

Microhabitat features associated with occupancy of artificial nestboxes by hazel dormice (*Muscardinus avellanarius*)

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Abstract

1. The severe decline of hazel dormice (*Muscardinus avellanarius*) is well documented and has led to increased legislative protection both in the UK and across Europe. Conservation measures for this species often include provision of nestboxes as a mitigation or enhancement technique after development projects. Previous research has offered some insights into how to select suitable general locations for nestboxes, but where to best place individual boxes to promote occupancy is less well understood. We hypothesised microhabitat variables related to proximity to food sources and nest building material will affect nestbox occupancy by dormice and should be considered when placing individual boxes within a selected site. 2. To assess individual nestbox occupancy by hazel dormice, 76 microhabitat variables were collected from 45 occupied and unused nestboxes in a deciduous woodland in Berkshire, UK. Variables were then used to predict probability of nestbox occupancy (observed from 2017 to 2021) using Random Regression models. 3. Results reveal nestboxes were more likely to be occupied by hazel dormice in sites with higher local cover and abundance of hazel trees (*Corylus avellana*), greater overall tree abundance but not fully closed canopies (best around 80-85%), more hawthorn (*Crataegus monogyna*) and honeysuckle (*Lolium periclymenum*), and when located further from footpaths. 4. Our results build on previous literature on habitat preferences of hazel dormice and importantly provide insight into relevant microhabitat variables that offer recommendations for where to place individual nestboxes to promote occupancy and facilitate recovery of hazel dormice.

Introduction

Over the past 50 years, the UK has seen a severe decline amongst many of its native mammal species, including hazel dormice (*Muscardinus avellanarius*), harvest mice (*Micromys minutus*) and hedgehogs (*Erinaceus europaeus*). Even populations thought to have been stable, and widespread, such as those of stoats (*Mustela erminea*) and weasels (*Mustela nivalis*), are being shown, through new research, to be decreasing at alarming rates (Coomber et al. 2021). Habitat loss through urban expansion and changes in farming practices are cited as being key drivers of population decline, as well as changes in forestry management. These changes decrease structurally complex and spatially heterogeneous woodlands (Hopkins & Kirby 2007) affecting vulnerable mammal species such as red squirrels (*Sciurus vulgaris*) (de Raad et al. 2021) and pine martens (*Martes martes*) (Caryl 2021). Many of our UK mammal species are vitally important contributors to biodiversity directly through interactions with various plant and invertebrate species, and also indirectly as prey for other species such as birds of prey and larger mammals (Occhiuto et al. 2021). It is therefore important that we understand the specific requirements of these vulnerable species to provide suitable mitigation and enhancement, and inform new protective legislation as required.

Hazel dormice have severely declined with a reported 50% reduction in population size since 2000 across the UK (Wembridge et al. 2019). This decline is primarily attributed to a reduction of traditional woodland

management techniques, specifically coppicing (Bright & Morris 1995) and habitat fragmentation (Bright & Morris 1994, Capizzi et al. 2002). Hazel dormice are habitat specialists and thus, particularly sensitive to environmental changes and habitat fragmentation (Capizzi et al. 2002). In addition, hazel dormice have slow reproduction rates and live at low densities (Bright & Morris 2008) which makes the species especially vulnerable to local declines and extirpation. The rarity of other dormice species, such as the garden dormouse, forest dormouse and mouse-tailed dormouse led to the creation of EU legislation which affords enhanced protection of individuals, prohibiting their capture, injury, killing, or deliberate disturbance, and their breeding sites and nests (UK Statutory Instruments: The Conservation of Habitats and Species Regulations 2017. No 1012).

The alarming decline of hazel dormice has prompted several conservation initiatives designed to protect the species and enhance or create suitable habitats (Bright & Morris 1994, 1995, Ramakers et al. 2014). For example, active woodland management has led to local recoveries (Goodwin et al. 2018). Management includes coppicing hazel to maintain a successional status, which slows the progression from an unshaded and productive shrub layer to a high forest with an overshaded understorey (Bright & Morris 1990). This provides dormice with habitat rich in foraging material that can support healthy populations of invertebrate species, which are a vital part of the diet of hazel dormice over the summer (Bright et al. 2006). Conservation initiatives have also involved reintroductions and in 2021 Natural England celebrated the reintroduction of the 1000th individual in Lancashire (People's Trust for Endangered Species 2021). Success has been linked to adequate habitat management (Bright & Morris 2002) and improved connectivity to allow population expansion (Mitchell-Jones & White 2009).

