represent the most energetically expensive part of hibernation with rewarming from torpor accounting for 19 % and inter-bout euthermia accounting for 51.6 % of energy expenditure during hibernation (Wang, 1978), although this can be somewhat mitigated by passive rewarming, which reduces energy expenditure (Schmid et al., 2000).

Species that reside in the Northern hemisphere are typically obligate hibernators, i.e. all individuals of a species will enter hibernation at some part of the winter (Mohr et al., 2020). Hibernation can be found in species across the globe, however, non-Holarctic species from tropical and arid regions in the southern hemisphere often display more variable patterns of hibernation and torpor due to their unpredictable environment and may use shorter and shallower torpor bouts (Nowack et al., 2023). In addition to variability in the length of torpor bouts, animals can also show variability in the pattern of hibernation dependent on many factors such as temperature, location, body mass or sex (van Breukelen and Martin, 2015).

Hibernators are notably vulnerable to changing environmental conditions, given their reliance on T_a as their T_b is closely related to T_a

^{*} Corresponding author.

E-mail addresses: K.Crawford@2024.ljmu.ac.uk (K. Crawford), rubyorsman@gmail.com (R. Orsman), lauraparry2011@hotmail.co.uk (L. Parry), tomohagan98@gmail.com (T. O'Hagan), J.Nowack@ljmu.ac.uk (J. Nowack).

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during torpor (Geiser, 2011) and arousal frequency typically increases at warmer temperatures (Geiser and Broome, 1993; Geiser and Kenagy, 1988). With the global increase in winter temperatures (Contosta et al., 2024) and European winter climates becoming increasingly unpredictable (Deser and Phillips, 2023), studies on hibernation pattern and individual variation in hibernation use of wild animals are needed in order to predict species' responses to climate change and formulate conservation strategies.

The Western European hedgehog (*Erinaceus europaeus*) is a small insectivorous, hibernating mammal with a wide geographic range, including most of the UK. In the UK, their population size is thought to be decreasing in rural areas but stabilising in urban areas (Hubert et al., 2011; Poel et al., 2015; Wembridge et al., 2022). Hedgehogs can have two breeding seasons in the UK, the first in May–June and the second around August–September, with an average of 4 young per litter (Jackson, 2006). Their main predator is the Eurasian badger (*Meles meles*), an intraguild predator whose presence in an area negatively impacts the likelihood of hedgehog presence (Hof et al., 2019). Studies on hedgehogs have previously focused on behaviour during the active period (e.g. Dowding et al., 2010) and while hedgehogs are considered obligate hibernators, so far not much is known about their hibernation pattern in the wild (but see Bearman-Brown et al., 2020; Dowding et al., 2010). Studies on the hibernation pattern of European hedgehogs to date have typically been limited to captive individuals rather than free ranging (South et al., 2020). The few studies on wild hedgehogs focused on overwinter survival (Bearman-Brown et al., 2020) or nest site use based on weekly checks of the activity of radio-tracked individuals (Rasmussen et al., 2019). These studies, while insightful, do not provide information about torpor pattern and arousal frequency. This study thus aimed to quantify the hibernation patterns of free ranging hedgehogs within a semi-rural habitat and mild winter-conditions in the north-west of England to determine how much individuals in the same habitat can vary in their use of torpor over the winter period.

2. Materials and methods

2.1. Location & night surveys

We conducted the study within a semi-rural, disused golf course covering approximately 54 hectares in the United Kingdom (N 53.344227, E –3.0221553) between May 25, 2023 and April 16, 2024, i.e. over one hibernation season. The golf course lies within a suburban area surrounded by both residential development and open green space, with a mix of habitats comprising woodland, grassland and ponds.

Animals were detected during their active period (spring to autumn) using a spotlight (Clulite DL1 Dust Lamp, Clulite, UK) and hand captured. We conducted a total of 38-night surveys that occurred weekly (active season) to twice a month (winter) and typically started at sunset and continued until early morning, covering the entire golf course. We examined and recorded sex, age (juvenile/adult), body condition (including body mass) and reproductive status in all individuals. To allow individual identification, we marked all animals with numbered and coloured heat shrink tubes attached to dorsal spines (following Reeve et al., 2019). It should be noted that sampling effort decreased during winter, with a mix of weekly and biweekly surveys between September and December, and predominantly biweekly surveys from January to March.

2.2. Hibernation data

Between the end of August and October, we equipped a subset of 5 hedgehogs (2m, 3f, see supplement, Table S1) with temperature-sensitive VHF radio transmitters (TW-3 single celled tag with thermistor, Lotek, UK) that allowed us to investigate hibernation patterns. These were attached to the back of the individual, with the thermal attachment touching the skin. We clipped the spines down and glued the

tag on using a combination of epoxy resin for attaching to spines and bonding cement (Torbot, Torbot Group Inc., US) to affix it nearer to the skin.

