



# What makes a house a home? Nest box use by West European hedgehogs (*Erinaceus europaeus*) is influenced by nest box placement, resource provisioning and site-based factors

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## ABSTRACT

Artificial refuges provided by householders and/or conservation practitioners potentially represent one mechanism for mitigating declines in the availability of natural nest sites used for resting, breeding and hibernating in urban areas. The effectiveness of such refuges for different species is, however, not always known. In this study, we conducted a questionnaire survey of UK householders to identify factors associated with the use of ground-level nest boxes for West European hedgehogs (*Erinaceus europaeus*), a species of conservation concern. Overall, the percentage of boxes used at least once varied with season and type of use: summer day nesting (35.5–81.3%), breeding (7.2–28.2%), winter day nesting (20.1–66.5%) and hibernation (21.7–58.6%). The length of time the box had been deployed, the availability of artificial food and front garden to back garden access significantly increased the likelihood that a nest box had been used for all four nesting types, whereas other factors related to placement within the garden (e.g., in a sheltered location, on hardstanding such as paving, distance from the house) and resource provisioning (bedding) affected only some nesting behaviours. The factors most strongly associated with nest box use were the provisioning of food and bedding. These data suggest, therefore, that householders can adopt simple practices to increase the likelihood of their nest box being used. However, one significant limitation evident within these data is that, for welfare reasons, householders do not routinely monitor whether their box has been used. Consequently, future studies need to adopt strategies which enable householders to monitor their boxes continuously. Ultimately, such studies should compare the survival rates and reproductive success of hedgehogs within artificial refuges versus more natural nest sites, and whether these are affected by, for example, the impact of nest box design and placement on predation risk and internal microclimate.

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## INTRODUCTION

The construction of urban areas is typically associated with the loss, fragmentation and degradation of natural habitats (*Fischer & Lindenmayer, 2007; Angel et al., 2011*). Such

changes frequently result in a reduction of the availability and quality of fundamental resources for wildlife including suitable sites for breeding, resting or hibernating (*Berthier et al., 2012; Shanahan et al., 2014; Reynolds et al., 2019*). Within urban areas, these sites can be lost because of changes at different spatial scales and for different underlying reasons. For example, areas of woodland and scrub may be cleared for building developments, native vegetation may be replaced with non-native species for aesthetic reasons, and individual trees may be removed where they affect built structures or pose a threat to human safety (*Reynolds et al., 2019; Wu, Liang & Li, 2019*). The loss or degradation of these sites can have significant impacts on populations if associated directly with reproductive output (*Franco, Marques & Sutherland, 2005; Chace & Walsh, 2006; Martin & Martin, 2007; Shanahan et al., 2014*), but can also disrupt resting (*Auslebrook et al., 2018; Grunst et al., 2021*) and hibernation patterns (*Grol, Voûte & Verboom, 2011*). One approach to help mitigate the loss of natural breeding and resting sites in urbanised areas is the use of artificial refuges.

Artificial refuges have been used as conservation tools in towns and cities (*Cowan et al., 2021*) to improve habitat connectivity, facilitate species introductions or translocations, and/or monitor species abundance and distributions (*Beyer & Goldingay, 2006; Williams et al., 2013; Goldingay, Rohweder & Taylor, 2020*). In addition to conservation organisations, individual householders may also provide a range of different types of refuges (e.g., bird nest boxes, bat boxes, insect hotels, toad houses, etc.) in their own gardens on an *ad hoc* basis (*Gaston et al., 2005; Davies et al., 2009*). Clearly, the physical structure of any refuge must meet the requirements of the focal species (e.g., *Latham & Knowles, 2008; Kaneko et al., 2010; Hodges & Seabrook, 2016; Ruegger, 2017; Larson et al., 2018; Shaw et al., 2021*), but householders can potentially purchase a wide range of commercial designs that vary in size and construction materials. Similarly, designs posted online by conservation or gardening organisations can be equally varied, and householders may also create their own designs based on the materials that are available to them and their own perceptions of species' requirements.