The installation of nestboxes is also widely employed in the UK to help reverse dormice declines (Morris et al. 1990). Nestboxes can improve local densities (Morris et al. 1990), potentially due to enhanced survival of young in consistently dry and secure boxes, or because boxes offer greater nesting opportunities than might be naturally available in some habitats. With entrances holes approximately 20mm in diameter, dormice nestboxes are less likely to be used by other woodland species, such as squirrels and woodpeckers, which reduces competition (Madikiza et al. 2010). While nestboxes can be important, their uptake by hazel dormice depends on the surrounding environment which needs to be carefully considered when placing boxes (Juškaitis et al. 2013, Mortensen et al. 2022). Placement near food and nesting material sources is likely beneficial. Hazel dormice feed on a variety of resources that vary seasonally. After coming out of hibernation in Spring, dormice feed on the nectaries and anthers of understorey tree species, including hawthorn (*Crataegus monogyna*) and rowan (*Sorbus aucuparia*), as well as herbaceous field layer species such as wild garlic (*Allium ursinum*) (Richards & Hurrell 1984, Eden 2009). Dormice can also consume pollen from certain canopy tree flowers, including oak (*Quercus* spp.) and sycamore (*Acer pseudoplatanus*) (Richards & Hurrell 1984). Spores of bracken (*Pteridium aquilinum*), bryophytes and fungi have also been found in faecal samples (Richards & Hurrell 1984). In the Summer dormice have an invertebrate-based diet, mainly feeding on aphids and lepidopteran larvae (Richards & Hurrell 1984, Eden 2009, Chanin et al. 2015). Finally, in Autumn, in preparation for hibernation, hazel dormice feed on high-calorie food such as hazelnuts (Grodziński & Sawicka-Kapusta 1970). Regarding nesting material, honeysuckle (*Lolium periclymenum*) is the preferred material, with graminoids providing an alternative (Bright & Morris 2005). Proximity to these resources is likely important, because while dormice can travel up to 50 m to collect materials, when resources are available regular travel is generally limited to within 10 m of the nest site (Bracewell & Downs 2017). In fact, a study found that over 70% of nests in nestboxes were made from the plant on which the nestbox was attached (Bracewell & Downs 2017). A shorter journey when encumbered by heavy nest materials reduces the risk of predation, and conserves energy, especially for lactating females (Prentice & Prentice 1988, Juškaitis 2014).

Proximity to key resources is important, but their accessibility is also key. As an arboreal species, hazel dormice require a well-developed tree canopy, and/or understorey layer with plenty of horizontal branches (Bright & Morris 2009). However, an extensive tree canopy and/or understorey layer could limit the amount of sunlight reaching field layer plants affecting flowering and fruiting and encouraging vertical growth which is less useful for travel (Bright & Morris 1990), so probably intermediate to high tree canopy and/or understorey

layer cover is optimal (Juškaitis & Augutė 2008). An extensive tree canopy and/or understorey layer could also shade the area beneath, leading to lower temperatures in nestboxes. At temperatures below 14-15, dormice often enter a state of torpor (Juškaitis 2005) that could be particularly detrimental during Autumn when foraging is key in preparing for hibernation. Temperature and sunshine hours have also been found to influence breeding success (Goodwin et al. 2018).

Previous research has described general habitat preferences of hazel dormice and explore how overall local conditions affect nestbox occupancy (Bright & Morris 1990, Panchetti et al. 2007). However, limited information is available on how microhabitat within a suitable local site influences nestbox use (Mortensen et al. 2022). After an area is identified as suitable for installing nestboxes it is still important to determine the optimal locations for nestboxes within the site. Here we address this knowledge gap, linking data from 76 microhabitat variables to dormice occupancy for 45 nestboxes installed in a UK National Trust woodland. Microhabitat variables were defined to test our hypotheses that the probability of nestbox occupancy increases with relatively high tree canopy and/or understorey coverage that facilitates movement but does not fully block sunlight, with greater abundance and diversity of key plant species for nest building and foraging resources in close proximity to the nest, and with increased distance from sources of anthropogenic disturbance. Our results offer recommendations for where to best place nestboxes and guide microsite management to aid in the protection and conservation of the hazel dormouse.

Materials and Methods

Study area and dormice surveys

Our study area was within the grounds of Basildon Park House (BPH), a National Trust property with extensive woodland, located in Berkshire, UK (Fig. 1). The woodland covers approximately 63 ha around the perimeter of BPH and is connected (western boundary) to a further 40 ha woodland (with a small road in between). Management at BPH includes seasonal coppicing over the winter months, and the creation of “wigwam” structures for trees as protection from deer browsing that improve habitat quality dormice (Reid et al. 2021).