Given that the transmitter was attached to the dorsal skin of the individual, temperature readings represent skin temperature (T_{skin}) rather than internal T_b . While this method does not allow for us to make assumption of torpor depth it allows us to detect onset of torpor bouts and arousals and is commonly used for non-implantation detection of hibernation patterns (e.g. Giroud et al., 2023). This reading is only accurate during torpor bouts as the individual is curled up in a nest and therefore represents individuals' skin temperature, whereas during movement the temperature reading is heavily influenced by T_a . Therefore, we discounted any data on temperature during a known movement event. All tags weighed approximately 12g, which is <5 % of the animal's body mass (adult body mass 700–1000g).

Hedgehog nests were located 2–3 times per week during the day in their active season (summer) using radio telemetry (TR-8, Telonics, US and LITEFLEX 3-Element VHF Yagi Antenna, Lotek, UK). Once individuals started to hibernate, we then located them once a day during their resting period to record nest site use and T_{skin} , this was around midday where possible but recording times did vary for some of the days. Additionally, all tagged individuals were located once a week or when possible, during the regular nightly surveys and, when found active we checked tag fixture and took data on body condition and health of animals as described above.

In addition to manual data recording once a day during the hibernation season, individual T_{skin} was monitored remotely every 10 min using two automated receiver stations (SRX-1200-D2, Lotek, US) that we shifted between the animals for a total of 316 recording days (2–3 recording periods of 8–75 days per individual, Supplement Table S2). This allowed us to collect fine scale data on torpor bout and arousal duration and timing.

Ambient temperature was recorded using calibrated temperature loggers (iButton, Maxim Integrated Products, Inc., Sunnyvale, California, USA, DS1922L-F5#, resolution: 0.0625 °C, accuracy improved by calibration (see below), logging interval: every 1 h) placed within a hedge on the edge of the golf course at approximately 5 cm off the ground. These recorded data for 276 consecutive days from June 2, 2023 until March 3, 2024. After the 3rd March, the iButton placed within the golf course was unable to be re-located, therefore obtained data on daily temperature and rainfall from the Met Office weather station at Crosby, SRC_ID 17309, approximately 17.3 km from the study site was used in Lieu of iButton data for the study period to provide a continuous data set. A Pearson correlation was conducted to evaluate the strength of relationship between iButton and Met office average/mean daily temperature values, concluding these two were highly correlated ($r = 0.993$, $r^2 = 0.986$, $p < 0.001$). Transmitters and iButtons were calibrated to the nearest 0.1 °C in a water bath from 5 to 40 °C using temperature probes (Omega PT-104A temperature logger, Omega Engineering, UK) for reference temperatures.

2.3. Hibernation use

Entry into hibernation was defined as the point at which a hedgehog entered the classical hibernation pattern, characterised by multiday torpor bouts interspersed by regular short arousal phases (typically bouts of torpor >3 days and arousal <2 days). We generally defined termination of hibernation by the end of use of deep torpor or via the occurrence of >3 days of normothermic T_{skin} coupled with extended activity. Instances where arousals were longer in duration than typical for hibernation (i.e. ≥ 3 days), coupled with comparatively shorter multiday torpor bouts (both in the context of hibernation and comparative to arousals) were described as flexible. In two instances where individuals lost their tag during the first long distance movement, we assumed that this marked the end of hibernation. Data from automated receiver stations were used to identify the length of arousal and torpor

phases and the date and time at which an individual entered and exited each phase. Within the automated box data (10-min interval) we used threshold crossing points to determine time of entry into torpor and arousal. We defined threshold temperatures for the start and end of arousals variably based on the respective T_a and we chose these conservatively with T_{skin} being at least 5 °C above T_a . This method follows other studies using the differential between T_a and T_b to define torpor bouts (e.g. Geiser and Mzilikazi, 2011). Although automated data were collected for all animals, box rotation meant that full data for the hibernation period was not collected for any one individual. As arousals were typically >24 h, we believe all arousals were likely captured through the combination of daily checks that gave us data on T_{skin} and nest site changes, and the data from automated boxes. However, without high resolution data for the entire hibernation period we cannot exclude the possibility that an arousal may have been missed. A total of 42 arousal entries and 42 torpor entries were recorded by the automated loggers, accounting to 33 full torpor bouts (entry to termination) and 37 full arousals (entry of arousal to re-entry into torpor), with a total recording time of 319 days (Supplement Table S2).

2.4. Statistics

All statistical analysis was performed in R version 4.4.1 (R Core Team, 2024). We present data as mean \pm SD unless stated otherwise; N = number of individuals, n = number of measurements where appropriate.