Well-designed artificial refuges can help to maintain local populations on a long-term basis (*Goldingay et al., 2015*) and potentially improve breeding success relative to conspecifics using natural nesting sites (*Bolton et al., 2004; Libois et al., 2012; Brazill-Boast, Pryke & Griffith, 2013*). The provision of nest boxes for the common dormouse (*Muscardinus avellanarius*), for instance, has been associated with a more than doubling in adult abundance (*Juškaitis, 2005*), and, for urban birds, has been known to aid the recovery of populations to approximately 50% of original levels within five years of the loss of original sites (*Dulisz et al., 2022*). However, a use of inappropriate designs, materials and/or positioning could result in negative outcomes for wildlife (*Larson et al., 2018*). For example, nest boxes with poor insulative properties can result in high temperature variability within the nesting chamber (*Larson et al., 2015; Larson et al., 2018*) which has been associated with declines in clutch size, nestling growth and fledging success of birds (*Larson et al., 2015; Bleu, Agostini & Biard, 2017*). For lactating mammals, warmer nest boxes could reduce nest attendance (*van der Vinne et al., 2014*) or occupancy (*Guillemette et al., 2008*) during breeding periods, but, for hibernators, could help to limit heat loss, and therefore energy expenditure, during torpor (*Nedergaard & Cannon, 1990; Madikiza et al., 2010*)

and aid passive rewarming when rousing (Hoeh *et al.*, 2018). Alternatively, if hibernacula experience unusually high temperatures, the resulting higher body temperatures could lead to substantial increases in energetic expenditure (Humphries, Thomas & Speakman, 2002) as well as more frequent arousals from torpor (Pretzluss & Dausmann, 2012). Different designs may also influence the risk of predation, conspecific parasitism and other forms of disturbance (Davison & Bollinger, 2000). For example, animals using artificial refuges which are more conspicuous than natural nest sites (Evans *et al.*, 2002), or those which lack anti-predator devices (Bailey & Bonter, 2017), might experience increased rates of predation. Furthermore, given that variability in refuge design may ultimately affect survival and/or reproductive rates, species might then be expected to exhibit preferences for those design elements that positively affect these outcomes such as material (Rueegger, Goldingay & Brookes, 2013), entrance type (Goldingay *et al.*, 2015) or orientation (Ardia, Pérez & Clotfelter, 2006). Ultimately, knowledge of these factors would enable conservation practitioners to optimise refuge design.

In addition to their physical design, the use of artificial refuges can be affected by factors relating to positioning (Madikiza *et al.*, 2010) and local- and landscape-level features (Nakamura-Kojo *et al.*, 2014; Le Roux *et al.*, 2016), such as the quality of nearby foraging habitat (Catry *et al.*, 2013) and availability of natural nest sites (Madikiza *et al.*, 2010). Even where good quality habitats are available, however, animals may display a preference for poor quality nest sites that inadvertently induces maladaptive breeding and fitness responses (Battin, 2004; Hale & Swearer, 2016). This concept is termed an ‘ecological trap’ and occurs when there is a mismatch between external cues of nest site selection (*e.g.*, food availability and suitable nest box design) and the actual quality of the site. For example, great tits (*Parus major*) in urban areas preferentially select nest boxes with larger cavities, yet these are associated with lower fledging success (Demeyrier *et al.*, 2016). Ultimately, the provision of artificial refuges may facilitate breeding within sub-optimal habitats (Mänd *et al.*, 2005), and such ecological traps might drive reductions in species abundance (Battin, 2004; Hale & Swearer, 2016).

An absence of knowledge of what constitutes effective design, appropriate placement and whether artificial refuges are used successfully can limit conservation efforts (Cowan *et al.*, 2020). Artificial refuges have been most widely studied (Brady, Risch & Dobson, 2000; Cowan *et al.*, 2021) and applied (Gryz, Jaworski & Krauze-Gryz, 2021) for birds both during and outside of breeding seasons (*e.g.*, Mainwaring, 2011); data relating to ground-dwelling terrestrial small mammals are comparatively limited (Cowan *et al.*, 2021) despite declines within urban areas (*e.g.*, Baker *et al.*, 2003; Gortat *et al.*, 2014; Łopucki & Kitowski, 2017). For example, in the UK, householders are commonly urged by wildlife organisations to install nest boxes in their gardens for the West European hedgehog (*Erinaceus europaeus*, hereafter ‘hedgehog’) (BBC, 2014; British Hedgehog Preservation Society, 2021; The Wildlife Trusts, 2021), a small (<1.5 kg), solitary, nocturnal hibernator of conservation concern (Mathews *et al.*, 2018; Mathews & Harrower, 2020).

