Sleeping hedgehogs in a changing environment

Influence of rising temperatures and supplementary feeding on the hibernation timing of the European hedgehog (Erinaceus europaeus)

Author: Philip Stecher

Supervisor: Dr. ir. Anouschka R. Hof

Chair group: Wildlife Ecology and Conservation

Author: Philip Stecher

Student number: 1326430

Title: Sleeping hedgehogs in a changing environment (Influence of rising temperatures and supplementary feeding on the hibernation timing of the European hedgehog (*Erinaceus europaeus*))

Thesis course: Thesis and Internships Wildlife Ecology and Conservation, WEC80436

Supervisor: Dr. ir. Anouschka R. Hof, Wildlife Ecology and Conservation chair group

Second examiner: Dr. Fred de Boer, Wildlife Ecology and Conservation chair group

Date of publication: 4th of March 2025

Acknowledgements

Many thanks to the 90 people involved in the camera trap project that was part of this study.

In addition, I want to thank Avolare, De Fugelhelling, Egelopvang Midden Nederland, Egelopvang Papendrecht, Egelopvang Stein, Egelopvang Haarlem, Wildopvang De Bonte Piet, Wildopvang Krommenie, Zorg voor Egels, which are the 9 wildlife sanctuaries in the Netherlands that provided data for this study.

And special thanks to dr. ir. Anouschka Hof who supervised this thesis and Nina Baradel, both of whom helped with the distribution of the camera traps.

Table of contents

Summary

Species' ranges and phenologies are changing due to environmental changes. Hibernation is a life strategy that is particularly linked to temperature, and for the European hedgehog (*Erinaceus europaeus*), a species that is in decline throughout most of its range, it remains unknown how and if rising temperatures influence the timing of hibernation. Furthermore, the provision of supplementary food to hedgehogs is gaining in popularity. It is not clear either how and if these practices affect hibernation patterns._ More knowledge on these aspects can provide insights for effective conservation of the hedgehog. The aim of this study was to determine how and if hibernation timing of hedgehogs has changed over the last 20 years, and to determine how and if supplementary feeding affects the timing of the onset of hibernation. Citizen science observation data throughout Europe and data from wildlife sanctuaries in the Netherlands were used to identify trends over the past 20 years in hibernation patterns. Temperature data over these years were used to determine the effect that temperature has on the timing of hibernation. Furthermore, camera traps were used to investigate the possible effect of supplementary feeding on the start date of hibernation. Based on observation data from Europe and data from the wildlife sanctuaries in the Netherlands, hibernation of hedgehogs started significantly later and ended significantly earlier over the last years. These trends were however not present in all data, and no correlation between the duration of hibernation and temperature was found. Supplementary feeding did not have an effect on the timing of the start of hibernation, but this is most likely due to limitations of the camera trap setup and the small amount of data. There are strong indications that hedgehog hibernation has been starting later and ending earlier over the years. These findings contribute to the understanding of hibernation patterns of European hedgehogs and add to the knowledge about hibernation in general, providing insights into future conservation of hedgehogs and changing hibernation patterns in other mammals.

Introduction

Climate change is affecting many species now already and effects are expected to increase (Bellard et al., 2012). Some species are for instance affected in their phenology by shifting their ranges in response to rising temperatures (Hewitt, 2004; Parmesan et al., 1999; Rubenstein et al., 2023), and by the occurrence of mismatches with the environment, when animals do not change their phenology in synchrony with their food source (Humphries et al., 2002; Møller et al., 2008; Renner & Zohner, 2018). For yet other species, we simply lack knowledge. It is further not known for many species if a lack of synchrony with species they depend on will occur. Lack of such knowledge hampers effective species conservation as well as limiting studies that investigate potential mitigating factors.

An important aspect of the phenology of species that may be affected by climate change is hibernation or diapause (Bellard et al., 2012). Hibernation or diapause (henceforth referred to as hibernation) is a strategy to deal with limited resources during the winter, is particularly connected to temperature, and present in about half of all mammalian orders (Turbill et al., 2011). It may thus be strongly affected by climate change (Findlay-Robinson et al., 2023). Effects of higher temperatures on hibernation (or torpor) have already been found in black bears (*Ursus americanus*), brown bears (*Ursus arctos*), several rodent and bat species (Wells et al., 2022), yellow-bellied marmots (*Marmota flaviventer*)(Cordes et al., 2020), arctic ground squirrels (*Urocitellus parryii*)(Chmura et al., 2023), and the frog species *Pelophylax nigromaculatus* (Gao et al., 2015). These effects include later start of hibernation in autumn, earlier end in spring, and an overall shorter duration. In the case of the frogs, hibernation timing was not affected by food availability, implying that a mismatch with the natural food source would occur when the frogs hibernate shorter in reaction to higher temperatures and their prey does not (Gao et al., 2015). Furthermore, with climate change, warm spells during which hibernating animals may temporarily awaken are expected to occur more frequently (Van Dorland et al., 2024). This may have large negative consequences, as it requires energy to wake up and food resources are low during these periods (Reeve, 1994).

Factors that may alter the effects of climate change on hibernation include supplementary feeding. Supplementary food can provide a food source during the period when a mismatch with the natural food source is occurring (Oja et al., 2014). Such a conservation strategy can be a relevant mitigation to potential negative effects of climate change, especially for species that live close to, or even within, human settlements where supplementary food is frequently provided (Gimmel et al., 2021). However, supplementary feeding could also delay the start of hibernation or cause the species to not hibernate at all by causing increased activity in the period prior to hibernation (Gazzard & Baker, 2020). Disruption of natural winter activity due to supplementary feeding has been found in brown bears (Bogdanović et al., 2024; Bojarska et al., 2019), migratory birds (Plummer et al., 2015), and eastern chipmunks (*Tamias striatus*, Humphries et al., 2003). The effect of the disruption of natural winter activity on survival or breeding success is yet unknown. Kirby et al. (2019) found that by causing a shortening of hibernation, supplementary feeding increased cellular aging in black bears (*Ursus americanus*). As per the optimal hibernation theory of Boyles et al. (2020), the energetic costs of hibernators decrease when ambient temperatures decrease until a minimum temperature, below which the energetic costs rise due to measures that prevent freezing. With rising ambient temperatures, maintaining hibernation costs more energy. This could suggest that additional energy in the form of supplementary food is needed to maintain hibernation under warmer climatic conditions at which it is still too cold to not hibernate at all and/or natural food is not available.

One hibernating species that may be affected by climate change is the European hedgehog (*Erinaceus europaeus*), a near threatened species (Gazzard & Rasmussen, 2023), hereafter referred to as hedgehog. And while this species is the most well studied among the other hedgehog species (Erinaceinae)(Gazzard et al., 2025), the timing of the hibernation of the European hedgehog has not yet been studied in the context of climate change. Hedgehog hibernation timing is dependent on latitude and shows a gradient throughout its distribution (Reeve, 1994). In Denmark, hedgehogs hibernate between late October/November and mid-April/mid-May (Rasmussen et al., 2019), while in Spain they do not hibernate at all (Marco-Tresserras & López-Iborra, 2022). Hedgehogs kept at a stable warm temperature, with food provided, do not start hibernation (Dimelow, 1963). This implies that temperature and food availability are the most important cues for starting hibernation. The effects

that rising temperatures have on the hibernation of hedgehogs are still unknown. However, an analysis of hedgehog hibernation surveys in the United Kingdom found no difference in hibernation timing between 1966 and 2012 (British Hedgehog Preservation Society, 2015), but the methods used to obtain and analyse data on hibernation timing are not specified in their report.
Starvation during hibernation is one of three large threats to hedgehogs, traffic deaths (Huijser & Bergers, 2000), and predation (mostly by the European badger (*Meles meles*))(Hof et al., 2019; Williams et al., 2018) being the other two. Up to 75% of young hedgehogs may die during hibernation because of starvation (*De Egel - Egelbescherming Nederland*, n.d.). Individuals that weigh below 600 grams are especially at risk (Bearman-Brown et al., 2020) and hedgehogs below 400 grams are not expected to survive hibernation at all (Cherel et al. 1995). An important fact related to this starvation is that hedgehogs do not build a food storage, which means that when they wake up intermittently or emerge too early, there may not be food available (Reeve, 1994). As starvation during hibernation forms a large threat and supplementary feeding of hedgehogs is increasing in popularity (Gazzard & Baker, 2020), obtaining a better understanding of how ongoing climate change and supplementary feeding may affect hibernation patterns, can inform conservation efforts.

As hedgehogs show a gradient of hibernation length with latitude (Reeve, 1994), an effect of rising temperatures on hibernation patterns, similar to found for other species, is to be expected. Hedgehogs hibernate on average when the minimum temperature drops below 8°C (Bexton, 2016). Persistent cold is the main factor in maintaining hibernation (Reeve, 1994), which highlights the importance of the before mentioned increasingly occurring warm spells. If the temperatures in autumn and winter rise due to climate change, this temperature will be reached later and consequently the hedgehogs are expected to start hibernation later. Rasmussen et al. (2019) already found that during a relatively warm autumn in Denmark, the hibernation was delayed by a month. Hilgers (2024) found that in the United Kingdom, the hedgehog hibernation start was delayed, the end advanced, and the overall duration shorter over the past two decades, all correlated with temperature variables. When higher temperatures cause young hedgehogs to emerge in the middle of winter, they may starve as they tend to be below 600 grams (Bearman-Brown et al., 2020). And when the higher temperatures cause hedgehogs to hibernate shorter, there is a longer time of exposure to roads and to predators (badgers, the main predator throughout large parts of its range, do not hibernate (Slamka, 2016)). Therefore, rising temperature due to climate change may have great negative consequences for hedgehog populations throughout Europe through its effect on hibernation patterns.
Hedgehogs are increasingly found in urban areas (Gazzard et al., 2025; Hof et al., 2012; Poel et al., 2015), where garden owners may feed them. The availability of supplementary feeding may affect hibernation patterns. First; supplementary feeding provided by people with hedgehogs in their gardens during winter could prevent starvation of young hedgehogs that temporarily emerge from hibernation. In that way, supplementary feeding may alleviate possible negative effects of rising temperatures. Second; it could also delay the start of hibernation or cause the hedgehogs to not hibernate at all by causing increased activity in the period prior to hibernation (Gazzard & Baker, 2020). For hibernation in general, the only relation that is well studied is with energy costs (Boyles et al., 2020). There is still little known regarding the effect that supplementary feeding has on the hibernation of hedgehogs. With a declining hedgehog population (*Egeltelling 2023 - Egelbescherming Nederland*, n.d.) and increasing attention from the public (that feeds hedgehogs) it is important to know the effect of supplementary feeding.

Research objectives, questions and hypotheses

The aim of this research was to get more insight into the effects of rising temperatures and supplementary feeding, on the hibernation patterns of hedgehogs. Such information would aid in designing effective conservation strategies for this near threatened species. The two main research questions were:

1. How have rising mean temperatures affected the start, end, and duration of the hibernation of hedgehogs throughout its range over the past decades?
2. How does supplementary feeding affect the onset of the hibernation of hedgehogs?