A linear mixed effect model was used ('lmer' in library 'lme4', (Bates et al., 2015)) to investigate differences in torpor bout duration between individuals. We also used a linear mixed effects model to test the effect of time in hibernation on torpor bout duration of the daily data collection. As it is known in other hibernators that arousals are more frequent at the end and start of hibernation (French, 1982), we split each individual's hibernation duration into three phases (33.3 %). The effect of phase on torpor bout duration was then tested using a linear mixed effect model with phase as a fixed effect and ID as a random effect. We used a type II ANOVA to test model significance. Pairwise comparisons of phase were then performed via a posthoc test ('emmeans' in library 'emmeans', (Lenth, 2024)). A linear mixed effects model was further used to investigate the effects of number of days in hibernation and average T_a on the previous day on torpor bout duration from the daily data collection ('lme' in library 'nlme', (Pinheiro and Bates, 2000)). We included animal ID as a random factor in order to account for repeated measures. For all models, normal distribution of residuals was checked visually through qq-plot visualization (library 'ggpubr', (Kassambara, 2020)), alongside a histogram of model residuals and using Shapiro-Wilk tests. A Rayleigh test was used to determine whether circular data (timing of torpor entry/exit from automated box data) differed significantly from random distribution and were significantly clustered around a mean for each phase ('rayleigh.test' in package 'circular' (Lund et al., 2017)).

We also used a linear mixed effect model to investigate whether euthermic bouts from the automated box data differed by individual and across month, with a type II ANOVA to test model significance.

3. Results

3.1. Ambient temperature

The range in monthly average T_a across the study period (May–April) was 13.3 °C (ranging from 5.2 to 18.5 °C). Total rainfall during the study period was 1075 mm with the heaviest month for rainfall being October and the heaviest day for rainfall being the 19th October (27 mm). Winter temperatures were relatively mild; The coldest month over the hibernation period, which started in September and lasted to April (see below), was January with an average T_a of 5.5 \pm 2.8 °C (minimum T_a : 4 °C, maximum T_a : 15 °C); the warmest month over the hibernation

period was September with an average T_a of 16.3 \pm 2.8 °C (minimum T_a : 8 °C, maximum T_a : 27 °C). The overall coldest temperature (−6 °C) was recorded in December during an 8-day cold spell (29th November – 6th December). The average T_a during the hibernation period was 9.2 \pm 4.2 (ranging from −6 to +27 °C) degrees. Variation in amplitude of daily T_a ranged from 0 °C (October)– 15.5 °C (September) throughout the hibernation period.

3.2. Population level data

A total of 26 animals (8 males, 11 females, 7 juveniles) were found during the study period (Fig. 1). Male sightings reached a peak in July with 13 sightings of three individuals through the month, then decreased to 9 and 8 in August and September, respectively. After September, only a single male sighting of a tagged hedgehog who was in a one-day arousal from hibernation was recorded on the 15th November (Fig. 1). Females remained active for longer than males with six repeated sightings of three individuals in November and one sighting in December; this was the last active hedgehog sighting until March. Males started activity in early spring, with five observations of four active males in March as opposed to a single female sighting. Juveniles were found active until mid-November. Only one juvenile was observed within the early spring of 2024 (March).

Breeding activity appeared to be spread from summer to autumn. The first lactating females were recorded on the 15th and 19th of June (with a confirmed parturition date between the 15th and 19th of June), respectively. Another two pregnant females were observed on the 3rd August, both were lactating by the 23rd. The last pregnant female was observed on the 5th September. Most juveniles were seen in September (N = 3 versus N = 0 between June and August).

The average body mass of individuals increased steadily from the start of surveys in May (average 711g \pm 99g) until the time when the majority of animals had entered hibernation (November; average: 965g \pm 260g). Males were generally heavier than females, with males weighing more on five out of seven months that had data points for both sexes. Males weighed more on average than females after termination of hibernation in early spring (by 137g in March and 36g in April, respectively).

3.3. Hibernation data

The first tagged individual (male) started hibernating on the 19th September (mean T_a during the day: 15.4 °C) and hibernation entry varied by up to 93 days between the five individuals (Table 1), with the last hedgehog entering hibernation on the 20th of December (mean T_a during that day: 9.5 °C). Notably, this hedgehog (female) used multiday torpor bouts (2–3 days) followed by extended activity of 3–5 days from the 30th of November before entering classical hibernation on the 20th of December (Fig. 2, middle panel, #302); T_a during the period of the multiday bouts dropped to a low of −6 °C. Both tagged males entered hibernation before the three females (Table 1, Fig. 2, two top panels).

The tagged individuals terminated hibernation between February 24, 2024 and April 10, 2024 (a range of 47 days) and the total hibernation duration varied by 59 days; the average length of hibernation was 140 days.

Over the whole hibernation season, arousals were recorded approximately every 5.9 days within the daily data (\pm 2.26 days) and torpor bout duration did not significantly differ between individuals (Table 1, $F_{4,96} = 0.9183$, $p = 0.4566$). On average, individuals spent 16.3 % of hibernation euthermic (range 14.0 %–18.8 %) and 83.7 % in torpor (range 81.2 %–86.0 %).