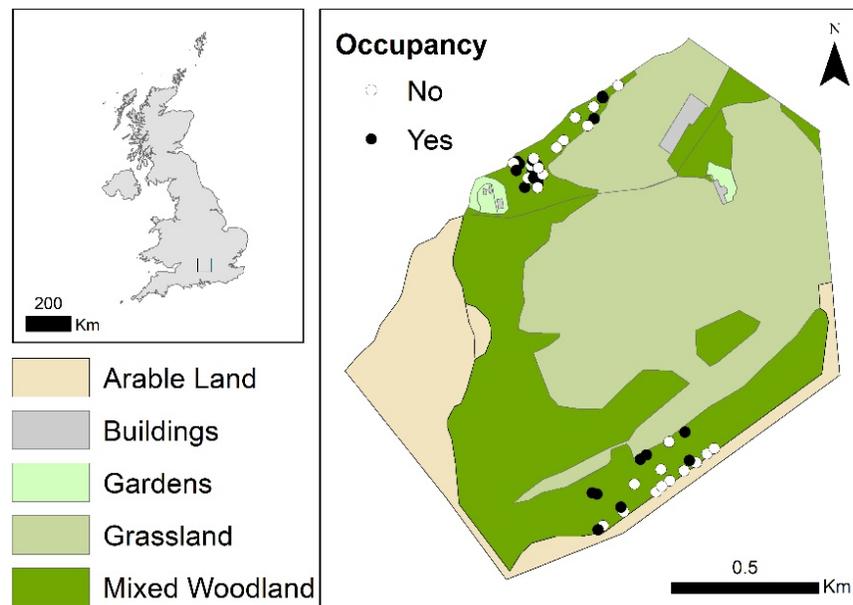


Figure 1 . Map of the surveyed nestboxes in Basildon Park House (UK) showing the main habitat types and the historical occupancy by hazel dormice *M. avellanarius* of 45 sampled nestboxes. The woodland site

is on the north boundary, with the *hedgeline* in the South on the southern boundary, adjacent to arable land. Top left inset shows the study area location in the UK.

In 2013, 144 nestboxes were erected at two different sites within BPH: 78 were located in the *woodland* site and 66 in the *hedgeline* site (Fig. 1). Within the *woodland* site, mature beech (*Fagus sylvatica*) is dominant in the tree canopy layer, ash (*Fraxinus excelsior*) and oak (*Quercus* spp.) frequent, and sweet chestnut and field elm occasional. Hawthorn (*C. monogyna*) and coppiced hazel (*C. avellana*) are dominant in the understorey layer, with holly and young sycamore frequent, and other species such as field maple, whitebeam and rowan occasional. Bramble (*Rubus fruticosus* agg.) and honeysuckle (*L. periclymenum*) are abundant in both the understorey and field layer. In the *hedgeline* site, most boxes are situated on the boundary between woodland and arable land (in 2021 the crop was rapeseed, *Brassica napus*), amongst what used to be a hedge, but is now a line of mature scrub. The main tree canopy species here are oak (*Quercus* spp.), lime and beech which are frequent, although there are some sections where there are no canopy tree species present. In the understorey cherry plum (*Prunus cerasifera*) is dominant, with spindle and young oaks occasional. The boxes within *hedgeline* site also extend northwards into a mature woodland, where the dominant tree canopy species are mature beech and oak, with hazel dominant in the understorey, and hawthorn and young sycamore frequent. Bramble is dominant in the understorey and field layer species.

All nestboxes at BPH have been regularly monitored by the Berkshire Mammal Group since 2017 as part of the National Dormouse Monitoring Programme (NDMP). No monitoring occurred between 2013 and 2016. As part of the NDMP systematic survey methods, nestboxes are typically surveyed monthly (between the 15th and 25th of each month) from May-September. At BPH the Berkshire Mammal Group check the boxes up to four times a year, dependent on the availability of a licensee. Routine cleaning takes place over winter. During each survey, nestboxes are recorded as empty or occupied by hazel dormice if individual dormice are present, or there is a new nest or an old nest with signs of recent occupation e.g. faeces (Panchetti et al. 2007). Individual dormice are sexed, classified within an age class, weighed, and assessed for breeding status. Using the full survey records between 2017 and 2020 and the first season survey of 2021, we classified nestboxes as historically *occupied* (occupied at least once since 2017) or *unoccupied* (not occupied since 2017) and selected 13 *occupied* nestboxes at the *woodland* site and all 8 *occupied* nestboxes at the *hedgeline* site (total 21 *occupied* nestboxes). For the *woodland* site we selected all boxes occupied frequently (in more than one survey) and recently (occupied at least once in the last three years). If two boxes in close proximity (<10m) met these criteria, we randomly selected one of them to avoid replicating microhabitat data. We also selected 24 historically *unoccupied* nestboxes (12 from each site) using the SelectRandomByPercent function in ARCGIS 10.5.1 excluding any nestboxes within 10m of selected *occupied* nestboxes. If two selected *unoccupied* nestboxes were in close proximity (<10m) we located an alternative pair in the area at least 10m apart.