These research questions were answered using various sources of information. Data from the Global Biodiversity Information Facility (GBIF.org, 2024a) were used to detect possible trends in hibernation patterns throughout its range (Europe, excluding Eastern Europe and Southeastern Europe). In addition, data from wildlife sanctuaries in the Netherlands were used to detect possible trends. Furthermore, camera traps were used to research the effect of supplementary feeding on the start date of hibernation. Camera traps were placed in private gardens throughout the Netherlands, either with or without supplementary feeding.
It was hypothesised that with increasing temperatures over the past decades, the start had been delayed, the end had been advanced, and the total duration had become shorter. In addition, a spatial relationship with later onset, earlier end, and shorter duration of hibernation in warmer regions was expected (Reeve, 1994). In relation to climate change it was therefore predicted that there is a trend over several years of delayed start, advanced end, and declining hibernation duration (Figure 1). Supplementary feeding is expected to cause a later start due to an increased food supply and subsequent increased activity (Figure 2, (Gazzard & Baker, 2020). It is therefore predicted that hedgehogs in gardens with supplementary food start their hibernation later.

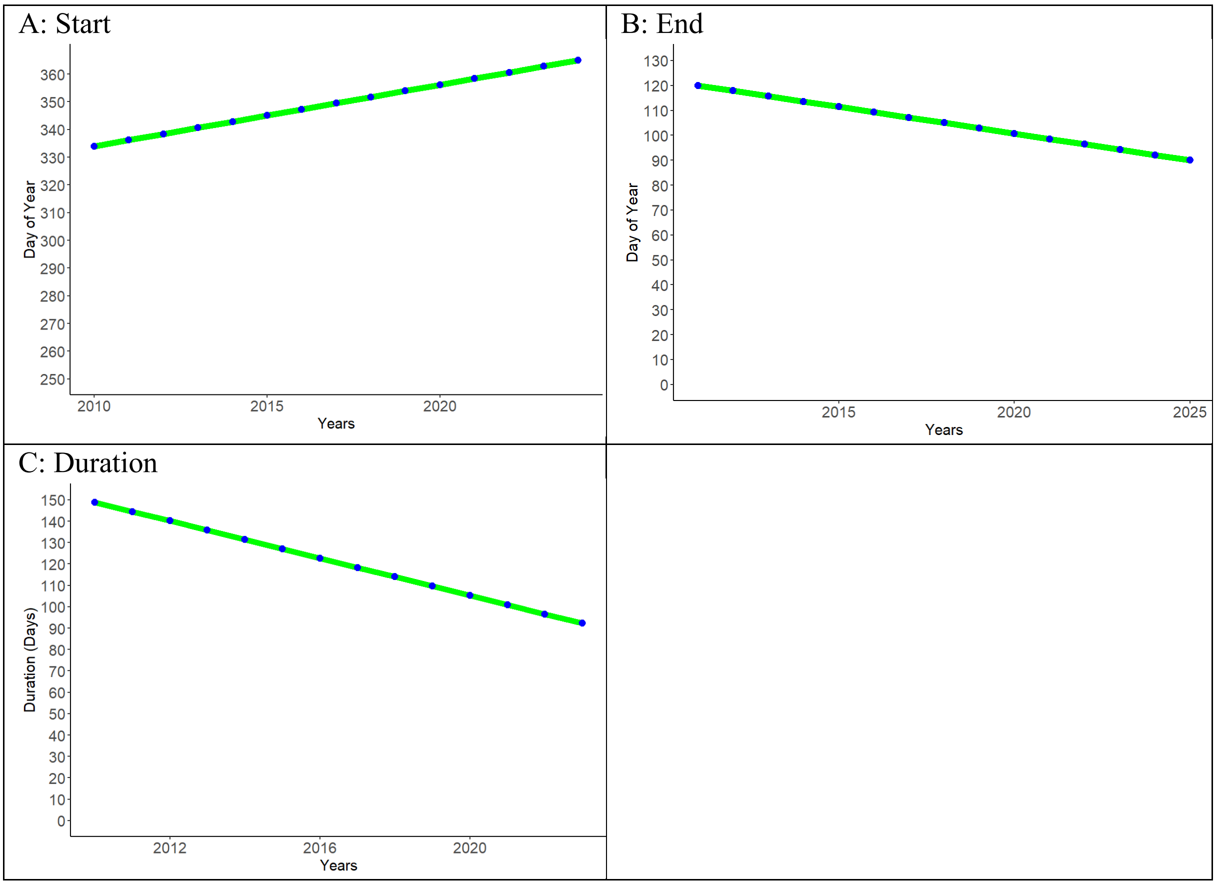


Figure 1: A: Hypothesised increase in start day of hibernation. B: Hypothesised decrease in end day of hibernation. C: Hypothesised decrease in duration of hibernation in days. All the plots have days on the y-axis and years on the x-axis.

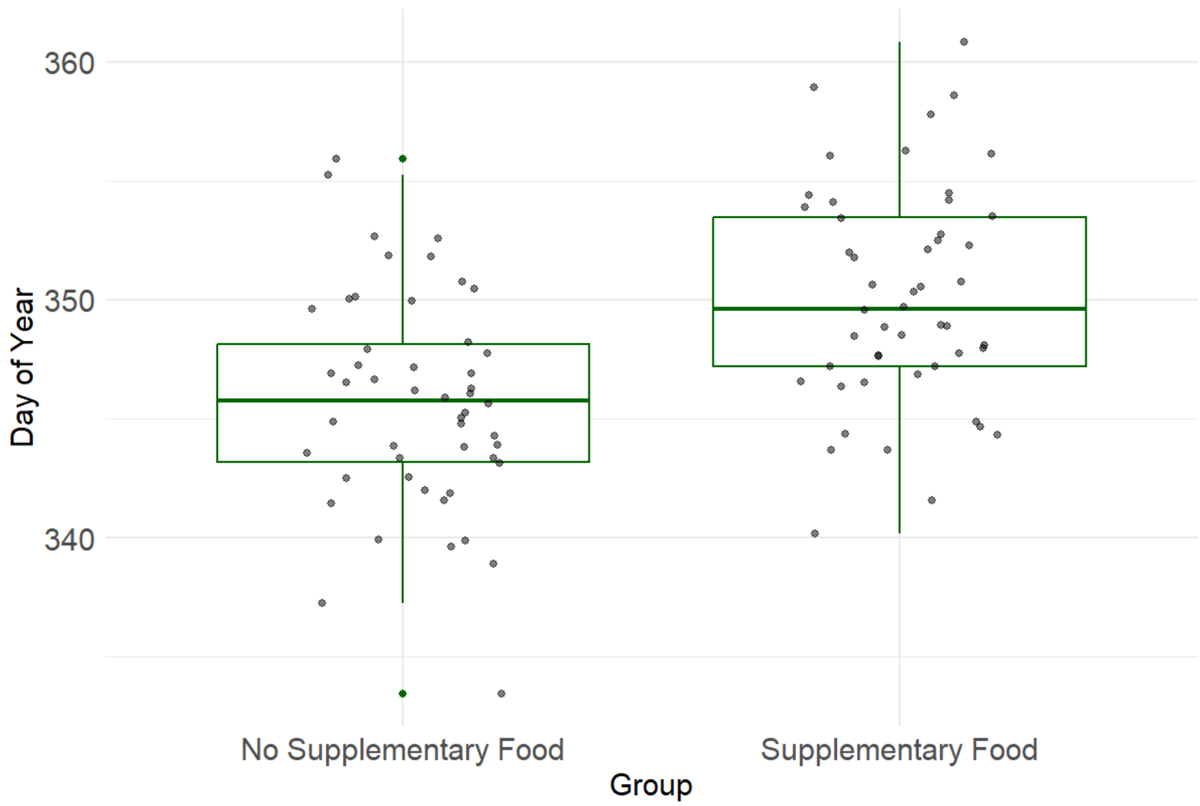


Figure 2: Hypothetical graph showing a difference between gardens where no supplementary food is provided versus gardens where it is provided. It is hypothesised that hedgehogs start their hibernation later when supplementary food is available. On the x-axis are the two groups, on the y-axis is day of year corresponding to around mid-December.

Methods

Hibernation patterns in relation to temporal and spatial differences in temperature

Patterns on European and country scale

Hedgehog observation data were used to assess the effect of temperature on the start, end, and duration of hibernation, through time. In addition, these observation data were used to test for potential differences in space in the start, end, and duration of hibernation. Citizen science observation data for the entire native range of the European hedgehog were obtained from the Global Biodiversity Information Facility (GBIF.org, 2024, Figure 3). The years 1980, 1983, 1993, 1996-1998, 2000, and 2003-2024 did have enough observations for analysis. A year for which a start date or end date could be calculated using the methods explained in the following sections is here regarded as a year with enough observations. Observations outside its native range were disregarded. As the majority (60%) of the available data originated from the United Kingdom and the Netherlands, data from these two countries were also analysed separately (GBIF.org, 2024b; GBIF.org, 2024c; GBIF.org, 2024d).

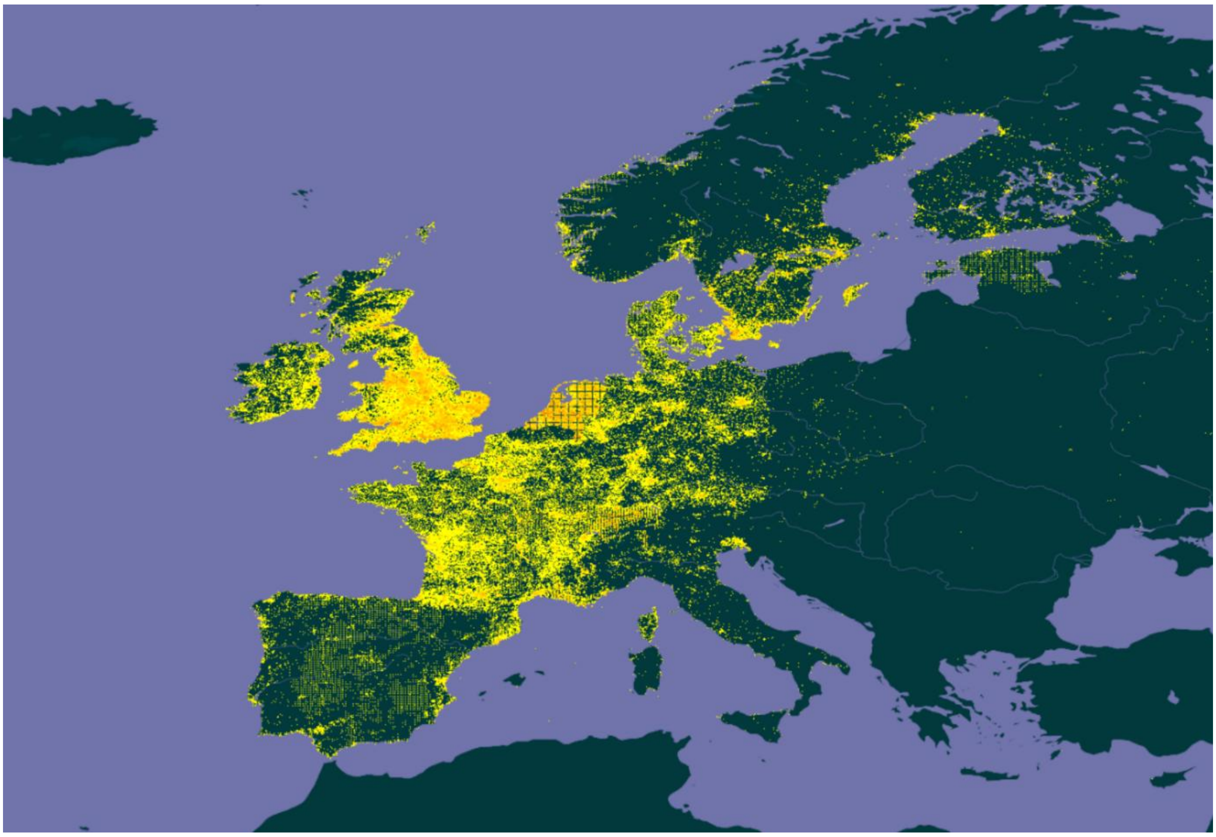


Figure 3: European hedgehog observations in Europe. Data from GBIF.org.