Torpor bout duration varied significantly between the phases in the daily data (Phase 1: 4.7 days \pm 2.2, Phase 2: 7.1 \pm 2.5, Phase 3: 6.5 \pm 2.2, $X^2 = 19.226$, $df = 1$, $p < 0.001$), with the middle phase of hibernation having the longest torpor bout duration and the first phase of hibernation having the shortest duration. Torpor bout duration was

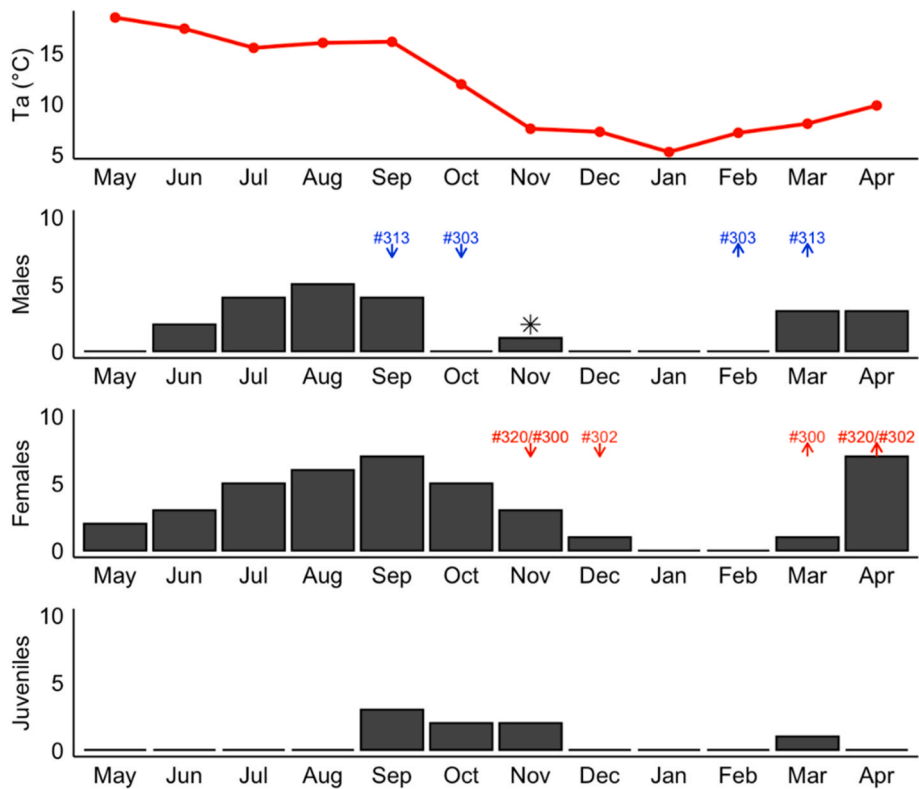


Fig. 1. Individuals found active over the study period per month split into males, females and juveniles along with monthly average ambient temperature (T_a). *Star*—The male sighting in November was a tagged male that changed nesting sites during hibernation. *Arrows* indicate hibernation entry (downward arrow) and exit (upward arrow) of tagged male (blue) and female (red) individual animals.

Table 1
Hibernation timings of each individual radio tagged, along with nest sites and hibernation pattern data and the last recorded body mass before hibernation. ¹¹ date tag fell off.

ID	Sex	Start Date	End Date	Flexible torpor use start date	Total duration (days)	TBD (days)	Number of Arousals	Days Torpid	Days Aroused	Body mass (g)	Post-hibernation body mass (g)	Days post hibernation of body mass recording	Nests	Nest changes (Days in nest)
#313	m	19/09/2023	04/03/2024 ¹	NA	168	5.8 ± 2.4	23	138	30	1084	NA	NA	6	8 (21 ± 14)
#303	m	12/10/2023	24/02/2024	NA	136	5.5 ± 2.2	19	117	19	914	668	8	4	6 (23 ± 8)
#320	f	25/11/2023	10/04/2024	10/04/2024	138	5.1 ± 2.4	21	112	26	1064	711	1	4	6 (27 ± 50)
#302	f	20/12/2023	06/04/2024	03/12/2023	109	6.6 ± 2.4	13	93	16	1051	NA	NA	4	5 (22 ± 18)
#300	f	04/11/2023	29/03/2024 ¹	NA	147	6.2 ± 3.4	18	123	24	936	774	13	3	5 (24 ± 22)

significantly different between phases 1 and 2 ($t = -4.49$, $p < 0.01$) and between phases 1 and 3 ($t = -3.36$, $p = 0.0032$), but no significance was found between phases 2 and 3 ($t = 0.88$, $p = 0.6527$). Torpor bout duration was significantly correlated with the number of days in hibernation ($t = 4.10$, $df = 89$, $p < 0.001$) and temperature on the day before arousal ($t = -2.01$, $df = 89$, $p = 0.0477$); there was no significant interaction between both variables ($t = 0.79$, $df = 88$, $p = 0.4285$).

Interbout euthermia lasted approximately 29.2 (range 8.5–88 h) (automated box data, $n = 40$, $N = 5$, Table S2, Fig. 3). Arousals were longer when associated with a nest site change (62.5 % of arousals >1 day were associated with a nest site change, $n = 16$, $N = 5$). Linear

models suggest that time spent in interbout euthermia was not significantly different between individuals in the automated box data ($F_{5,35} = 2.01$, $p = 0.10$) or across months ($F_{5,31} = 0.50$, $p = 0.77$). The timing of arousal entry and exit were significantly different from random, with the average time of arousal entry being around midday (1110h; Raleigh test, $p < 0.05$) and early morning for re-entry into torpor (0120h; Raleigh test, $p < 0.0001$).