Microhabitat surveys

In March 2021, all nestboxes were cleaned and any old nests found were collected to analyse their composition. For each nestbox we noted: GPS coordinates, tree species on which the nestbox was installed, height from the base of the nestbox to the ground, and the orientation of the front of the nestbox. Microhabitat data were collected during May and June 2021 at four scales: directly above the nestbox, within a 5 m radius of each box, in four 2 m x 5 m quadrats starting 5 m from the nestbox, and using existing GIS layers (Fig 2, Table 1). Within the 5 m radius cover was estimated within four levels: tree canopy, understorey, field layer and ground layer (Eden 2009). Tree canopy reflected trees taller than 4 m, with trees < 4m classified as part of understorey (Berg & Berg 1998). The four 2 m x 5 m quadrats started at the edge of the 5m radius running with orientations N, E, S and W. Fig. 2). Sampling areas which intersected footpaths or trackways were still assessed as dormice can occasionally cross open ground when foraging or looking for nesting materials (Mortelliti et al. 2013).

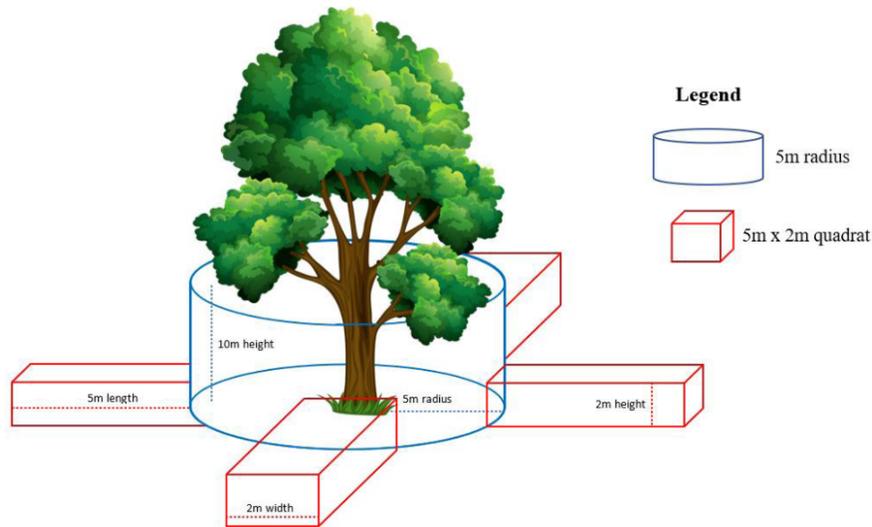


Figure 2. Schematic of the vegetation microhabitat sampling scheme used to study factors influencing nestbox occupancy by hazel dormice *M. avellanarius* in a UK woodland. The central tree is the site of a studied nestbox and we show the radius and quadrat sampling areas. See Table 1 for details on the variables measured at these scales.

GIS information

Nestbox locations were collected via GPS with a minimum of 3m accuracy and mapped using ARCGIS. Footpaths around the site, and the woodland margin were walked and recorded using GPS and added as a new layer. These layers were then used to calculate the minimum distance to the woodland margin, the closest footpath, and the nearest nestbox.

Statistical analysis

We evaluated the role of microhabitat variables in nestbox occupancy using machine learning Random Forest regression methods (Cutler et al. 2007). This approach ensembles multiple regression or classification trees allowing the estimation of variable importance and conditional effects (Breiman 2001). Random Forests were generated based on 10,000 classification trees using the function “randomForest” from the R package “randomForest” (Liaw & Weiner 2002). We first defined a model with all 74 measured variables

(Table 1) plus the height from the ground to the nestbox and a categorical variable for site (*woodland* or *hedgeline*). We evaluated variable importance with the package “randomForestExplainer” (Paluszynska et al. 2020) considering seven metrics: mean minimal depth from top trees, total number of nodes that use the variable to split the data, the total number of trees in which the variable is used, mean decrease in prediction accuracy after the variable is permuted, mean decrease in the Gini index of node impurity by splits based on the variable, total number of trees in which the variable is used for splitting the root node, p-value from a binomial test comparing the number of nodes in which the variable was used compared to the expected number if variables were assigned to nodes at random. To facilitate the selection of the most relevant variables we focused on variables with significant p-values in the binomial test, which were explored in detail using plots representing all metrics and further confirmed via the function “important_variables” from the package “randomForestExplainer”. We then built a simplified model for prediction based on the most important variables (relationships between importance metrics shown in Appendix S1). Based on this simplified model we generated dependence plots to show how each variable influences the probability of occupancy using the function “partial” from the R package “pdp” (Greenwell 2017). For the complete and simplified models we report OOB (Out-Of-Bag) overall error, false positive, and false negatives rates (and

their reciprocals: model accuracy, specificity, and sensitivity). OOB samples represented approximately one-third of the observations drawn with replacement (the default setting). In addition to the OOB validation we further validated the model by comparing predictions for sampled nestboxes with observed dormice occupancy between June and October 2021 (this information was not used to define occupancy for model fitting).