It is known that citizen science data are biased (Kosmala et al., 2016). These biases consist for example of a higher probability of observations during weekends and holidays, but also of misidentification of species. Despite these biases it can still be useful and has often been used in conservation science (Dickinson et al., 2010; McKinley et al., 2017). Regarding the hedgehog dataset, misidentifications are not very likely, as the hedgehog is quite unmistakable. The bias is particularly related to differences in observer effort over the years. In the last two decades the amount of hedgehog observations has drastically increased from 1700 observations in 2000 to 94000 observations in 2024 in its whole range. These biases were corrected using an effort-adjusted threshold method. The bias in observation effort was adjusted by defining hibernation onset as the time when sightings dropped below a set threshold of the maximum daily level per year.

Analysis

The start of hibernation was defined as the first day of a sequence of days on which the number of hedgehog observations was below a threshold percentage of the maximum daily number per year. A threshold was chosen because the intakes never drop to 0 during hibernation as hedgehogs often wake up intermittently. For the these data a threshold of 10% and a sequence of seven days was used. The crossing of this threshold coincided best with the reported start of hibernation during the period from the end of November till the end of December, roughly in the middle of its range (The Netherlands)((*De Egel - Egelbescherming Nederland*, n.d.) and with the stabilisation of the number of observations in the obtained data (Figure 4). Multiple threshold values were tested, and 10% reflected the current knowledge about the hibernation best. The end of hibernation was defined as the last day of the last sequence of seven days on which the number of hedgehog observations was below 10% of the maximum number per year. With a larger sequence, the possibility of a lack of observations due to chance and citizen science bias is lower, but not all years had enough data for this. Therefore, choosing a sequence length was a compromise between a large enough sequence that can more accurately show the hibernation patterns, and a small enough sequence that includes all years.

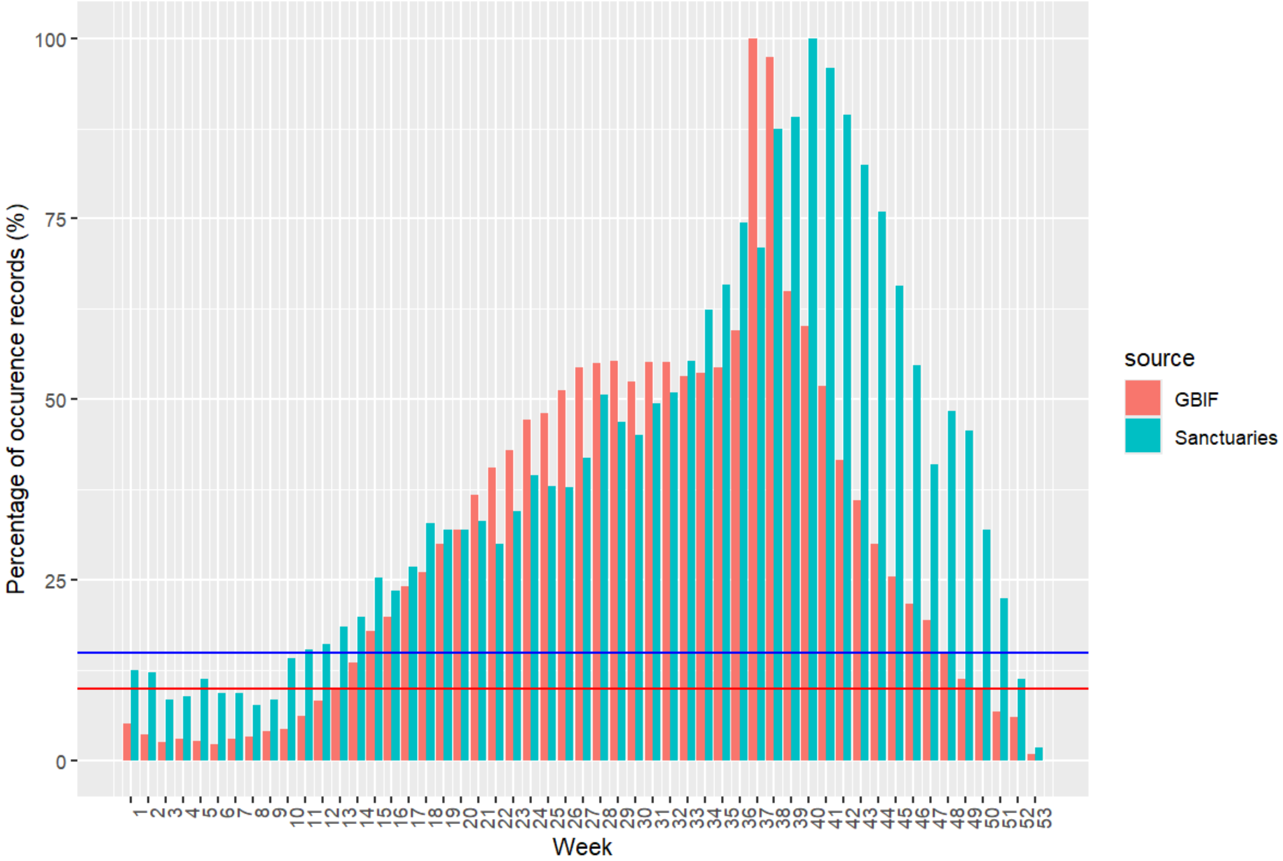


Figure 4: Percentage of hedgehog observations or take ins, based on the maximum number per week. Data from observations from GBIF in red and data from sanctuaries in blue. On the y-axis is the relative number of observations, standardized on the week with the most observations. On the x-axis are week numbers with week 53 also included even though this week is not present in all years. The blue line represents a 15% threshold for the sanctuary data, the red line represents a 10% threshold for the GBIF data. The data from GBIF is from 1953 till 2024, and the data from the sanctuaries is from 2015 till 2024. The maximum number of hedgehogs in one week was 978 for the sanctuary data and 7040 for the GBIF data.

For analysis of the temperature at which hedgehogs started and ended their hibernation, data from the European Centre for Medium-range Weather Forecasts Reanalysis v5 (ERA5) were used (Bell et al., 2021). To test for correlations in start date, end date, and duration of hibernation with mean temperature during the hibernation period, the mean temperature during the months October till April was used. This was done to test whether the mean temperature during the hibernation period has an effect on its start, end, and length. For analysis of the Europe data, due to logistic constraints, the mean minimum temperature at two meters above ground over the whole period for the whole range was used to correlate with the start and end dates and duration. For the Netherlands specifically, each observation was assigned a temperature based on its location, date, and time of day. For this, hourly temperature at two meters above ground was obtained from ERA5 for all months, excluding February, June, and July (due to logistic constraints). The temperatures on the start and end dates were calculated as the mean temperature of all the observations on the corresponding day. Dates were converted to day of year for the analysis. All data were tested for normality. Pearson correlation tests were used when the data were normally distributed, and otherwise in the case of trends Mann-Kendall trend tests were used and in the case of correlations, Spearman rank correlation tests were used.
To test whether a spatial gradient in hibernation timing due to differences in temperature is present within the whole range of the European hedgehog, the data were divided into four latitudinal regions: south, central south, central north, and north. This was also done for specifically the United Kingdom and the Netherlands, to test whether a gradient is present within these countries. A one-way ANOVA

was used to test for differences between these four groups. These data were analysed using RStudio (R Core Team, 2024).

Patterns in wildlife sanctuary hedgehog take-ins
Dates at which hedgehogs were admitted to wildlife sanctuaries from 2016 till 2024 were obtained by emailing and calling all wildlife sanctuaries in the Netherlands that take care of hedgehogs. In total there are 25, and 9 of them provided their data (Figure 5, Appendix 1).

Analysis
Since hedgehogs that are admitted to wildlife sanctuaries are generally sick or admitted, there is a certain degree of bias in the data that had to be dealt with. The data were therefore similarly analysed as the observation data, using an effort-adjusted threshold method in R in RStudio (R Core Team, 2024). As the individual contribution per sanctuary to the total dataset ranged from 1.8% to 26.5%, the data of all 9 centres were pooled together, assuming similar trends over the years in each sanctuary.
Based on sensitivity analysis, a threshold of 15% and a sequence of five days coincided best with the known start of hibernation (end of December), in the Netherlands (De Egel - Egelbescherming Nederland, n.d., Figure 4).
Data from the meteorological institute of the Netherlands (Koninklijk Nederlands Meteorologisch Instituut, hereafter named KNMI) were used to obtain minimum temperature data for each date a hedgehog was taken in (*KNMI - Daggegevens van Het Weer in Nederland*, n.d.). This temperature was taken for each wildlife centre from the nearest meteorological station, so that based on the date and the sanctuary, each observation was assigned a temperature. The mean minimum temperatures on the start and end dates were calculated by averaging the (minimum) temperatures of the corresponding day of all 9 sanctuaries combined, as the individual data contributions were too small to analyse separately. To test for correlations of hibernation timing with the average temperature during the hibernation period, the mean temperature during the months October till April was used, calculated using the before mentioned temperatures. The dates in the data were converted to day of year and correlation tests were done. All data were tested for normality. When normal distributed, a Pearson correlation test was performed. When not normal distributed, non-parametric Mann-Kendall trend tests were used for trends, and Spearman rank correlations tests were used for correlations.

Figure 5: Locations within the Netherlands of the 9 sanctuaries that provided data for this research.

Camera trap data

Camera trap data were used to assess the effect of supplementary feeding on the start of hibernation. Camera traps were installed in private gardens with known hedgehog presence throughout the Netherlands, ranging from small city centre gardens to multiple hectare size rural gardens. Suitable gardens were identified using private networks, social media requests, and email lists of two chair groups of the university. Suitable gardens were defined as secure gardens (no communal gardens or parks) with access for hedgehogs and in which hedgehogs were observed in the past. Most gardens were in low traffic neighbourhoods or allotment garden parks, with a few exceptions. The type of camera traps used in this study are of the type Reconyx Hyperfire 2. The cameras were pointed toward locations with a large probability of hedgehogs being detected. These locations included feeding houses, sleeping places, garden access points (holes or gates), or they were placed so that they had a wide view of the garden. The height at which the camera was placed ranged from 0 cm when no tree or pole was available, to 20 cm above ground. In total, 53 cameras were distributed over a large part of the Netherlands (Figure 6). The cameras were installed between 7-10-2024 and 10-11-2024. The cameras stayed in place till the beginning of January 2025. In addition nine people that had their own cameras provided data (Figure 6). Supplementary food (cat food from various brands) for hedgehogs was provided in 29 out of the 62 gardens. In addition, all garden owners noted down their garden characteristics in a form (Appendix II). These garden characteristics included for example the surface area, degree of urbanization, amount of trees, and the presence of pets, feeding stations, and nearby parks.