Both males terminated hibernation before the females (Fig. 2, Table 1). All females started to increase the length of interbout euthermia and showed increased activity during arousal phases towards the end of their hibernation (from March). While one female re-entered a

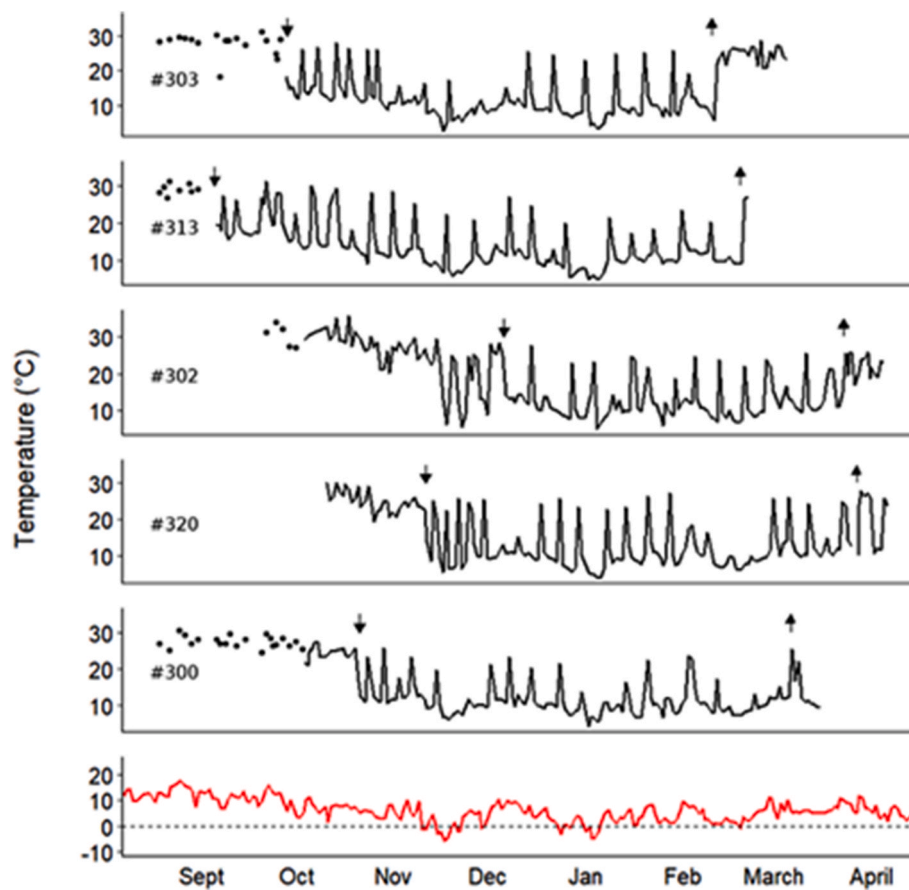


Fig. 2. Daily skin temperature pattern of all five individuals (listed with ID numbers) over the hibernation period collected through manual data collection (one datapoint/day) along with minimum ambient temperature on the bottom panel in red. The top two panels represent male, the bottom three panels female individuals, dots represent intermittent data collection, downward arrows represent start times of hibernation, and upward arrows represent the end of hibernation. Flexible short bouts of multiday torpor use can be seen in #302 prior to hibernation onset in December followed by long phases of euthermia of 3–5 days and #320 in April followed by five days of euthermia before the final termination of hibernation.

long 7-day torpor bout after an extended 3-day activity before exiting hibernation, the other two females underwent more frequent arousals of 2–3 days towards the end of their hibernation and shorter torpor bouts.

3.4. Nest site changes during hibernation

Nest site changes were observed on average 5 times per animal (range: 4 to 7, $N = 5$, Table 1) over their hibernation. Although arousals occurred every 5.9 days, duration of nest use varied, and average time spent in a nest site in succession was 23.4 days (range: 1–117 days, $N = 5$, Fig. 3). During our study, males on average changed nest site more often than females and spent approximately 5.4 fewer days in the nest compared to females. All hedgehogs used at least one nest site twice on separate occasions during hibernation, with an individual using the same nest on three separate occasions. Hibernation nesting sites were typically leaf nests within shrubs ($n = 5$ nests, $n = 152$ days used, $N = 5$ individuals) with two individuals also using nesting sites under a log or within a tree ($n = 2$ nests, $n = 80$ days used). While most hibernation nesting sites were located with the furthest possible distance to human settlements, animals were also seen to occasionally use gardens ($N = 1$ individual, $n = 3$ nests, $n = 10$ days used) or hedges on the edge of a garden ($N = 1$ individual and nest, $n = 13$ days used) as well as a storage container for hibernation.