Results

We found a diversity of tree and field layer plant species across different areas of the *woodland* and the *hedgeline* sites (summary in Appendix S2). The complete random forest model with all 76 variables had an OOB error rate of 26.67%, with 25% false positives and 28.6% false negatives. Variable importance metrics from this full model revealed 27 variables with significant binomial test p-values, and among those ten were consistently identified as relevant based on the other six importance metrics (Fig 3; for display purposes variable importance is shown based on the three less correlated metrics, Fig S1). These ten variables included vegetation measurements at different scales, human impact and nestbox position variables (Fig 3).

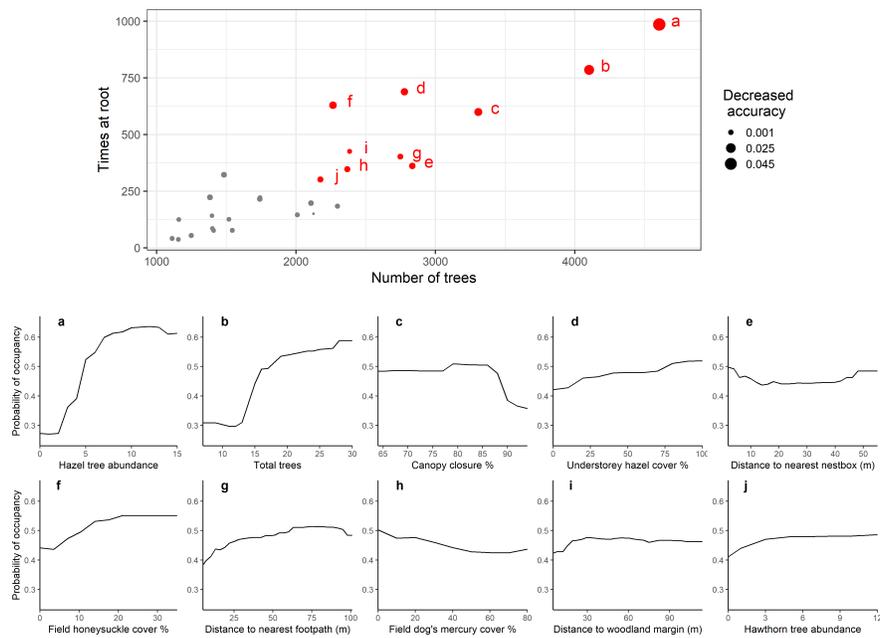


Figure 3 . Variable importance and dependence plots for the top selected variables linking microhabitat to nestbox occupancy by hazel dormice *M. avellanarius* in a UK woodland. Top large panel shows the 27 variables with binomial test p-values<0.05 with values for the three importance metrics that were less correlated in their ranking (chosen to showcase differences in variable importance among metrics. Fig S1). The three metrics are used for displaying purposes, but all seven metrics were considered to identify the most important variables shown in red colour and labelled with letters that correspond to the bottom dependence plot panels. Bottom panels (labelled a to j) show changes in predicted probability of nestbox occupancy by hazel dormice for the ten most relevant predictors (red symbols on the top panel) in descending order of variable importance (from left to right, top to bottom).

The random forest model based on these ten variables had a OOB error rate of 22.22% (model accuracy 77.78%) with 20.8% false positives (specificity=79.2%) and 23.8% false negatives (sensitivity =76.2%). The model predicted increased probability of nestbox occupancy with more trees within ten metres, particularly more hazel *C. avellana* and hawthorn *C. monogyna* trees and at intermediate to high levels of tree canopy and/or understorey closure (values above 90% cover resulted in lower probability of occupancy). Occupancy was also more likely in areas with higher percentages of understorey cover by hazel and honeysuckle *L.*

periculum but lower ground cover of dog's mercury *Mercurialis perennis* , and for nestboxes located nearer to other boxes (within 10-15m distance) or isolated (lower probability for intermediate distances) and located further from footpaths and slightly away from woodland margins which may be sources of disturbance (Fig 3).