Hedgehog numbers have declined substantially in rural areas in the UK over the last few decades (Roos, Johnston & Noble, 2012), which is likely attributable to agricultural intensification (Hof & Bright, 2010; Yarnell & Pettett, 2020), vehicle collisions (Wright *et*

*al.*, 2020), direct predation by or intraguild competition with the European badger (*Meles meles*) (Young *et al.*, 2006; Trewby *et al.*, 2014; Williams *et al.*, 2018a) and habitat loss and fragmentation (Rondinini & Doncaster, 2002; Moorhouse *et al.*, 2014): the latter is most commonly discussed in the context of the loss of hedgerows, a habitat feature that is thought to be particularly important for hedgehogs for nesting, foraging or providing cover from predators (Hof, Snellenberg & Bright, 2012; Pettett *et al.*, 2017). Conversely, however, hedgehogs seem to be attracted to (Doncaster, Rondinini & Johnson, 2001; Pettett *et al.*, 2017) and abundant within (Hubert *et al.*, 2011; Van de Poel, Dekker & Van Langevelde, 2015; Schaus *et al.*, 2020; Schaus Calderón, 2021) areas of human habitation where residential gardens are a widely-used and favoured habitat (Baker & Harris, 2007; Hof & Bright, 2009; Dowding *et al.*, 2010; Williams, Stafford & Goodenough, 2015; Pettett *et al.*, 2017; Williams *et al.*, 2018b; Rasmussen *et al.*, 2019; Gazzard & Baker, 2020; Gazzard, Yarnell & Baker, 2022). Residential gardens (private, typically enclosed, areas adjoining dwellings that may contain lawn(s), ornamental plantings, vegetable plots, ponds, paved areas, decking, sheds and/or other outbuildings) in Britain average 188 m<sup>2</sup> in size (Office for National Statistics, 2020) but collectively can form up to 47% of total green space in some cities (Loram *et al.*, 2007). In this habitat, householders commonly leave out food for hedgehogs in the form of soft (*e.g.*, canned pet or hedgehog foods) or solid (*e.g.*, pet kibble) products, though the natural diet of hedgehogs is primarily insectivorous (Haigh, Butler & O’Riordan, 2012a; Haigh, O’Riordan & Butler, 2012b). Given that householders have a high affinity for hedgehogs (Morris, 2018), the implementation of hedgehog-friendly activities within gardens could have a significant positive impact on this species.

Hedgehog nest boxes (also known as hedgehog houses; Fig. 1) are thought to have grown in popularity over recent years and are now widely commercially available (see Stone, 2020), with numerous guidelines on how to construct homemade versions also available online (*e.g.*, British Hedgehog Preservation Society, 2021; Hedgehog Street, 2021; The Wildlife Trusts, 2021). These are simple boxes or box-like structures within which hedgehogs construct nests out of vegetative material found in the environment or supplied by householders. To date, no studies have been conducted to quantify the frequency with which hedgehogs use nest boxes, whether certain design features or positioning influence their use, and whether influencing factors change between seasons. Such information is fundamental for advising householders and conservation practitioners on how to most effectively provide refuges.

Throughout the annual cycle, hedgehogs construct nests for four different purposes: daytime nesting outside the hibernation period (hereafter ‘summer day nesting’ for brevity), breeding, daytime nesting during the hibernation period (hereafter ‘winter day nesting’) and winter hibernation. In the UK, hedgehogs hibernate between November–April, but typically rouse several times (Reeve, 1994; Morris, 2018). Summer day nesting is therefore defined as day nesting at any time during March–October inclusive. Breeding nests may also be formed at any point during this period: the majority of litters in the UK are produced early in the annual cycle (May–June: Deanesly, 1934; Jackson, 2006; Haigh, 2011), although ‘late litters’ are not uncommon in August–October (Dowler Burroughes, Dowler & Burroughes, 2021). Breeding nests tend to be occupied by the mother and usually 3–6 young