Of the five hedgehogs that were tagged, three were recaptured in spring. One of these, a female, was first recaptured during an interbout arousal period 23 days before the end of her hibernation, during which she was observed feeding. She was subsequently observed interacting

with a male one day after emerging from hibernation after which she entered a 3-day long torpor bout (Fig. S1, Table 2). This female was discovered dead 10 days after termination of hibernation; the likely cause of death was a dog attack. A male was captured 8 days after hibernation exit and a female was captured 13 days after hibernation termination. The remaining two hedgehogs were not recaptured the following spring. The average body mass at the start of hibernation was $1010\text{g} \pm 170\text{g}$ ($N = 5$), the average body mass coming out of hibernation was $718\text{g} \pm 106\text{g}$ ($N = 3$). Therefore, the average body mass loss for the duration of hibernation was 292g ($N = 3$) or 28.9 %.

4. Discussion

Our study quantified hibernation patterns of wild European hedgehogs in a temperate-zone habitat with a mild winter climate to investigate whether animals subjected to mild conditions during winter show flexibility in torpor use. Despite the relatively warm winter temperatures, all hedgehogs in our study entered hibernation at one point during the winter, confirming the view of hedgehogs being obligate hibernators, and all tagged hedgehogs survived hibernation. However, despite all individuals being subject to the same environmental conditions, we found a surprisingly high variability in timing and duration of hibernation between individuals, with only one winter month without any sign of hedgehog activity.

Our data showed no correlation between entry into hibernation and environmental temperature and photoperiod. Males entered hibernation earlier than females, a trend generally seen in hibernators as females

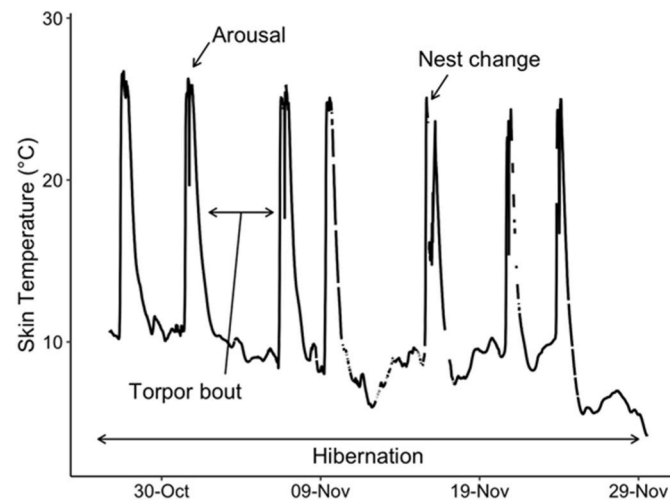


Fig. 3. Skin temperature trace of an individual (#303) over a period of 35 days, illustrating the typical hibernation pattern seen in this species. Nest site changes are relatively infrequent compared to arousal frequency. The continuous high temperature during arousals indicates that the animal did not leave the nest; activity during an arousal is indicated by a drop in skin temperature when animals leave the sheltered microclimate of the nest (the animal moved to a new nesting site that was still in range of the automated box).

Table 2
Flexible torpor bout dates and durations of two female individuals, one prior to hibernation onset and one post hibernation, showing extended periods of arousal with shorter torpor bouts preceding this. Individual #302 used multiple bouts prior to onset of a more typical hibernation pattern.*Found dead.

ID	Date of arousal start	Arousal end date	Arousal duration (days)	Preceding torpor bout duration (days)
#302	03/12/2023	05/12/2023	3	3
#302	08/12/2023	11/12/2023	4	2
#302	15/12/2023	19/12/2023	5	3
#320	10/04/2024	14/04/2024	5	3
#320	18/04/2024	20/04/2024*	3*	3

rear young during the active season and subsequently need to get back up to a good weight after the demanding lactation period before entering hibernation, where they live off their fat reserves (Neuhaus, 2000). While the sample size of our tagged hedgehogs was small, our population level data further confirmed our observation that males disappeared from September, while females and juveniles were sighted until December. Male hedgehogs did not only enter hibernation earlier but also terminated hibernation before the females. Hibernation timing has been found to differ between the sexes for several species. For example, a study on yellow-bellied marmots (*Marmota flaviventer*) found significant differences in hibernation termination date of 58 days, with heavier individuals and males exiting hibernation earlier than females (Edic et al., 2020). This has also been reported in Richardsons ground squirrels (*Urocitellus richardsonii*) and Northern Idaho ground squirrels (*Urocitellus brunneus*) and seems to be related to the need of males to promote their individual reproductive success as spermatogenesis is paused at low body temperatures during torpor (Allison et al., 2023; Michener, 1983; Lee et al., 1990). Early emergence allows spermatogenesis to be initiated and territories to be established before female emergence (Michener, 1992).