Occupancy data from 2021 available for model validation was limited, as only 11 boxes in total across the site were occupied during June to October (ten in the *woodland* site and only one in the *hedgeline*) and from those, five boxes in the *woodland* site were not included in our dataset (thus, we lacked habitat data and could not predict occupancy). The random forest model based on the top ten variables correctly predicted occupancy for five of the six nestboxes occupied in summer 2021 resulting in a 16.7% false negative rate. The single false negative (predicted to be empty but found to be occupied) was a nestbox that had not been occupied in any previous years and was found with an unwoven nest with green leaves in October, but no dormice were present. Due to low numbers of hazel dormice in 2021 (nestbox occupancy was very low), our predictions had a higher false positive rate (41.0%) with 16 boxes predicted to be occupied by the model but found empty during the surveys (the remaining 23 were predicted to be empty and found empty). Predictions based on the complete model with all variables were identical.

Discussion

Microhabitat variables describing vegetation within 10 metres of a nestbox and local human disturbance effects influence occupancy by hazel dormice. In particular, we found that nestboxes were more likely to be occupied by dormice in sites with higher abundance of key vegetation resources (hazel, hawthorn and honeysuckle), with tree abundance that we hypothesized offered multiple movement routes but without creating fully closed canopies that would limit understorey growth and solar radiation, and when located further from human disturbances (footpaths and woodland margins). These are features that should be considered when selecting where to place nestboxes in mitigation and conservation actions and also to guide specialised woodland management promoting favourable features to encourage use of nestboxes by hazel dormice.

Hazel dormice can adapt their diet to their surroundings (Eden 2009), but proximity to preferred and suitable resources is likely beneficial and previous research found a positive effect of tree diversity locally on nest box occupancy (Mortensen et al. 2022). In our study area, increased probability of nestbox occupancy was linked to abundance of three plant species (hazel, hawthorn and honeysuckle). Hazel and hawthorn were also associated with higher occupancy in a managed forest in Denmark (Mortensen et al. 2022). High abundance and cover of hazel trees was a key predictor of occupancy, perhaps not too surprising for a species named after the plant. Hazel is a source of high-calorie food between July and October when dormice need to build up fat reserves to overwinter (Tooke & Battey 2010, Bracewell & Downs 2017). Hazel leaves are also a favoured nest material, thus, close range availability should reduce energy costs and predation risk (Prentice & Prentice 1988). Nestboxes located in areas with higher abundance of hawthorn were also more likely to be occupied. Previous research found dormice seek out hawthorns when emerging from hibernation (Juškaitis 2013). This tree flowers in April/May providing valuable resources at a critical time. The third key plant was honeysuckle, one of the few plant with leaves eaten by dormice (Richards & Hurrell 1984). Honeysuckle leaves can represent half of dormice's diet during May (Richards & Hurrell 1984) and are also a commonly used nesting material (Bracewell & Downs 2017). Honeysuckle bark can be peeled away from the stem in small strips offering a light, easy to transport, material that is readily available as dormice come out of hibernation. Dormice can use leaves of other plants for nesting (eg. beech and oaks) but often these leaves are not available until later in spring (Lechowicz 1984, Roberts et al. 2015). Our analyses also showed that proximity to some plants, in particular dog's mercury *M. perennis* , could reduce occupancy. Whilst there are many ground flora plants which are not utilised by dormice for food or nest material, dog's mercury is a poisonous plant toxic to many mammals and, dormice might specifically avoid it because of this (Rugman et al. 1983). Further research into its toxicity would be valuable. In addition, dog's mercury is very prolific and can completely cover large areas of the field layer, competing with other species which are suitable for dormice.

Our results also reveal the importance of tree abundance and tree canopy cover for hazel dormice, predicting that the probability of occupancy should double when the relative abundance of trees goes from 10 to 30 within 10 metres of a nestbox. Dormice are arboreal and can travel up to 152 metres from their nestbox in search of food, this movement is facilitated by an abundance of trees with suitable branching structures (Bright & Morris 2009). Indeed, previous research indicated dormice prefer nestboxes in forest stands with higher cover or denser (Bright & Morris 1990, Juškaitis & Augutė 2008, Mortensen et al. 2022). However, we show here that very high tree canopy and understorey cover (>85%) is likely not ideal, with an apparent optimal around 80-85%. An effect that may not be detectable when using coarser density indices (Mortensen et al. 2022). Very closed canopies can prevent solar radiation leading to lower temperatures and may also limit sunlight reducing plant growth below the tree canopy. On the other hand, open canopies allow too much radiation and occur under limited tree cover that limit arboreal movement.