**Figure 1** Examples of homemade (A–F) and commercially available (G–I) artificial refuges for hedgehogs. Hedgehog nest boxes vary in size and design, but average nest box dimensions reported in this study ( $N = 4,509$ ) were  $629 \times 726 \times 423$  mm (width  $\times$  depth  $\times$  height) for homemade nest boxes, and  $499 \times 478 \times 311$  mm for manufactured nest boxes. Image credits: (A) G. Northcott; (B) C. Gazzard; (C) S. Wilkinson; (D) L. Pearse; (E) V. Yates; (F) R. Brenton. Commercially available nest box images: A. Gazzard; produced by (G) Home & Roost, (H) Coopers of Stortford and (I) Tom Chambers.

Full-size  DOI: [10.7717/peerj.13662/fig-1](https://doi.org/10.7717/peerj.13662/fig-1)

(*Morris, 1977; Kristiansson, 1981; Walhovd, 1984*), with the litter becoming independent by approximately six weeks of age (*Morris, 2018*).

Rural hedgehogs appear to favour nesting in hedgerows and woodlands (*Haigh, O’Riordan & Butler, 2012b; Bearman-Brown et al., 2020*); knowledge of nest site selection in urban habitats is lacking, but hedgehogs have been known to nest in gardens (*British Hedgehog Preservation Society, 2022*). Nests are constructed at ground level under shelter, for example, under hedging, scrub or log piles, though are sometimes also formed in rabbit (*Oryctolagus cuniculus*) burrows or cavities beneath garden sheds or decking (*Jackson & Green, 2000; Morris, 2018*). Day nests are loosely formed (*Rautio et al., 2014*) compared to the compact hibernacula or larger breeding nests (*Reeve, 1994; Morris, 2018*). In all cases, a central nesting core is created under a dome of bedding material that typically contains dry broadleaves, grass and other foliage (*Reeve & Morris, 1985; Rautio et al., 2014; Pettett et al., 2017*). Nest-sharing by adults is very rare (*Reeve, 1994*), but hedgehogs will readily make use of multiple day and hibernation nests (*Haigh, O’Riordan & Butler, 2012b; Rautio et al., 2014; Morris, 2018; Yarnell et al., 2019; Bearman-Brown et al., 2020*), including those that have been used by other individuals (*Riber, 2006; Haigh, O’Riordan & Butler, 2012b;*

*Rautio et al., 2014*). Distances between successive nest sites have been recorded to range from 2–323 m (*Jensen, 2004; Yarnell et al., 2019*).

Nesting at ground level exposes hedgehogs to numerous risks: they can be disturbed by humans, companion animals or livestock (*Bearman-Brown et al., 2020*); are potentially accessible to predators including badgers, foxes (*Vulpes vulpes*) and domestic dogs (*Canis lupus familiaris*); are vulnerable to damage or destruction caused by activities associated with land management, garden maintenance (e.g., mowing or strimming/weed whacking) and construction works; and flooding (*Morris, 2018*). Disturbances including noise, light or the accidental uncovering of a nest can prompt hedgehogs to relocate nests more frequently than usual, thereby increasing energetic expenditure (*Rast, Barthel & Berger, 2019*) as well as the risk of mortality from companion animals and road traffic, but can also potentially cause the abandonment or killing of young (*Morris, 2018*). Furthermore, hedgehogs are likely to be sensitive to changes in the internal microclimate of nests: high levels of humidity have been linked to the advanced decay of broad-leaved nesting material (*Morris, 1972*), ectoparasite presence (*Heeb, Kölliker & Richner, 2000*) and the efficiency of animal evaporative heat loss mechanisms (*McComb et al., 2021*). During hibernation, low temperatures inside nests can accelerate heat loss of individuals in torpor and cause fat stores to rapidly deplete (*Soivio, Tähti & Kristoffersson, 1968; Jensen, 2004; Morris, 2018*). Last, if different individuals use or reuse the same box in quick succession, this could potentially increase the risk of parasite transmission (*Tomás et al., 2007*).