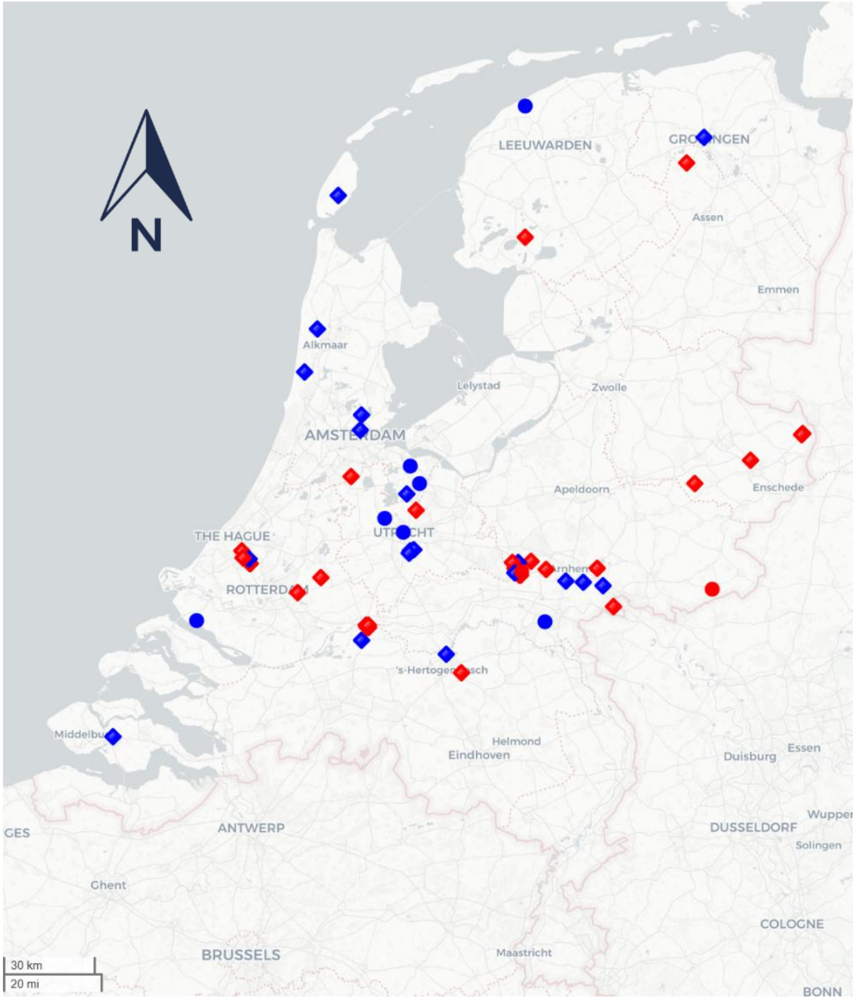


Figure 6: Camera trap distribution in the Netherlands. In green are the gardens where supplementary food was provided, in red the gardens where this was not provided. Diamonds are borrowed WUR cameras, circles are privately owned cameras.

The camera traps were set to take three pictures with one second in between when motion was detected. In addition they were set to night mode, only taking pictures between sunset and sunrise. This was done to save storage and battery life during the study period. All pictures from the cameras were stored in Agouti (Agouti.eu). Pictures were analysed per camera to find the last picture of a hedgehog. This last picture was accepted as the last observation before hibernation if it was at least the tenth night a hedgehog was observed on camera within a month and if there were at least seven days after it with no hedgehog present. This was rather arbitrarily chosen, in practice most hedgehogs either visited a garden on a daily basis, or only once or twice during the whole study period (or no visits at all). The camera trap data were analysed using a linear model, in R (R Core Team, 2024). All assumptions were met. In this model the date at which a hedgehog was seen last on camera was used as response variable. The binary variable 'supplementary food provision' was the explanatory variable. In addition, four variables were controlled for: temperature, degree of urbanisation, garden surface area, and the presence of nearby parks. The temperature variable was the temperature recorded by the camera itself during the last picture, or taken from the nearest KNMI weather station in the case of privately owned cameras. Degree of urbanisation was either Urban, Urban edge, or Rural. Garden surface area was in square meters and presence of nearby parks was binary. Degree of urbanisation, garden surface, and presence of nearby parks were submitted by the garden owners using the garden characteristics form (Appendix II).

Results

Hibernation patterns in relation to temporal and spatial differences in temperature

European scale patterns

First the results on the scale of the entire European hedgehog range are presented. In total there were 696,528 hedgehog observations throughout Europe, after cleaning the data. An increase in the start date of hibernation, and a decrease in end date, was found in the period 1980-2024 (Mann-Kendall trend test, Start: n = 29, S = 144.00, p = 0.007, End: n = 24, S = -88.00, p = 0.03, Figure 7A, B). There was no significant change in duration of hibernation over time (Mann-Kendall trend test: n = 21, S = -64.00, p = 0.06). Analysis of all data, excluding the United Kingdom (44% of the total data), resulted in no significant trends in the start and end dates (Start: Mann-Kendall trend test: n = 16, S = -38.00, p = 0.10; End: Pearson correlation: $r(16) = 0.13$, p = 0.62). Furthermore, no correlations between mean minimum temperature during the hibernation period and the start date, end date, and duration were found (Start: Spearman correlation: $r(28) = -0.07$, p = 0.76; End: Spearman correlation: $r(23) = 0.02$, p = 0.93; Duration: Spearman correlation: $r(20) = -0.21$, p = 0.36). In addition, a difference between the north and south was found in the start date, with the start date being significantly earlier in the north than in the south (Tukey's HSD test: p = 0.001, 95% C.I. [-60.8, -12.0], Figure 8). There was not enough data to test for a difference in end date or duration between the north and south.

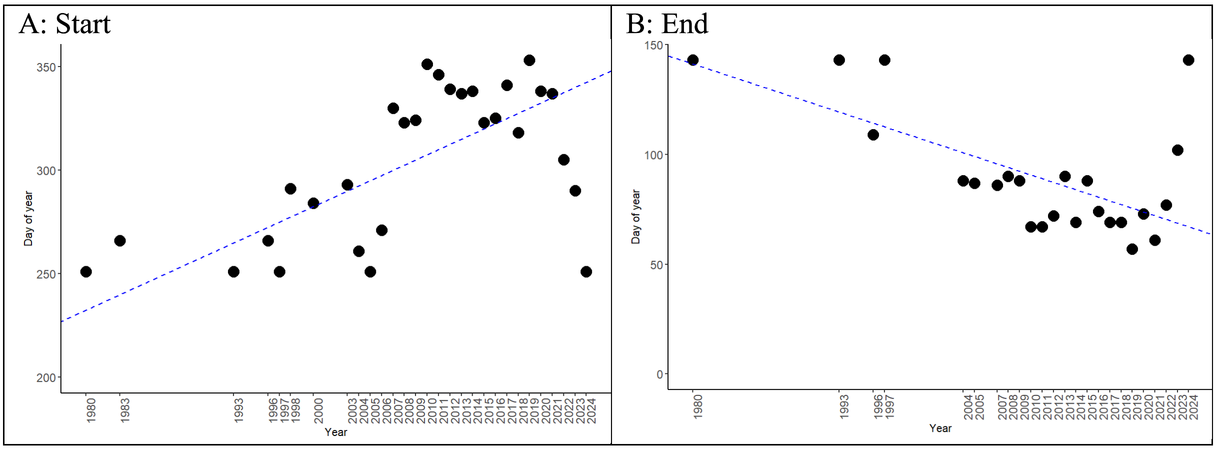


Figure 7: Trends in observation data from Europe. A: Significant delay in the start of hibernation. On the y-axis is the start date, given in day of year. On the x-axis is the year in which the measured hibernation started. B: Significant advance in the end of hibernation. On the y-axis is the end date in day of year. On the x-axis is the year in which the measured hibernation ended.

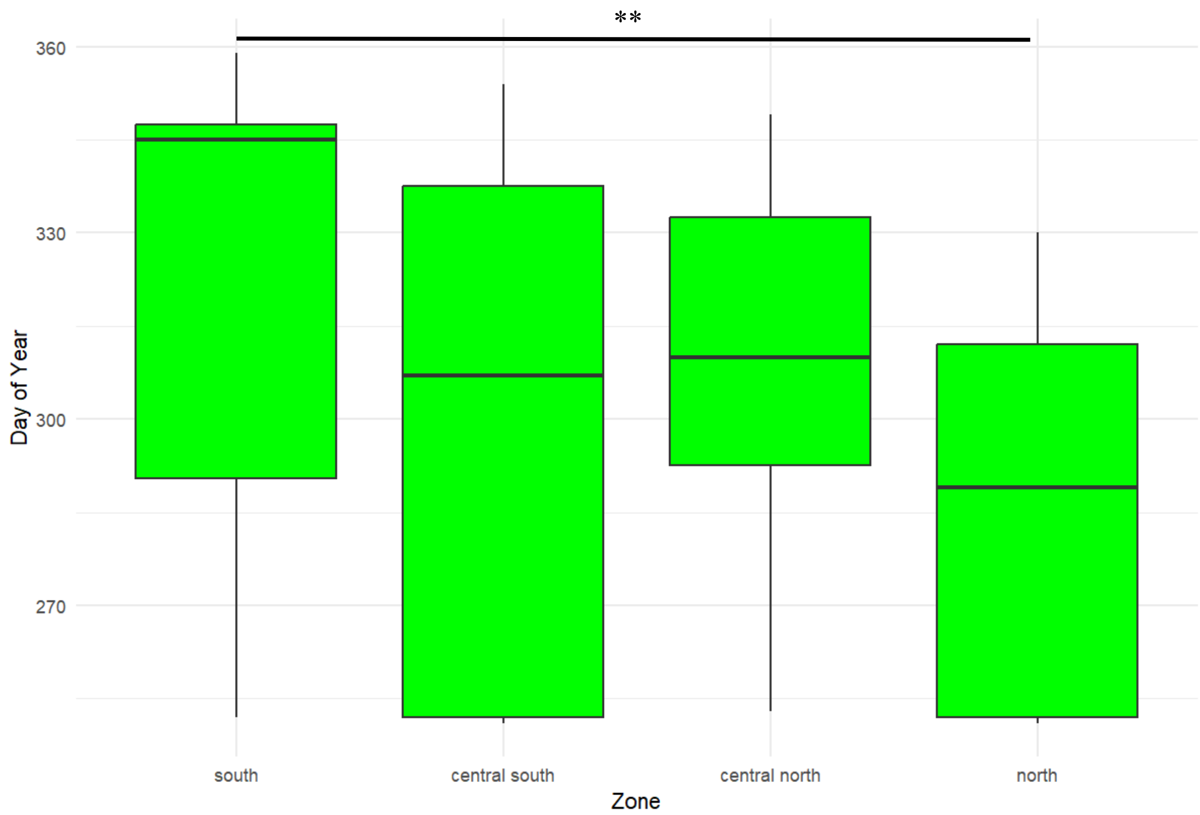
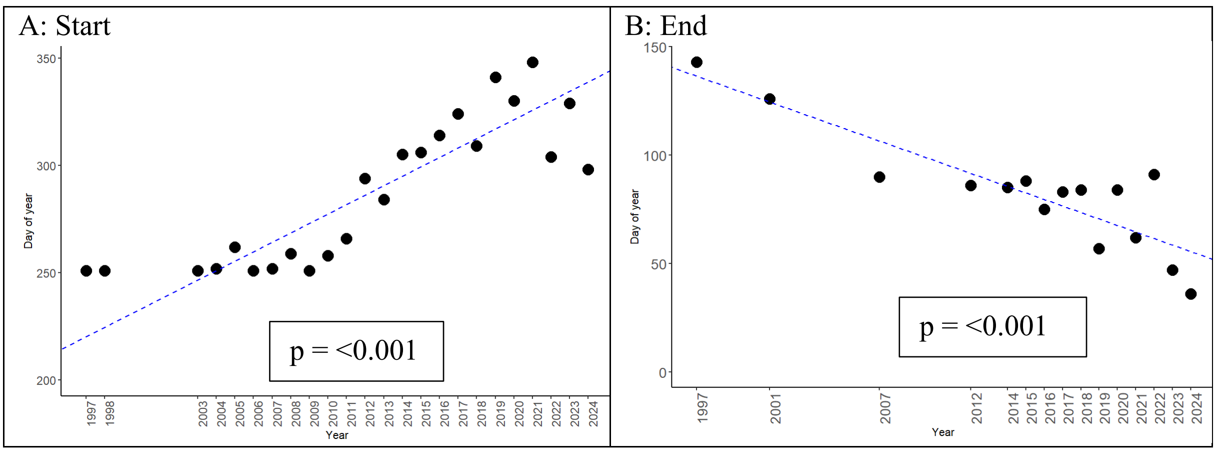