Previous research on European hedgehogs also showed a variation in hibernation onset and termination, with juvenile wild hedgehogs in different Danish suburbs showing up to 52 days difference in entry and 30 days difference in termination of hibernation (Rasmussen et al., 2019). However, our study indicates that this variation in hibernation

onset and termination is likely not due to environmental variables such as temperature, but likely a form of individual variability. Despite the high variation in timing that we observed, the average time spent aroused/torpid was similar amongst all hedgehogs. All individuals generally used the same pattern when in hibernation that is seen in ‘classical hibernators’ characterised by multiday torpor bouts interspersed by short arousals (Geiser, 2011). Typically, hibernators will have longer torpor bouts in the middle phase of hibernation and shorter bouts at the start and end of hibernation (French, 1985; Twente and Twente, 1965), as was the case in our study. Our data were also in line with previous studies showing that torpor bout duration shortens and arousal frequency increases with a higher T_a (Geiser and Ruf, 2023). While arousal timing varied, arousals were most often observed at around midday, a time when T_a is approaching its daily maximum. This may allow animals to save energy by passively rewarming with T_a as the first phase of rewarming, followed by an active phase of rewarming past T_a , therefore animals rewarming from torpor without passive heating would increase energetic costs of arousal by 181 % (Schmid et al., 2000). Passive rewarming is typically associated with daily heterotherms and more commonly documented in species on the Southern hemisphere which save considerable amounts of energy by augmented rewarming (Mzilikazi et al., 2002), however, instances of passive rewarming in northern hemisphere hibernators have been documented (Halsall et al., 2012; Arnold, 1988).

Interestingly, male sightings ceased between October to February (with the exception of one sighting of an animal that changed nesting sites), while females were sighted during all months except January and February, indicating a much higher variability in the timing of hibernation in females than males. Furthermore, the tagged female individuals in our study used multiday torpor bouts interspersed with longer active phases of up to 5 days, both before entering hibernation and at the end of hibernation, which indicates that individuals have the option of using a more flexible form of torpor than the rigid hibernation pattern that is often seen as characteristic for most Northern hemisphere hibernators (Nowack et al., 2023). A long-term study on Arctic ground squirrels (*Urocitellus parryii*) showed that global warming caused a shortening of the hibernation season in females, but not males, indicating a sex difference in phenological flexibility. While females terminated hibernation later than males in our study, these data reveal the general risk of climate change to cause phenological mismatches in hibernation termination between sexes that could have implications on breeding success (Chmura et al., 2023; Kucheravy et al., 2021).

The extreme variation in hibernation timing and the flexible torpor use that we saw in our study may have also been influenced by the unusual warm autumn temperatures in 2023. The winter of 2023/24 was the 5th warmest on record for the UK (Met Office, 2024). Energy savings during hibernation vary with species and can be up to 75 % for larger species such as brown bears (*Ursus americanus*) (Tøien et al., 2011) and up to 97.5 % in smaller species such as pygmy possums (*Cercartetus nanus*) (Geiser, 2007). Arousals are the most energetically expensive part of hibernation, therefore more energy is used when arousals become more frequent with warmer temperatures and animals are consequently using shorter torpor bouts (Wang, 1978). Hibernators generally rely on their fat or food reserves during hibernation that they have to accumulate prior during the hibernation season in autumn (Ruf and Geiser, 2014). While some hibernators, such as Richardsons ground squirrels, are known to enter hibernation at high T_a of $>20^\circ\text{C}$ (Michener, 1992), generally, higher winter temperatures lead to a high risk for hibernating animals to lose critical fat reserves as they increase the metabolic rate during torpor bouts (Buck and Barnes, 2000; Nowack et al., 2019) and cause an increase in expensive arousals (Twente et al., 1977). Therefore, strict hibernation may not be an ideal strategy in a mild climate when conditions would allow for foraging, while flexibility in hibernation timing and use of shorter torpor bouts could allow animals to save energy during colder days, while they still have the option to be active and forage during warmer days and higher food availability. This strategy could be explained by the optimal hibernation theory which postulates that both energetic and non-energetic costs influence the expression of hibernation (Boyles et al., 2019) and considers non-energetic factors influencing torpor depth and duration such as the missed opportunity costs and predation risk. However, hedgehogs have little natural predation risk other than from badgers that undergo a seasonal reduction in activity (Harlow, 1981).

Flexibility in hibernation may be more widespread than currently realised. Some previous studies have noted so called ‘test drops’ in some individuals prior to full hibernation onset (eg. Strumwasser, 1958). These are usually characterised as short torpor bouts of increasingly longer duration and decreasing T_b prior to onset of a typical hibernation pattern, seen in species such as Columbian ground squirrels (*Urocyon columbianus*) (Young, 1990) or Californian ground squirrels (*Citellus beecheyi*) (Strumwasser, 1958). These are thought to be physiological preparation for prolonged torpor phases during hibernation but could also allow animals to respond flexibly during phases of variable ambient conditions such as seen in our study.