Given the lack of quantified information on many aspects relating to the deployment of hedgehog nest boxes by householders, and their use by hedgehogs, we used a questionnaire survey of householders in the UK to identify the factors associated with the use of hedgehog boxes for summer day nesting, breeding, winter day nesting and hibernation. Based on these results, and the associated limitations of these data, we make suggestions for future studies to collect data that would form the basis for recommendations made to householders about how to optimise the deployment of nest boxes (and associated materials such as bedding), as well as identifying the role that artificial refuges may have in the future conservation of this species.

## MATERIALS & METHODS

Data were collected using an online questionnaire survey (15/08/2017-31/10/2017 inclusive) of UK householders who had installed at least one hedgehog nest box in their garden. The questionnaire was promoted as ‘The Hedgehog Housing Census’ by the Hedgehog Street campaign (run jointly by the People’s Trust for Endangered Species and British Hedgehog Preservation Society) and advertised through social media, local radio interviews and newspaper articles. As some of the information requested may have led respondents to be tempted to open their box(es) to see if hedgehogs were using them, a statement was included at the start of the questionnaire that explicitly instructed respondents not to do so as this may have adverse effects on the welfare of nesting animals. Additionally, since this survey was focussed on the use of nest boxes as refuges for sleeping, breeding and/or hibernating, a second statement outlined that respondents were not to complete the survey

if they had installed hedgehog nest boxes solely for the purpose of feeding hedgehogs: many householders in the UK use covered feeding stations to protect hedgehogs from other species (*e.g.*, cats (*Felis catus*), foxes and badgers) whilst simultaneously protecting the food from inclement weather and from competition with these other species (see [Finch et al., 2020](#)). Householders with >1 nest box were asked to complete one survey for each box. Responses that were incomplete, or those that appeared to describe nest boxes being used in locations other than domestic gardens (*e.g.*, in wildlife rescue centres or for rehabilitated individuals at ‘soft release’ sites), were removed prior to analyses.

The questionnaire requested information on a wide range of variables including: the respondent’s geographical location; characteristics of their garden; whether they owned a dog; the size and design features of the box; the length of time that the box had been installed and how it was positioned in the garden; if and where, relative to the location of the nest box, the respondent put food out for hedgehogs; whether they had put any natural or artificial bedding material in the box; whether they fed garden birds; whether they had seen foxes and/or badgers in their garden; and whether the nest box had ever been used by hedgehogs for day nesting in the summer (March-October) or winter (November-February), breeding or hibernating. Nest box use was defined on the basis of direct or indirect observations (*e.g.*, through the use of motion-activated trail cameras or other monitoring devices) of a hedgehog entering or exiting the box. The aerial coverage of urban, arable, woodland and grassland habitat within a 500 m radius around each site (500 m was chosen given existing hedgehog movement data: ([Dowding et al., 2010](#); [Schaus Calderón, 2021](#); [Gazzard, Yarnell & Baker, 2022](#))), and the distance to the nearest patch of each of these habitats, were quantified with PostGIS and using a 2017 Land Cover Map of the UK (UK Centre for Ecology & Hydrology; [Morton et al., 2020](#)); the aggregate habitat classes in the Land Cover Map are based on Broad Habitat Classifications used in the government’s 1994 UK Biodiversity Action Plan ([Jackson, 2000](#)). Variables are defined in [Table 1](#).

To assess factors affecting whether nest boxes had been used by hedgehogs, we fitted generalised linear models (GLMs) with binomial distributions and logit link functions. Many participants were not aware of whether their nest box had been used for every category of nesting but could indicate whether the nest box had been used for at least one type. Therefore, the data were separated into four groups representing nest boxes that were known to have been or not have been used for: (a) summer day nesting, (b) breeding, (c) winter day nesting or (d) hibernation. In addition, as many nest boxes had only been installed recently, the response variable indicated whether the nest box had been used at any point since it had been deployed rather than the extent of use over time. When the binary responses comprised a greater number of “events” (nest box used) than “non-events” (nest box not used), we opted not to balance (subsample the dataset to obtain an even split of events and non-events) the data in favour of treating each of the four GLM analyses in the same way. Furthermore, the imbalances in proportions of boxes used were not extreme, and biases in maximum likelihood estimates are reduced in larger sample sizes (see [Jiménez-Valverde, Lobo & Hortal, 2009](#); [Salas-Eljatib et al., 2018](#)).