Figure 8: The start date (in day of year) of hibernation of four equal zones based on latitude in Europe. North and south differ significantly (p = 0.001), whereas the other differences are not significant.

Country scale patterns

United Kingdom

Focusing on the country level, first the results from the United Kingdom are presented. In total there were 308,779 hedgehog observations in the United Kingdom, for the years 1997 onwards. An increasing trend in the start date of hibernation, was found over the period 1997-2024 (Mann-Kendall trend test: n = 24, S = 195.00, p = <0.001, Figure 9A). For both the end date of hibernation and the overall duration, a decreasing trend was found over time (End date: Pearson correlation: $r(22) = 0.86$, p = <0.001, Duration: Mann-Kendall trend test: n = 13, S = -69.00, p = <0.001, Figure 9B, C). No north to south gradient was found in the start date (F(3) = 0.55, p = 0.65). Furthermore, there was too little data to test for a gradient in the end date and the duration.



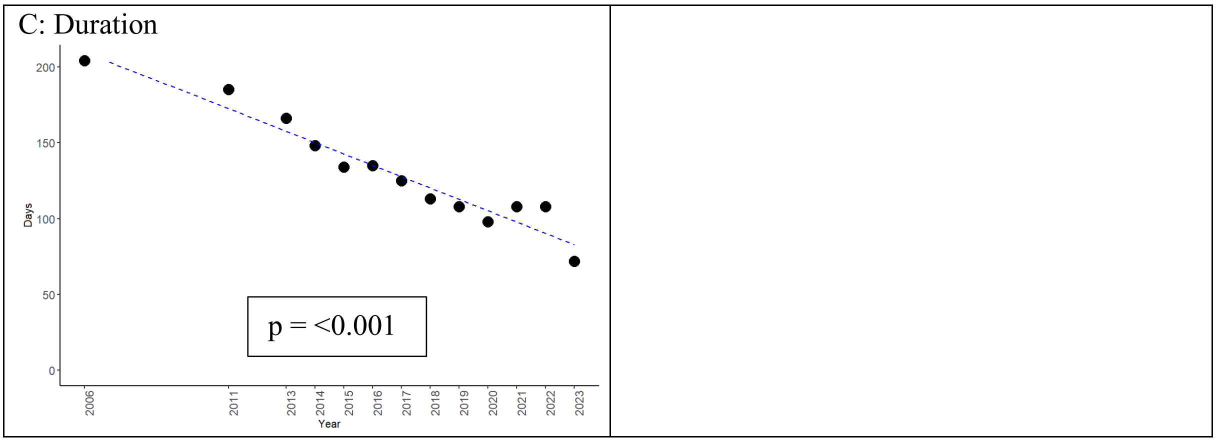


Figure 9: Data from the United Kingdom. A: Increase in start of hibernation. On the y-axis is the start date, given in day of year. On the y-axis is the year in which the measured hibernation started. B: Decrease in end of hibernation. On the y-axis is the end date, given in day of year. On the y-axis is the year in which the measured hibernation ended. C: Decrease in the duration of hibernation. On the y-axis is the duration in days. On the x-axis is the year in which the measured hibernation started.

Netherlands

And last, here the results from the Netherlands on the country level are presented. In total there were 114,234 hedgehog observations over the years 2006-2024. The mean temperatures at the start and end date were 7.64 ± 2.37 °C and 7.77 ± 1.35 °C, respectively. No trends over the period 2006-2024 were found in the start and end dates of hibernation (Start: Pearson correlation: $r(9) = 0.001$, $p = 0.99$, End: $r(14) = 0.45$, $p = 0.08$). Furthermore, no trend was found in the duration of hibernation over this same period (Pearson correlation: $r(7) = 0.15$, $p = 0.70$). Regarding temperature, no significant correlations of minimum temperature with the start and end date were found (Start: Pearson correlation: $r(9) = -0.36$, $p = 0.27$, End: Mann-Kendall trend test: n = 14, S = 25.00, $p = 0.19$), and no correlations of mean temperature during the hibernation period with the start date, end date, and duration of hibernation (October till April) were found (Start: Pearson correlation: $r(11) = -0.15$, $p = 0.63$; End: Pearson correlation: $r(14) = 0.26$, $p = 0.33$; Duration: Pearson correlation: $r(7) = -0.07$, $p = 0.86$). In addition, no gradient within the Netherlands from the north to the south was found in the start of hibernation ($F(3, 29) = 0.252$, $p = 0.86$), and there was too little data to test for spatial gradients in the end date and the duration.

Patterns based on wildlife sanctuary hedgehog take-ins

Similar to the observation data, but from a different source, in this section the results from the wildlife sanctuaries in the Netherlands are shown. In total there were 20,690 hedgehogs taken in care over the years 2016-2024 by the nine sanctuaries included in this study.

An increasing trend in the start date of hibernation was found over the years 2016-2023 (Mann-Kendall trend test: n = 7, S = 17.00, $p = 0.02$, Figure 10A). Furthermore, decreasing trends in end date and duration of hibernation over the same period were found (End date: Pearson correlation: $r(7) = -0.79$, $p = 0.01$, Duration: $r(5) = -0.95$, $p < 0.001$, Figure 10B, C). The temperature at the start date of hibernation showed no correlation with year (Pearson correlation: $r(5) = -0.07$, $p = 0.88$). The mean temperature on the start day of hibernation was 4.88 ± 3.55 °C. In contrast, a slightly significant decreasing trend in the mean minimum temperature of the end date was found over the period 2016-2024 (Pearson correlation: $r(7) = -0.70$, $p = 0.04$). In addition, a correlation between the start date and mean temperature during the hibernation period was found, but no correlations were found in the end date and duration of hibernation with the mean temperature during hibernation (Start: Spearman correlation: $r(5) = 0.86$, $p = 0.024$); End: Pearson correlation: $r(7) = -0.35$, $p = 0.36$; Duration: Pearson correlation: $r(5) = -0.24$, $p = 0.61$).

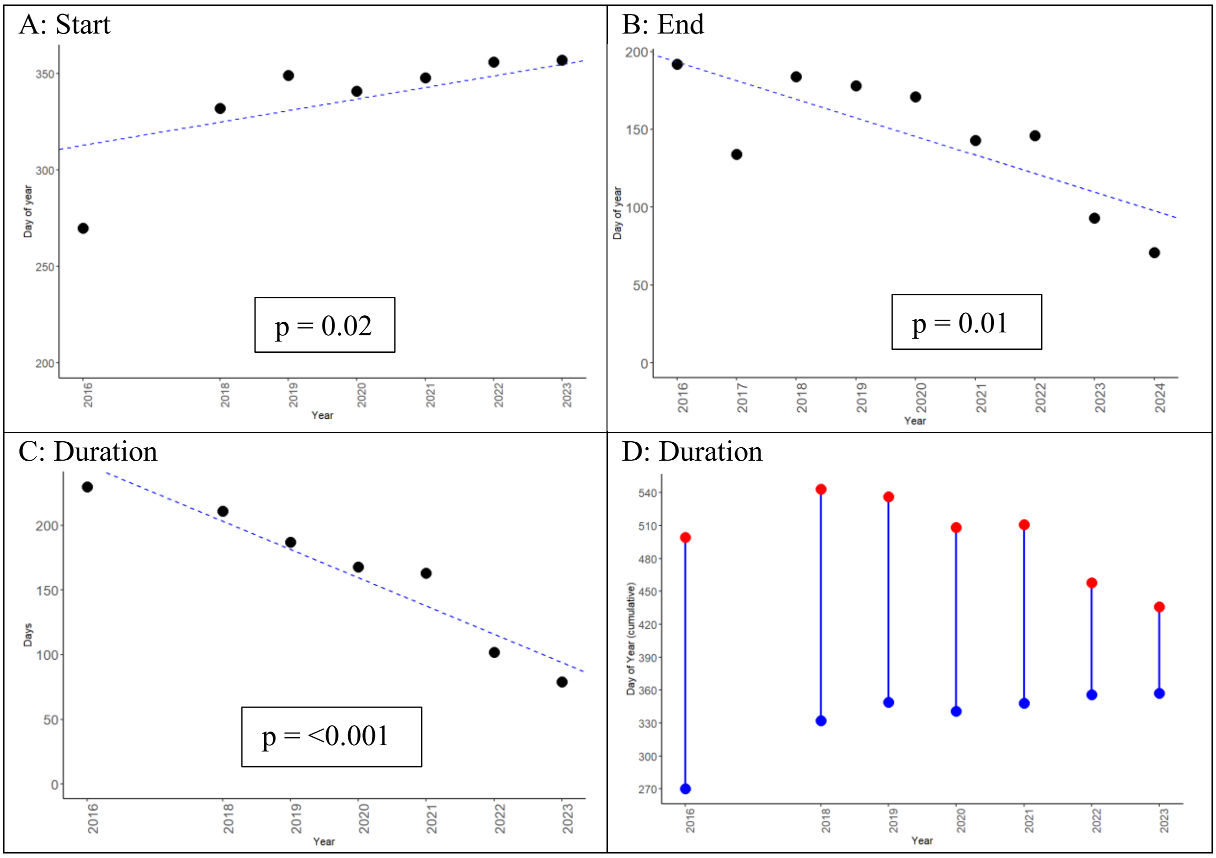


Figure 10: Trends in Sanctuary data. A: Start of the hibernation, showing an increase over time. On the y-axis is the start day of the hibernation, given in day of year. On the x-axis is the year in which the measured hibernation started. B: End of hibernation, showing a decrease over time. On the y-axis is the end day, given in day of year. On the x-axis is the year in which the measured hibernation ended. C: Duration of hibernation, showing a decrease over time. On the y-axis is the duration in days. On the x-axis is the year in which the measured hibernation started. D: Duration visualised as lines between the start date (blue dots) and the end date (red dots, with numbers exceeding 365, counting on from the year of the start).