Higher occupancy was also associated with lower human disturbance. Occupied nestboxes were more likely to be located further from woodland edges and footpaths. Hazel dormice do not completely avoid disturbed sites, and have been reported at roadside habitats in Germany (Schulz et al. 2012). However, our study site is a well-visited National Trust property with high footfall of people, especially at weekends and in the Spring and Summer when dormice are active. Nestboxes located closer to the footpaths and woodland margins are likely exposed to higher noise levels and potentially people could disrupt dormice (trying to look inside nestboxes) if these are visible from paths.

Collectively, these results lead to management recommendations for the placement of nestboxes and site management that build on previous research that focused on wider habitat and nestbox design (Morris et al. 1990, Juškaitis 1997, Madikiza et al. 2010). In particular, given footpath effects, larger and less visited woodlands should be preferable sites for nestbox placement. Within those, nestboxes should be placed preferentially in core woodland areas with high abundance of hazel, hawthorn and honeysuckle, good tree abundance and a late-spring tree canopy and understorey cover around 80-85%. If these conditions are not present, management to promote them should be implemented through felling or coppicing. Coppicing is often employed as a management strategy but the planting of honeysuckle, a fast-growing species, is not generally considered and based on our results could improve dormice occupancy. Management of trees can also be important to avoid fully closed canopies. Finally, the spacing between nestboxes should be considered. Our results show higher occupancy for nestboxes within 5 metres of each other and when located around 50 m away. The first result may reveal individual dormice moving among nestboxes located in very closed proximity, which is an optimal outcome if the aim is to increase population size (i.e., maximize the number of distinct dormice using nestboxes). While additional research is necessary and may not be practical in smaller settings, we tentatively suggest placing nestboxes around 50 metres from each other if possible and within the optimal microhabitat conditions described above.

In conclusion, our study addressed a knowledge gap to understand the role of microhabitat on nestbox occupancy by hazel dormice. However, additional information is still needed to facilitate the recovery of the hazel dormouse. For example, despite collecting data on dozens of plant species during our vegetation surveys, dormice occupancy seems to be influenced by just a handful of key plants. Surveys required working closely to nestboxes, and thus, to minimize disturbance we completed these during the scheduled monthly monitoring by a Natural England dormouse class licensee. More frequent surveys may identify rarer but potentially important plants or seasonal changes we were unable to monitor. In addition, our occupancy time-series did not allow analysis of temporal patterns, but it would be interesting to consider how past occupancy influence future use. Research on variation among individual dormice in their preferences will also be valuable. Marking dormice using pit-tags and camera traps could be used to understand temporal and individual patterns of nestbox use. While we wait for this additional understanding, our results reveal microhabitat variables that influence hazel dormice occupancy of nestboxes offering advice to placement and local scale management to promote conservation of this little mammal.

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Table 1. Microhabitat variables measured at four different scales to assess factors influencing nestbox occupancy by hazel dormice *M. avellanarius* in a UK woodland site. Some variable types are described in general but were calculated for multiple species (all measured species are indicated under definition).

Variable/scale	Definition
<i>Above nestbox scale</i>	<i>Above nestbox scale</i>
Tree canopy closure	Total percentage of tree canopy and understorey vegetation cover above the focal nestbox estimated as the average cover from two measurements in May and July (to account for seasonal variability in leaf growth). Cover was defined as the percentage of black pixels in processed photos taken with an Apple iPhone 11 levelled-flat on a tripod set at 1 metre from the ground and as close to the nestbox as possible without including the box in the photo. Original photos were desaturated to grayscale with the colour curve adjusted to make all pixels either black or white using GIMP 2.10.24.
<i>5m radius</i>	
Tree canopy cover	Percentage of the tree canopy (in 10% increments) occupied by trees of the same species taller than 4 m within a 5m radius circular area around the focal nestbox. <i>10 separate variables</i> for each identified species: Ash <i>Fraxinus excelsior</i> , Beech <i>Fagus sylvatica</i> , Field Elm <i>Ulmus minor</i> , Field Maple <i>Acer campestre</i> , Holly <i>Ilex aquifolium</i> , Lime <i>Tilia x europaea</i> , Oak <i>Quercus</i> spp., Sweet Chestnut <i>Castanea sativa</i> , Sycamore <i>Acer pseudoplatanus</i> , Yew <i>Taxus baccata</i> .