Correlations between explanatory variables were checked prior to analysis, and further examined using generalised variance inflation factors (GVIFs) during the modelling

**Table 1** Variables considered in the analysis of hedgehog nest box use within gardens. Source: Q = the variable was derived from the questionnaire survey; LC = data were quantified using a UK land class dataset (Morton et al., 2020).

Theme	Variable	Description	Variable type	Source
Nest box use	SUMMERDAY	How long, in months, the respondent believed that the nest box had been used for summer day nesting (March–October), breeding, winter day nesting (November–February) or hibernation	Converted to binary variable for analysis: (0) Box had not been used (1) Box had been used	Q
	BREEDING			
	WINTERDAY			
	HIBERNATION			
Time installed	MONTHS INSTALLED	The number of months the nest box had been installed in the respondent's garden	Continuous	Q
Nest box design	TYPE	Whether the nest box was homemade or purchased	(0) Purchased (1) Homemade	Q
	MATERIAL	The primary material the nest box was constructed with	(0) Timber (1) Plywood/plyboard (2) Brushwood (3) Plastic (4) Other (including wicker, woodcrete and brick)	Q
	HEIGHT	Nest box height (cm)	Continuous	Q
	WIDTH	Nest box width (cm)	Continuous	Q
	DEPTH	Nest box depth (cm) (front to back)	Continuous	Q
	CAPACITY	Maximum capacity (cm <sup>3</sup> ) of the nest box (Height * Width * Depth)	Continuous	Q
	BASE	Whether the nest box had an integral base	(0) No base (1) Base	Q
	TUNNEL	Whether the nest box had an external tunnel entrance	(0) No tunnel entrance (1) Tunnel entrance	Q
	PARTITION	Whether the nest box had an internal tunnel or partition	(0) No internal partition (1) Internal partition	Q
	VENT	Whether the nest box had ventilation holes	(0) No vent (1) Vent	Q
	LINING	Whether the nest box had a waterproof lining	(0) Nest box is unlined (1) Nest box is lined	Q
Nest box positioning	FRONT OR BACK	Whether the nest box was positioned in a front or back garden	(0) Front garden (1) Back garden	Q
	HARD STANDING	Whether the nest box was located on hardstanding ( <i>i.e.</i> , patio, paved or decked areas)	(0) Not on hardstanding (1) On hardstanding	Q
	SHELTERED	Whether the nest box was under shelter ( <i>e.g.</i> , shrubbery)	(0) Not in sheltered location (1) In a sheltered location	Q
	DISTANCE BUILDING	Whether the nest box was located <5 m from a building	(0) ≥5 m from a building (1) <5 m from a building	Q

(continued on next page)



Table 1 (continued)

Theme	Variable	Description	Variable type	Source
	FACING	Whether the nest box entrance was facing into the open or elsewhere	(0) Facing a wall/fence (1) Parallel to a wall/fence (2) Facing shrubs/planting (3) Facing the open (4) Other	Q
	ORIENTATION	The direction that the nest box entrance was facing	(0) North (1) East (2) South (3) West	Q
	RAISED	Whether the nest box was raised off the ground or not	(0) Not raised (1) Raised	Q
Garden characteristics	CONNECTED	The number of neighbouring back gardens which were accessible to hedgehogs from the respondent's back garden	Continuous	Q
	FRONT BACK ACCESS	Whether a hedgehog could access the respondent's back garden from their front garden	(0) No front-to-back access (1) Front-to-back access	Q
	OTHER NESTS	Whether the respondent had directly observed, or found evidence of, hedgehogs nesting outside of a nest box elsewhere in their back garden	(0) No alternative nesting sites observed (1) Alternative nesting sites observed	Q
	POND	Whether the garden contained a pond	(0) No pond (1) Pond	Q
	GOOD HAB	The proportion of "good" habitat present in the garden, including shrubs, a wild area, woodpile, compost heap, shed or decking with cavity beneath, lawn, vegetable patch and/or flowerbeds	Continuous (proportion)	Q
Resources for hedgehogs	BEDDING	Whether the respondent provided artificial ( <i>e.g.</i> , newspaper) or natural ( <i>e.g.</i> , leaves, hay) bedding within the nest box, or both	(0) None provided (1) One type of bedding (2) Both types of bedding	Q
	HEDGEHOG FOOD	The location in which food was provided for hedgehogs in the garden	(0) None provided (1) Scattered in varying locations (2) <0.5 m from nest box (3) 0.5–5 m from nest box (4) 5.1–10 m from nest box (5) >10 m from nest box	Q
Other animals	BIRD FOOD	Whether the respondent supplied food for birds in their garden	(0) None provided (1) Food provided	Q
	BADGERFOX	Whether the respondent ever observed badgers or foxes in their garden (NB badger and fox sightings were merged due to the low number of positive sightings)	(0) Not sighted (1) Sighted	Q