Camera trap data

Regarding the effect of supplementary feeding on the timing of the start of hibernation in the Netherlands, here are the results from the camera traps presented. In total 28 gardens of the 62 had enough hedgehog activity to be useful for analysis, of which supplementary food was provided in 19 gardens. Analysis was done on the garden level, instead of on individual hedgehogs, as hedgehogs could not be individually identified with certainty.

The mean temperature at the moment of the last observation for all gardens together was 4.43 ± 2.91 °C, and the mean date at which the hedgehogs were last seen on camera was the 2nd of December (day 336 of 2024) ± 22.0 days. No difference in start date between the two supplementary food groups was found ($F(1) = 2.85$, $p = 0.11$, Figure 11). The mean last date for the supplementary fed group was the 30th of November ± 21.9 days, compared to the 7th of December ± 22.8 days for the control group. No correlation was found between the date of the last observation and the temperature of the last observation ($F(1) = 0.48$, $p = 0.50$). In addition, the temperature at which the hedgehogs started their hibernation was not correlated with the supplementary food provision ($F(1) = 0.34$, $p = 0.57$).

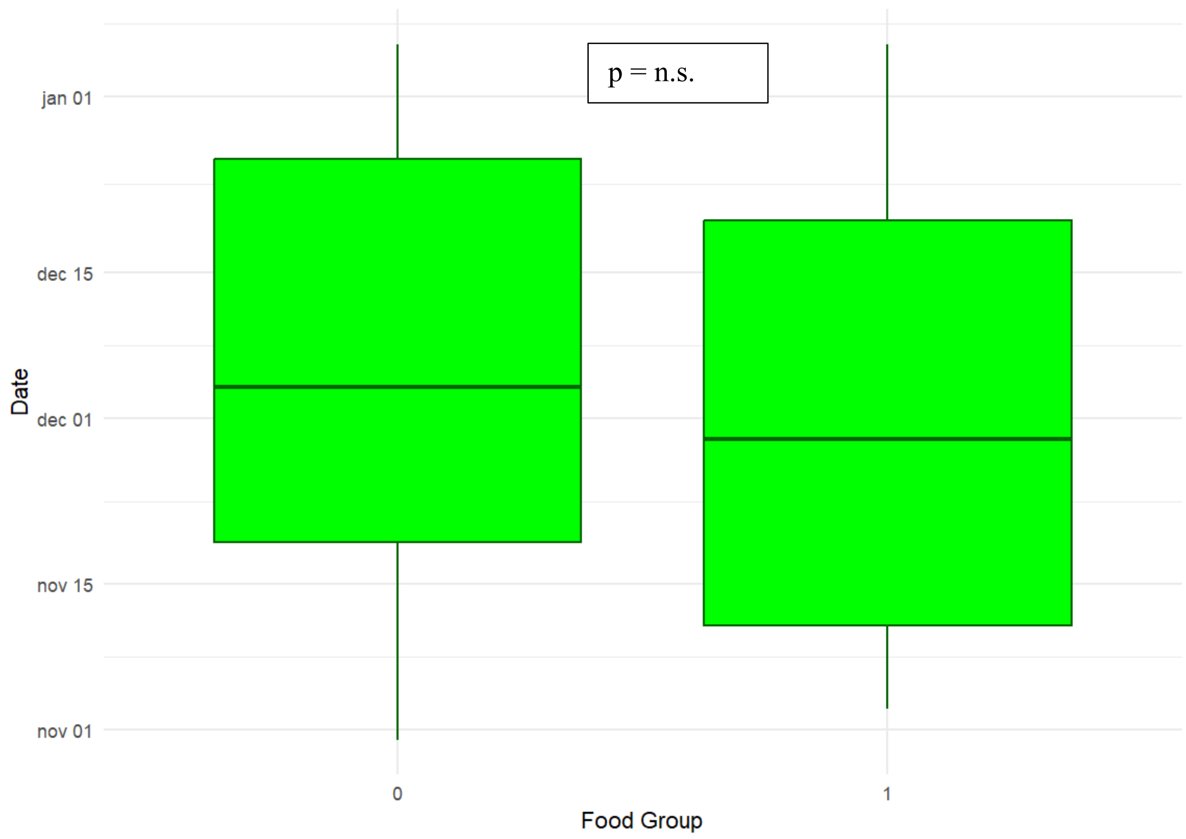


Figure 11: No difference in start date of hibernation between the two food groups (p = 0.11). The control group is 0, the supplementary food group is 1.

Discussion

Climate change can have large effects on the phenology of species. Thus far little is known regarding the impact of climate change on hibernation, an important life history strategy found in about 50% of mammalian orders (Turbill et al., 2011). Although for some species the effects of rising temperatures on their hibernation timing are known, for hedgehogs this was largely unknown (Findlay-Robinson et al., 2023). The effect of supplementary feeding on the hibernation is especially unknown (Gazzard & Baker, 2020). The aim of this study therefore was to determine how and if hibernation timing of European hedgehogs is affected by rising temperatures and supplementary feeding.

Here, it was found that based on citizen science data, hedgehogs start their hibernation later ($p = 0.007$), and end earlier ($p = 0.03$) on a European scale, and in the United Kingdom specifically. However, these trends were not present in the observation data from the Netherlands. Related to this, a difference was found between the north and the south of the whole range of the hedgehog, but this difference was not found within the United Kingdom or the Netherlands.

In contradiction to observed from citizen science data from the Netherlands, based on data from wildlife sanctuaries in the Netherlands, hedgehogs have significantly changed their hibernation timing over the past years. These changes are a delayed start, advanced end, and shorter duration of hibernation.

Based on the camera trap data from this study, supplementary food provision has no effect on the timing of the start of hibernation. Furthermore, the temperature at the last observation was not correlated with the start date, and no difference between the two groups in mean temperature at the last observation was found.

The results regarding changing hibernation patterns over time were in line with the hypothesised delayed start, advanced end, and shorter duration. The mean temperatures on the start (7.64 ± 2.37 °C) and end dates (7.77 ± 1.35 °C) that were found using the observation data from the Netherlands are in

line with what Bexton (2016) found. The absence of trends in mean temperature of the start and end dates of hibernation, in the observation data from the Netherlands, the wildlife sanctuary data (only start date), and the camera trap data (only start date), shows that hedgehogs time their hibernation based on ambient temperature and not based on day of year (light). Hilgers (2024) found that, in the United Kingdom, temperature influenced the timing of the start, end, and duration of hibernation. Her results were in line with the results (regarding the United Kingdom) of this study and with the hypothesis that hibernation started later, ended earlier and lasted shorter over the past two decades. These results are also in line with studies into other small hibernating mammals, such as two species of ground squirrels (*Urocitelles parryii* and *Urocitelles columbianus*)(Chmura et al., 2023; Lane et al., 2012; Wells et al., 2022). However, the absence of correlations in start date, end date, and duration with the mean temperature during the hibernation period in the whole range of the hedgehog and within the Netherlands are contrary to the hypothesis and to what others found for hedgehogs and other species (Boyles et al., 2020; Hilgers, 2024; Reeve, 1994). There was nonetheless a correlation between the mean temperature of the hibernation period and the start date, in the data from the wildlife sanctuaries in the Netherlands. The strong influence that the United Kingdom data has on the whole GBIF dataset can be explained by the relatively large amount of data it comprises in comparison with other countries in Europe, making up 44% of the total data. A possible explanation for the trends that are present in the data from the United Kingdom are the extensive surveys that have been conducted there, specifically focused on the hibernation period (British Hedgehog Preservation Society, 2015). These surveys have collected the largest amount of data available on the subject of hedgehog hibernation, and are part of the GBIF dataset. The trends not being present in the data from only the Netherlands and data from the rest of Europe is therefore likely the cause of a lack of data. This would then also be the explanation for the absence of correlations with the mean temperature of the hibernation period.
The difference in hibernation start date between the north and south of the whole range of the hedgehog is in line with other studies (Marco-Tresserras & López-Iborra, 2022; Rasmussen et al., 2019; Reeve, 1994). A likely explanation for the absence of a gradient in hibernation timing within the Netherlands is that the difference in mean minimum temperature within the country is not large enough (1,5 °C, Wolters et al. (2011)) to cause a difference in the date at which hedgehogs start their hibernation. It is however unknown why such a gradient was not found in the data subset of the United Kingdom.

Regarding the effect that supplementary feeding has on the hibernation timing, no difference in start date between the two groups was found ($p = 0.11$), so the hypothesis cannot be accepted. The absence of a difference can possibly be explained by the small amount of data (19 supplementary food gardens, 9 control gardens). The results are not in line with the results of Gazzard & Baker (2020), regarding hedgehogs, and to what is found in brown bears regarding increased winter activity due to supplementary feeding (Bogdanović et al., 2024; Bojarska et al., 2019). One explanation, and major limitation of this setup, is that it is likely that many hedgehogs in the control group were in fact supplementary fed in neighbouring gardens. Alternatively, it is possible that hedgehogs in fact do not start their hibernation later when supplementary fed, with the explanation that they have already built a sufficiently large fat reserve to survive the hibernation. This contradicts however the knowledge that a low availability of food at the beginning of winter is a cue to start hibernation in mammals (Vuarin & Henry, 2014). So it is likely a combination of the small amount of data and the probable availability of food in other gardens which causes the absence of a difference. As for the no difference in temperature on the last day between the two groups, this would imply that hedgehogs despite having supplemental food available, start their hibernation based on the ambient temperature.
One reason for the small amount of data is that 73 percent of the gardens where no food was provided, did not have enough documented hedgehog activity (or no hedgehogs at all). In contrast, this was 34 percent for the other group of gardens. This is another major limitation of the study and a logical consequence of the provision of supplementary food and the setup of the cameras. The cameras in gardens with supplementary food were pointed at the feeding stations, whereas these were not present in gardens without supplementary food. In those gardens the cameras were pointed towards hiding spots, suspected sleeping spots, garden access points, or so that they had a large view of the garden.

The probability of hedgehogs appearing at feeding stations was higher than them appearing at one of those other locations.
In general, the assumption was made that when hedgehogs were not captured by camera traps anymore, they started their hibernation. This was also done in a study investigating the activity throughout the year of the Asian black bear (*Ursus thibetanus*)(Zahoor et al., 2021). Yet, hedgehogs may also have moved to a neighbouring area or died, in traffic or by predation. However, the onset of hibernation was a more probable reason for lack of further camera captures, especially since all gardens (that had enough hedgehog activity) were in low traffic neighbourhoods, and had no known badger activity. Furthermore, mortality by road traffic peaks during the breeding season and affects mostly adult males (Haigh et al., 2014), whereas this study was conducted during October till January and most recorded individuals were young hedgehogs, which are born between May and October (Heaton-Jones, 1993).
In this study no differences between male and female, and between young and adult hedgehogs were investigated, because this information could not be obtained from all data sources, and because it was not the focus of this study. This is another limitation of this study, as there are known differences between these age and sex classes in hibernation timing (Gazzard & Baker, 2020). Although this limitation is not as limiting as the limitations of the supplementary food setup, it is possible that the hibernation timings of each of the ages and sex classes are affected differently by rising temperatures or supplementary feeding.