Variable/scale	Definition
Understorey cover	Percentage of the canopy (in 10% increments) occupied by trees of the same species smaller than 4 m within a 5m radius circular area around the focal nestbox. <i>19 separate variables</i> for each identified species: Alder buckthorn <i>Frangula alnus</i> , Ash <i>Fraxinus excelsior</i> , Beech <i>Fagus sylvatica</i> , Blackthorn <i>Prunus spinosa</i> , Cherry Plum <i>Prunus cerasifera</i> , Elder <i>Sambucus nigra</i> , Field Elm <i>Ulmus minor</i> , Field Maple <i>Acer campestre</i> , Hawthorn <i>Crataegus monogyna</i> , Holly <i>Ilex aquifolium</i> , Lime <i>Tilia x europaea</i> , Oak <i>Quercus</i> spp., Rowan <i>Sorbus aucuparia</i> , Spindle <i>Euonymus europaeus</i> , Sycamore <i>Acer pseudoplatanus</i> , Wayfaring Tree <i>Viburnum lantana</i> , Whitebeam <i>Sorbus aria</i> , Wild Cherry <i>Prunus avium</i> , Hazel <i>Corylus avellana</i> .
Field layer cover	Percentage of the field layer (in 10% increments) occupied by plants of the same species within a 5m radius circular area around the focal nestbox. Climbing species cover was estimated up to a height of 10 m. <i>16 separate variables</i> for each identified species or group: Bluebells <i>Hyacinthoides non-scripta</i> , Bramble <i>Rubus fruticosus</i> agg., Cleavers <i>Galium aparine</i> , Cow Parsley <i>Anthriscus sylvestris</i> , Dogs Mercury <i>Mercurialis perennis</i> , Ground Ivy <i>Glechoma hederaceae</i> , Hedge Woundwort <i>Stachys sylvatica</i> , Speedwell <i>Veronica</i> spp., Herb Robert <i>Geranium robertianum</i> , Honeysuckle <i>Lonicera periclymenum</i> , Lords and Ladies <i>Arum maculatum</i> , Meadow Buttercup <i>Ranunculus acris</i> , Nettles <i>Urtica dioica</i> , Yellow Archangel <i>Lamium galeobdolon</i> , Fern (group, not identified to species)", Grass (graminoid group, not identified to species).
Ground cover	Percentage of the ground (in 10% increments) occupied by bryophytes within a 5m radius circular area around the focal nestbox. [Data were also collected for cover of fungi, leaf litter and bare ground too but due to low variability among sites were not considered in the analyses].
<i>Quadrat</i> Quadrat cover	Mean percentage cover of individual species over four 2m x 5m quadrats starting 5 m from the focal nestbox and running North, South, East and West. <i>2 separate variables</i> for each key species identified: Bramble <i>Rubus fruticosus</i> agg. and Honeysuckle <i>Lolium periclymenum</i> .
<i>5 m + quadrat</i>	

Variable/scale	Definition
Tree abundance	Relative abundance of individual tree species within a 10m radius from the focal nestbox. Obtained by adding the total number of individual trees with a trunk circumference >40cm within a 5m radius circular area and in four 2m x 5m quadrats starting 5 m from the focal nestbox and running North, South, East and West. Abundance within the 5m radius area included every individual tree, whilst the four quadrats provided relative abundance within the area 5m-10m from the nestbox based on quadrat totals. <i>20 separate variables</i> for each identified species: Ash <i>Fraxinus excelsior</i> , Beech <i>Fagus sylvatica</i> , Blackthorn <i>Prunus spinosa.</i> , Cherry Plum <i>Prunus cerasifera</i> , Elder <i>Sambucus nigra</i> , Field Elm <i>Ulmus minor</i> , Field Maple <i>Acer campestre</i> , Guelder Rose <i>Viburnum opulus</i> , Hawthorn <i>Crataegus monogyna</i> , Hazel <i>Corylus avellana</i> , Holly <i>Ilex aquifolium</i> , Lime <i>Tilia x europaea</i> , Oak <i>Quercus</i> spp., Plum <i>Prunus domestica</i> , Spindle <i>Euonymus europaeus</i> , Sweet Chestnut <i>Castanea sativa</i> , Sycamore <i>Acer pseudoplatanus</i> , Wayfaring Tree <i>Viburnum lantana</i> , Wild Cherry <i>Prunus avium</i> , Yew <i>Taxus baccata</i> .
Total trees	Combined relative tree abundance. Sum of “Tree abundance” for all 20 recorded species at each nestbox.
Tree richness	Observed tree species richness calculated adding all species with “Tree abundance”>0 for each nestbox.
<i>Local (GIS)</i>	
Distance to nearest footpath	Distance in metres from focal nestbox to the nearest footpath. Collected via GPS with minimum 3m accuracy and mapped using ARCGIS
Distance to nearest nestbox	Distance in metres from focal nestbox to the nearest nestbox. Collected via GPS with minimum 3m accuracy and mapped using ARCGIS
Distance to nearest woodland margin	Distance in metres from focal nestbox to the nearest woodland margin. Collected via GPS with minimum 3m accuracy and mapped using ARCGIS

Appendix S1. Relationship between the variable importance metrics

Appendix S2. Brief description of plant species present at the survey sites