Notably, desert hedgehogs (*Paraechinus aethiopicus*) living in a warm climate of Saudia Arabia do not undergo hibernation at all, but display irregular short torpor bouts, between $<24\text{ h}$ and 101 h (Boyles et al., 2017), indicating that other (albeit distantly related) hedgehog species can exhibit a flexible pattern of torpor in response to the environmental conditions. Laboratory studies looking into torpor variation within individuals kept at different temperatures during hibernation indicate differences between species in the ability to change torpor pattern: While studies on garden dormice (*Eliomys quercinus*) hibernating under laboratory conditions at 3°C or 14°C did not indicate a change of torpor pattern to a more flexible torpor use, even if food was available (Giroud et al., 2023; Nowack et al., 2019), a study on ground squirrels (*Ictidomys tridecemlineatus*) with *ad libitum* food availability found that animals used short daily bouts of torpor instead of the traditional hibernation pattern when hibernating at 25°C , with one individual not hibernating at all over the winter period (MacCannell and Staples, 2021). Interbout arousal also lasted significantly longer, and time spent torpid by animals housed at 25°C was less than 50 % than in animals housed at both 5°C and 16°C . Similarly, free-ranging Western pygmy-possum (*Cercartetus concinnus*) in a habitat with Mediterranean climate were found to use more flexible torpor patterns of shorter and prolonged torpor bouts instead of classical hibernation (Turner et al. 2011). In contrast, Eastern pygmy possums (*Cercartetus nanus*) were found to continue to hibernate even at temperatures of 22°C in a laboratory study (Geiser and Ruf,

2023), although torpor bout duration was with 1–2 days significantly shorter in animals hibernating at 22°C than at 7°C and the number of days of survival on body fat reserves decreased from 310 days to 127 days (Geiser and Ruf, 2023).

Dependent on species, hibernators can either feed or fast during arousals in the hibernation period. Those that fast will typically have dramatically altered gut microbiomes during hibernation, with lower diversity of gut microbiota (Gao et al., 2024; Zhang et al., 2024). This has been noted in species such as arctic ground squirrels (*Urocyon parryi*) (Stevenson et al., 2014) brown bear (*Ursus Arctos*) (Sommer et al., 2016) and greater horseshoe bats (*Rhinolophus ferrumequinum*) (Xiao et al., 2019), although no data on hedgehogs are available yet. Interestingly, we found one hedgehog feeding on a slug during an interbout arousal in March; The same hedgehog was observed in a different arousal during a period of flexible torpor use whereby the individual used short torpor bouts interspersed with longer arousals, with a male hedgehog, presumably mating, although this was not confirmed. While Western European hedgehogs show the typical pre-hibernation fattening of species that live off their fat reserves during hibernation, captive hedgehogs have been discovered feeding during arousal periods with *ad libitum* food availability (South et al., 2020), although it is unclear whether these hedgehogs used deep torpor.

Hedgehogs only changed nesting sites on approximately every fourth arousal (approx. every 23 days versus every 6 days), indicating that nest site changes are not a reliable method to estimate torpor bout duration of hibernating hedgehogs. Arousals associated with a nest site change were usually longer than arousals without nest site changes. A small number of total nest sites were used by individuals and all individuals cycled between a small number of nesting sites that were used repeatedly. Other research indicates a wide variety of nest sites being used by hedgehogs to provide opportunities for feeding, predator evasion and reproduction (Gago et al., 2023; Rasmussen et al., 2019; Riber, 2006) and hedgehogs preferring permanent winter nests within forested patches of urban areas (Gago et al., 2023; Korslund et al., 2023). While hedgehogs in our study almost exclusively used the forested areas of the golf course away from residential development for their winter nests, they were observed to regularly change between nests, indicating that a number of suitable nesting sites were available. The preference for forested areas in comparison to the residential areas that were more frequently used in summer (personal observation JN) is perhaps due to decreased anthropogenic disturbance as well as increased cover from woodland areas and possibly a more stable microclimate in these areas. Research on hazel dormice (*Muscardinus avellanarius*) has highlighted the importance of nest microclimates, with stable humidity and soil temperature influencing site selection (Findlay-Robinson and Hill, 2024). These factors likely also influence site selection in hedgehogs seeking a stable microclimate for hibernation.

In conclusion, our results indicate that hedgehogs hibernate even at relatively mild winter conditions but show a high degree of flexibility in hibernation onset and termination timing which seems to be dependent on individual body condition and varies between sexes. The increasing urbanisation in the UK and elsewhere (Kundu and Pandey, 2020) that is causing habitat loss and fragmentation, resource availability, increased disturbance and often warmer microclimates (Deilami et al., 2018) in cities could pose significant challenges for hibernators. Flexibility in hibernation use could thus be crucial for their survival under these altered conditions.

CRedit authorship contribution statement

Katie Crawford: Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Ruby Orsman:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Laura Parry:** Writing – review & editing, Investigation, Formal analysis, Data curation. **Thomas O’Hagan:** Writing – review & editing, Investigation, Data curation. **Julia Nowack:** Writing – review &

editing, Visualization, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Ethics

Ethical approval for the study was obtained by Liverpool John Moores University (licence number: JN_KC/2024-5) and a Licence issued by Natural England in order to carry out the study methods (licence number: 2022-61869-SCI-SCI-2).

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Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2025.104186>.

Data availability

Data are accessible through figshare: <https://figshare.com/s/978a9c2953f8896d7b8f>.

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