With hibernation possibly starting later, ending earlier and being overall shorter each year, threats to hedgehog populations could worsen. Potential starvation during hibernation is an especially important threat (Bearman-Brown et al., 2020; Cherel et al., 1995), as it is possible that a mismatch between hibernation and the availability of food will occur (Humphries et al., 2002). When hedgehogs wake up intermittently due to higher temperatures, they use large amounts of energy (Walhovd, 1979), highlighting the importance of supplementary feeding. This was also found in other species, such as the bat species *Myotis lucifugus* (Humphries et al., 2002; Nedergaard & Cannon, 1990). The optimal hibernation theory of Boyles et al. (2020) states that higher temperatures will lead to higher energy costs of hibernation, which also could imply an important role for supplementary feeding in the future. Effects of supplementary feeding on winter activity vary between different species. An experimental study into the hibernation of eastern chipmunks (*Tamias striatus*) found that individuals of this species woke up more intermittently during hibernation when their food storages had been supplemented, which is in line with the hypothesised increased activity of hedgehogs that were supplementary fed, but which was not found in this study. An indirect effect of supplementary feeding was found for wild boar (*Sus scrofa*), which showed an increased population size when supplementary fed (Oja et al., 2014). Putman & Staines (2004) found that with red deer (*Cervus elaphus*), supplementary feeding can have negative effects, such as the abandoning of natural food sources and completely relying on the supplementary food source. Supplementary feeding did not have an influence on the population level in mountain hares (*Lepus timidus*)(Newey et al., 2010), but did cause earlier breeding. Wells et al. (2022) found that rising temperatures can increase breeding success in hibernating mammals. In hedgehogs earlier breeding could imply earlier births in the year and subsequently larger young individuals at the start of hibernation and a higher chance of survival.

The effects of climate change, and specifically rising temperatures, on hibernation patterns in general remain largely unknown, debated, and different per species. While there is among all hibernating species the suspicion of hibernation shortening, evidence is still lacking for many species (Findlay-Robinson et al., 2023). There is however evidence of shortening of the hibernation period for some species, but the consequences of this shortening on for example survival or breeding success are not yet researched (Chmura et al., 2023; Gazzard et al., 2025; Inouye et al., 2000; Lane et al., 2012).
This study gives some insight into the changing hibernation timing of hedgehogs. This knowledge can give important insights for further research into changing hibernation patterns, and for future conservation of the species in the light of climate change and further declining population sizes (Gazzard et al., 2025).

Recommendations

This study investigated changes in hibernation timing. To get a better understanding of how the timing of hibernation of hedgehogs is changing as a result of rising temperatures, more large-scale surveys like those performed in the United Kingdom should be performed throughout its range. The data from the wildlife sanctuaries in the Netherlands and the observation data from the United Kingdom suggest that hedgehogs are changing their hibernation patterns. However, a lack of observation data in large parts of its range or a bias towards the non-hibernation period therein likely causes these trends to not be visible in the observation data outside of the United Kingdom. This further highlights the importance of extensive surveys carried out during the hibernation period. In addition, the correlations between hibernation timing and temperature that Hilgers (2024) found in the United Kingdom should be further researched, as these were not found in this study (in the data from the Netherlands), but are a probable cause of the changes over the years in hibernation timing.

For further research into the effect that supplementary feeding has on the start of hibernation, a more controlled experimental setup should be created, as a lack of data and limitations of the setup were the probable reason that in this study no effect was found. In such a setup the possibility of the hedgehogs being fed in a neighbouring garden could be excluded and there could be two groups with an equal number of hedgehogs. In addition, the possibility of hedgehogs having moved to neighbouring gardens or being killed during the research could be ruled out.

Furthermore, the effect that supplementary feeding has on survival or breeding success of hedgehogs could not be studied here due to time constraints, and further research into this is needed for successful conservation (Gazzard & Baker, 2020).

To understand what influence the changes in hibernation timing, that were found in this study, have on hedgehog populations, more research has to be done into the effect of a shorter hibernation period on hedgehog populations (Gazzard et al., 2025). Observation of individual hedgehogs before, during, and after hibernation would be useful for that purpose, as well as the monitoring of whole populations in different climate conditions. Differences in sex and age class could be present and research into these differences could provide crucial information for conservation of the species.

Conclusion

To conclude, the aim of this study was to determine how and if hibernation timing of European hedgehogs has changed over the past decades and how it is affected by supplementary feeding. The results show that hedgehog hibernation patterns show a delay in the start, an advance in the end, and a shortening of the overall duration of hibernation, but these trends are not present in all data sources. Hedgehogs that are supplementary fed do not start their hibernation later or earlier than hedgehogs that are not. This absence of a difference is likely caused by limitations of the setup and the small amount of data.

The findings in this study add to the knowledge about hedgehog hibernation, and about hibernation timing in general. Nonetheless, much still remains unknown about hedgehog hibernation. This includes patterns in hibernation timing in other parts of the hedgehogs range than the United Kingdom, geographical patterns on country scale, the effect of supplementary food provision, and differences in patterns of hibernation timing between different age and sex classes in hedgehogs. These should all be further researched to obtain full understanding of the changing hibernation patterns of the European hedgehog. In general, still little is known about changing hibernation patterns. Further research into these patterns could be crucial to successful conservation of hibernating species in further changing climates.

References

Bearman-Brown, L. E., Baker, P. J., Scott, D., Uzal, A., Evans, L., & Yarnell, R. W. (2020). Over-Winter Survival and Nest Site Selection of the West-European Hedgehog (Erinaceus europaeus) in Arable Dominated Landscapes. *Animals 2020, Vol. 10, Page 1449*, *10*(9), 1449. https://doi.org/10.3390/ANI10091449

Bell, B., Hersbach, H., Simmons, A., Berrisford, P., Dahlgren, P., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Radu, R., Schepers, D., Soci, C., Villaume, S., Bidlot, J. R., Haimberger, L., Woollen, J., Buontempo, C., & Thépaut, J. N. (2021). The ERA5 global reanalysis: Preliminary extension to 1950. *Quarterly Journal of the Royal Meteorological Society*, *147*(741), 4186–4227. https://doi.org/10.1002/QJ.4174

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity. *Ecology Letters*, *15*(4), 365–377. https://doi.org/10.1111/J.1461-0248.2011.01736.X

Bexton, S. (2016). Hedgehogs. *BSAVA Manual of Wildlife Casualties*, 117–136. https://doi.org/10.22233/9781910443316.12

Bogdanović, N., Zedrosser, A., Hertel, A. G., & Ćirović, D. (2024). Cozy den or winter walk: the effects of climate and supplementary feeding on brown bear winter behavior. *Journal of Zoology*, *323*(4), 292–304. https://doi.org/10.1111/JZO.13174

Bojarska, K., Drobniak, S., Jakubiec, Z., & Zyśk-Gorczyńska, E. (2019). Winter insomnia: How weather conditions and supplementary feeding affect the brown bear activity in a long-term study. *Global Ecology and Conservation*, *17*, e00523. https://doi.org/10.1016/J.GECCO.2019.E00523

Boyles, J. G., Johnson, J. S., Blomberg, A., & Lilley, T. M. (2020). Optimal hibernation theory. *Mammal Review*, *50*(1), 91–100. https://doi.org/10.1111/MAM.12181

British Hedgehog Preservation Society. (2015). *Hedgehog Hibernation Survey*. https://www.hedgehogstreet.org/hibernation-survey/

Cherel, Y., El Omari, B., Le Maho, Y., & Saboureau, M. (1995). Protein and lipid utilization during fasting with shallow and deep hypothermia in the European hedgehog (Erinaceus europaeus). *Journal of Comparative Physiology B*, *164*(8), 653–658. https://doi.org/10.1007/BF00389807/METRICS

Chmura, H. E., Duncan, C., Burrell, G., Barnes, B. M., Buck, C. L., & Williams, C. T. (2023). Climate change is altering the physiology and phenology of an arctic hibernator. *Science*, *380*(6647), 846–849. https://doi.org/10.1126/SCIENCE.ADF5341/SUPPL_FILE/SCIENCE.ADF5341_MDAR_REPRODUCIBILITY_CHECKLIST.PDF

Cordes, L. S., Blumstein, D. T., Armitage, K. B., CaraDonna, P. J., Childs, D. Z., Gerber, B. D., Martin, J. G. A., Oli, M. K., & Ozgul, A. (2020). Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(30), 18119–18126. https://doi.org/10.1073/PNAS.1918584117/SUPPL_FILE/PNAS.1918584117.SAPP.PDF

De egel - Egelbescherming Nederland. (n.d.). Retrieved September 4, 2024, from https://www.egelbescherming.nl/de-egel/de-egel-algemene-informatie/

Dickinson, J. L., Zuckerberg, B., & Bonter, D. N. (2010). Citizen science as an ecological research tool: Challenges and benefits. *Volume 41, Pages 149 - 172*, *41*, 149–172. https://doi.org/10.1146/annurev-ecolsys-102209-144636

Dimelow, E. J. (1963). Observations on the feeding of the hedgehog (Ericaceus europaeus L.). *Proceedings of the Zoological Society of London*, *141*(2), 291–309. https://doi.org/10.2/JQUERY.MIN.JS

Egeltelling 2023 - Egelbescherming Nederland. (n.d.). Retrieved September 26, 2024, from https://www.egelbescherming.nl/egeltelling-2023/

Findlay-Robinson, R., Deecke, V. B., Weatherall, A., & Hill, D. L. (2023). Effects of climate change on life-history traits in hibernating mammals. *Mammal Review*, *53*(2), 84–98. https://doi.org/10.1111/MAM.12308

Gao, X., Jin, C., Llusia, D., & Li, Y. (2015). Temperature-induced shifts in hibernation behavior in experimental amphibian populations. *Scientific Reports 2015 5:1*, *5*(1), 1–11. https://doi.org/10.1038/srep11580

Gazzard, A., & Baker, P. J. (2020). Patterns of Feeding by Householders Affect Activity of Hedgehogs (Erinaceus europaeus) during the Hibernation Period. *Animals 2020, Vol. 10, Page 1344*, *10*(8), 1344. https://doi.org/10.3390/ANI10081344

Gazzard, A., Macdonald, D. W., & Rasmussen, S. L. (2025). Conservation concern for Europe's hedgehog species (Erinaceidae): Current statuses, issues and needs. *Biological Conservation*, *304*, 111033. https://doi.org/10.1016/J.BIOCON.2025.111033

Gazzard, A., & Rasmussen, S. L. (2023). Erinaceus europaeus assessment. *IUCN Red List of Threatened Species*. https://doi.org/10.2305/IUCN.UK.2024-2.RLTS.T29650A213411773.EN

Gimmel, A., Eulenberger, U., & Liesegang, A. (2021). Feeding the European hedgehog (Erinaceus europaeus L.)—risks of commercial diets for wildlife. *Journal of Animal Physiology and Animal Nutrition*, *105*(S1), 91–96. https://doi.org/10.1111/JPN.13561

Haigh, A., O'riordan, R. M., Butler, F., Haigh, A., O'riordan, R. M., & Butler, F. (2014). Hedgehog Erinaceus europaeus mortality on Irish roads. *Wildlife Biology*, *20*(3), 155–160. https://doi.org/10.2981/WLB.12126

Heaton-Jones, K. (1993). Hand Rearing Hedgehogs—from Birth to Release. *Veterinary Nursing Journal*, *8*(3), 80–86. https://doi.org/10.1080/17415349.1993.11012531

Hewitt, G. M. (2004). Genetic consequences of climatic oscillations in the Quaternary. *Volume 359, Issue 1442, Pages 183 - 195*, *359*(1442), 183–195. https://doi.org/10.1098/rstb.2003.1388

Hilgers, N. (2024). *The effects of climate change on hibernating patterns of hedgehogs in the United Kingdom*.