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Table 1 (continued)

Theme	Variable	Description	Variable type	Source
	DOGS	Whether the respondent owned any pet dogs that were allowed access to the garden	(0) No dogs (1) Dogs	Q
Habitats	URBAN500 ARABLE500 WOOD500 GRASS500	The quantity (m <sup>2</sup> ) of urban/arable/woodland/grassland habitats within 500 m of the respondent's location (estimated from the central point of their postcode)	Continuous	LC
	URBANDIST ARABLEDIST WOODDIST GRASSDIST	Distance (m) to the nearest urban/arable/woodland/grassland habitat patches from the respondent's location (estimated from the central point of their postcode)	Continuous	LC

process (Fox & Monette, 1992). For the former, the threshold of 'high' correlation was set at a Pearson coefficient value  $< -0.5$  or  $> 0.5$ , and for the latter, the GVIF threshold was chosen to be  $< 2$  (see Zuur, Ieno & Elphick, 2010). Models were constructed by sequentially adding variables and examining Akaike's Information Criterion (AIC) values (Burnham & Anderson, 1998). In some cases, nonsignificant variables were retained if they improved model fit and/or if it was considered informative to highlight their importance across different nesting types (e.g., BEDDING, BADGERFOX, DOGS). Final model fit was assessed with the Hosmer-Lemeshow test which compares the number of expected events—as deduced from the regression model—to the number of observed events, commonly for 10 divisions of the dataset (Hosmer & Lemeshow, 1980). Additionally, Nagelkerke pseudo- $R^2$  values are provided for each final model to give an indication of the amount of variance in the dependent variable that was explained by the independent variables (Nagelkerke, 1991). Analyses were performed in R 4.0.3.

## RESULTS

In total, 4,309 questionnaire responses were available for analysis: 1,717 (39.8%) responses were associated with homemade nest boxes, and 2,592 (60.2%) with commercially purchased nest boxes. However, 1,492 respondents did not monitor the use of their nest box and could not provide information on whether it had been used for any type of nesting. Considering only those respondents who stated that they knew whether their nest box had been used or not, 81.3% ( $N = 1,868$ ), 28.2% ( $N = 1,104$ ), 66.5% ( $N = 1,300$ ) and 58.6% ( $N = 1,592$ ) reported that hedgehogs had used the box at least once for summer day nesting, breeding, winter day nesting or hibernation, respectively.

Of all nest boxes reported, 46.3% had been installed for  $< 1$  year, 42.0% for 1–5 years, 8.2% for 5–10 years and 3.6% for  $> 10$  years. Overall, 77.9% of homemade boxes and 79.5% of commercial boxes had been installed only after hedgehogs had been sighted in the garden: this is equivalent to 78.9% of all the boxes in the survey. Respondents

also collectively directly observed, or observed evidence of, at least 2,546 other nest sites used by hedgehogs within their gardens, which equates to an average of 0.6 per garden. These comprised nests constructed under garden vegetation (46.0%), woodpiles (14.5%), compost heaps (6.3%), decking (5.7%), sheds (21.5%) and buildings (6.1%).

### Factors affecting nest box use

The number of survey responses that were available for modelling factors affecting the use of nest boxes varied between nesting types: 1,868 for summer day nesting, 1,104 for breeding, 1,300 for winter day nesting, and 1,592 for hibernation. Multicollinearity checks showed that some of the nest box design variables, as well as habitats variables, were correlated. Consequently, the following variables (Table 1) were excluded from the analyses: BASE, TUNNEL, PARTITION, VENT, LINING, ARABLE500, WOOD500, and GRASS500. In addition, URBANDIST was omitted as most participants lived directly within urban areas; <6% of respondents resided outside of land classified as urban.