Hof, A. R., Allen, A. M., & Bright, P. W. (2019). Investigating the Role of the Eurasian Badger (Meles meles) in the Nationwide Distribution of the Western European Hedgehog (Erinaceus europaeus) in England. *Animals 2019, Vol. 9, Page 759*, *9*(10), 759. https://doi.org/10.3390/ANI9100759

Hof, A. R., Snellenberg, J., & Bright, P. W. (2012). Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. *Animal Behaviour*, *83*(4), 1099–1106. https://doi.org/10.1016/J.ANBEHAV.2012.01.042

Huijser, M. P., & Bergers, P. J. M. (2000). The effect of roads and traffic on hedgehog (Erinaceus europaeus) populations. *Biological Conservation*, *95*(1), 111–116. https://doi.org/10.1016/S0006-3207(00)00006-9

Humphries, M. M., Kramer, D. L., & Thomas, D. W. (2003). The role of energy availability in mammalian hibernation: An experimental test in free-ranging eastern chipmunks. *Physiological and Biochemical Zoology*, *76*(2), 180–186. https://doi.org/10.1086/367949

Humphries, M. M., Thomas, D. W., & Speakman, J. R. (2002). Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature 2002 418:6895*, *418*(6895), 313–316. https://doi.org/10.1038/NATURE00828

Inouye, D. W., Barr, B., Armitage, K. B., & Inouye, B. D. (2000). Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences*, *97*(4), 1630–1633. https://doi.org/10.1073/PNAS.97.4.1630

Kirby, R., Johnson, H. E., Alldredge, M. W., & Pauli, J. N. (2019). The cascading effects of human food on hibernation and cellular aging in free-ranging black bears. *Scientific Reports 2019 9:1*, *9*(1), 1–7. https://doi.org/10.1038/s41598-019-38937-5

KNMI - Daggegevens van het weer in Nederland. (n.d.). Retrieved November 7, 2024, from https://www.knmi.nl/nederland-nu/klimatologie/daggegevens

Kosmala, M., Wiggins, A., Swanson, A., & Simmons, B. (2016). Assessing data quality in citizen science. *Frontiers in Ecology and the Environment*, *14*(10), 551–560. https://doi.org/10.1002/FEE.1436

Lane, J. E., Kruuk, L. E. B., Charmantier, A., Murie, J. O., & Dobson, F. S. (2012). Delayed phenology and reduced fitness associated with climate change in a wild hibernator. *Nature 2012 489:7417*, *489*(7417), 554–557. https://doi.org/10.1038/nature11335

Marco-Tresserras, J., & López-Iborra, G. M. (2022). The effect of sex on home range in an urban population of European hedgehogs *Erinaceus europaeus* at the southern edge of its distribution. *Animal Biodiversity and Conservation*, *45*(2), 269–279. https://doi.org/10.32800/ABC.2022.45.0269

McKinley, D. C., Miller-Rushing, A. J., Ballard, H. L., Bonney, R., Brown, H., Cook-Patton, S. C., Evans, D. M., French, R. A., Parrish, J. K., Phillips, T. B., Ryan, S. F., Shanley, L. A., Shirk, J. L., Stepenuck, K. F., Weltzin, J. F., Wiggins, A., Boyle, O. D., Briggs, R. D., Chapin, S. F., … Soukup, M. A. (2017). Citizen science can improve conservation science, natural resource management, and environmental protection. *Volume 208, Pages 15 - 28*, *208*, 15–28. https://doi.org/10.1016/j.biocon.2016.05.015

Møller, A. P., Rubolini, D., & Lehikoinen, E. (2008). Populations of migratory bird species that did not show a phenological response to climate change are declining. *Volume 105, Issue 42, Pages 16195 - 16200*, *105*(42), 16195–16200. https://doi.org/10.1073/pnas.0803825105

Nedergaard, J., & Cannon, B. (1990). Mammalian hibernation. *Philosophical Transactions - Royal Society of London, B*, *326*(1237), 669–686. https://doi.org/10.1098/RSTB.1990.0038

Newey, S., Allison, P., Thirgood, S., Smith, A. A., & Graham, I. M. (2010). Population and individual level effects of over-winter supplementary feeding mountain hares. *Journal of Zoology*, *282*(3), 214–220. https://doi.org/10.1111/J.1469-7998.2010.00728.X

Oja, R., Kaasik, A., & Valdmann, H. (2014). Winter severity or supplementary feeding—which matters more for wild boar? *Acta Theriologica*, *59*(4), 553–559. https://doi.org/10.1007/S13364-014-0190-0/METRICS

Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A., & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature 1999 399:6736*, *399*(6736), 579–583. https://doi.org/10.1038/21181

Plummer, K. E., Siriwardena, G. M., Conway, G. J., Risely, K., & Toms, M. P. (2015). Is supplementary feeding in gardens a driver of evolutionary change in a migratory bird species? *Global Change Biology*, *21*(12), 4353–4363. https://doi.org/10.1111/GCB.13070

Poel, J. L. V. De, Dekker, J., & Langevelde, F. Van. (2015). Dutch hedgehogs Erinaceus europaeus are nowadays mainly found in urban areas, possibly due to the negative Effects of badgers Meles meles. *Wildlife Biology*, *21*(1), 51–55. https://doi.org/10.2981/WLB.00072

Putman, R. J., & Staines, B. W. (2004). Supplementary winter feeding of wild red deer Cervus elaphus in Europe and North America: justifications, feeding practice and effectiveness. *Mammal Review*, *34*(4), 285–306. https://doi.org/10.1111/J.1365-2907.2004.00044.X

R Core Team. (2024). *R: A Language and Environment for Statistical Computing*. https://www.R-project.org/

Rasmussen, S. L., Berg, T. B., Dabelsteen, T., & Jones, O. R. (2019). The ecology of suburban juvenile European hedgehogs (Erinaceus europaeus) in Denmark. *Ecology and Evolution*, *9*(23), 13174–13187. https://doi.org/10.1002/ECE3.5764

Reeve, Nigel. (1994). *Hedgehogs*. 313.

Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Volume 49, Pages 165 - 182*, *49*, 165–182. https://doi.org/10.1146/annurev-ecolsys-110617-062535

Rubenstein, M. A., Weiskopf, S. R., Bertrand, R., Carter, S. L., Comte, L., Eaton, M. J., Johnson, C. G., Lenoir, J., Lynch, A. J., Miller, B. W., Morelli, T. L., Rodriguez, M. A., Terando, A., & Thompson, L. M. (2023). Climate change and the global redistribution of biodiversity: substantial variation in empirical support for expected range shifts. *Environmental Evidence*, *12*(1), 1–21. https://doi.org/10.1186/S13750-023-00296-0/FIGURES/5

Slamka, M. (2016). *Winter activity of European badger (Meles meles) in Slovakia*. *43*(1).

Turbill, C., Bieber, C., & Ruf, T. (2011). Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1723), 3355–3363. https://doi.org/10.1098/RSPB.2011.0190

Van Dorland, R., Beersma, J., Bessembinder, J., Bloemendaal, N., Van Den Brink, H., Brotons Blanes, M., Drijfhout, S., Groenland, R., Haarsma, R., Homan, C., Keizer, I., Krikken, F., Le Bars, D., Lenderink, G., Van Meijgaard, E., Meirink, J. F., Overbeek, B., Reerink, T., Selten, F., … Van Der Wiel, K. (2024). KNMI National Climate Scenarios 2023 for the Netherlands. *2023 | Scientific Report*, *2*.

Vuarin, P., & Henry, P. Y. (2014). Field evidence for a proximate role of food shortage in the regulation of hibernation and daily torpor: A review. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, *184*(6), 683–697. https://doi.org/10.1007/S00360-014-0833-0/METRICS

Walhovd, H. (1979). Partial arousals from hibernation in hedgehogs in outdoor hibernacula. *Oecologia*, *40*(2), 141–153. https://doi.org/10.1007/BF00347932/METRICS

Wells, C. P., Barbier, R., Nelson, S., Kanaziz, R., & Aubry, L. M. (2022). Life history consequences of climate change in hibernating mammals: a review. *Ecography*, *2022*(6), e06056. https://doi.org/10.1111/ECOG.06056

Williams, B. M., Baker, P. J., Thomas, E., Wilson, G., Judge, J., & Yarnell, R. W. (2018). Reduced occupancy of hedgehogs (Erinaceus europaeus) in rural England and Wales: The influence of habitat and an asymmetric intra-guild predator. *Scientific Reports 2018 8:1*, *8*(1), 1–10. https://doi.org/10.1038/s41598-018-30130-4

Wolters, D., Homan, C., & Bessembinder, J. (2011). *Ruimtelijke klimatologische verschillen binnen Nederland met speciale aandacht voor de regio's Haaglanden en Rotterdam*.

Zahoor, B., Liu, X., Wu, P., Sun, W., Jia, X., Lv, Z., Zhao, X., He, X., He, B., Cai, Q., & Songer, M. (2021). Activity pattern study of Asiatic black bear (Ursus thibetanus) in the Qinling Mountains, China, by using infrared camera traps. *Environmental Science and Pollution Research*, *28*(20), 25179–25186. https://doi.org/10.1007/S11356-020-12325-3/FIGURES/3

Appendix 1: Sanctuaries

List of sanctuaries that contributed by sharing their data regarding hedgehog take-ins.

- Avolare. Boersberg 2, Doorwerth
- De Fugelhelling. De Feart 1, Ureterp
- Egelopvang Midden Nederland. Landweg 3, Huizen
- Egelopvang Papendrecht. Admiraal de Ruyterweg 1a, Papendrecht
- Egelopvang Stein. Sittarderweg 4, Born
- Stichting Egelopvang Haarlem. Van Oosten de Bruijnstraat 64, Haarlem
- Wildopvang De Bonte Piet. Broerdijk 32a, Midwoud
- Wildopvang Krommenie. Busch 2, Krommenie
- Zorg voor Egels. Reigerstraat 65, Alphen aan den Rijn

Appendix 3: Use of AI

AI was used in this thesis to assist with code in RStudio. In addition, it was used to check for spelling and grammar errors.