For all types of nest box use, the length of time it had been installed, positioning within the garden, the provisioning of resources and site-based factors significantly influenced whether it had been used or not (Tables 2 and 3). Nest boxes were significantly more likely to have been used for all four patterns of use the longer they had been installed, if the back garden could be accessed from the front, if the householder put out food for hedgehogs, and if other nest sites were present in the garden (Table 3). Positioning on hardstanding (such as paving, patio or decking), in a sheltered location and the supply of bedding each increased the likelihood that the box was used in three of the four contexts, but these were not consistent. Boxes in close proximity to a building, those that were raised off the ground and were homemade were more likely to have been used in two contexts, but again these patterns were not consistent. Factors that significantly negatively impacted nest box use included whether the entrance to the box faced into the open, the presence of a garden pond, an increase in the extent of potentially valuable habitat (including shrubs, a wild area, woodpile, compost heap, shed or decking with cavity beneath, lawn, vegetable patch and/or flowerbeds) within the garden, and the presence of dogs (Table 3).

## DISCUSSION

The percentage of nest boxes reported to have been used at least once varied between nesting types: summer day nesting (81.3%), breeding (28.2%), winter day nesting (66.5%) and hibernation (58.6%). These are, however, maximum figures because of the way in which data were collated for analysis; we were only able to include respondents who had evidence that their box had, or had not, been used for these purposes. If we assume that all additional boxes owned by respondents who did not have such evidence had never been used, then these figures would be markedly reduced: summer day nesting (35.3%), breeding (7.2%), winter day nesting (20.1%) and hibernation (21.7%). This lack of definitive information about patterns of use is, in part, related to the fact that conservation organisations recommend that householders should not look in their box to check if they are being used due to the risks associated with disturbing hedgehogs. Instead, householders are advised to use motion-activated cameras outside the box or other approaches, such as

**Table 2** Results of generalised linear models examining factors affecting hedgehog nest box use for (a) summer day nesting, (b) breeding, (c) winter day nesting and (d) hibernation. Reference levels for variables are indicated in parentheses. SE = standard error; OR = odds ratio. Variables that had a significant effect ( $p < 0.05$ ) are highlighted in bold.

(a) Summer day nests ( $N = 1,868$ ). Hosmer and Lemeshow Test:  $\chi^2_8 = 10.226$ ,  $p = 0.250$ ; Nagelkerke  $R^2 = 0.235$ .

Variable	Estimate	SE	<i>z</i> value	<i>p</i>	OR	95% CI
(Intercept)	-1.250	0.524	-2.384	0.017	0.287	0.103–0.810
<b>MONTHS INSTALLED</b>	<b>0.009</b>	<b>0.002</b>	<b>3.843</b>	<b>&lt;0.001</b>	<b>1.009</b>	<b>1.005–1.015</b>
TYPE (Purchased)						
Homemade	0.261	0.140	1.860	0.063	1.298	0.988–1.712
<b>FRONT OR BACK (Front garden)</b>						
Back garden	<b>0.528</b>	<b>0.220</b>	<b>2.398</b>	<b>0.016</b>	<b>1.696</b>	<b>1.094–2.599</b>
<b>HARD STANDING (Not on hardstanding)</b>						
On hardstanding	<b>0.430</b>	<b>0.190</b>	<b>2.266</b>	<b>0.023</b>	<b>1.538</b>	<b>1.068–2.251</b>
<b>SHELTERED (Not in sheltered location)</b>						
In a sheltered location	<b>0.529</b>	<b>0.168</b>	<b>3.158</b>	<b>0.002</b>	<b>1.698</b>	<b>1.219–2.354</b>
<b>DISTANCE BUILDING (<math>\geq 5</math> m from a building)</b>						
<5 m from a building	<b>0.421</b>	<b>0.158</b>	<b>2.667</b>	<b>0.008</b>	<b>1.524</b>	<b>1.122–2.085</b>
<b>FACING (Entrance faces wall/fence)</b>						
Parallel to wall/fence	0.001	0.302	0.003	0.997	1.001	0.541–1.780
Faces shrubs/plantings	-0.043	0.314	-0.138	0.890	0.957	0.507–1.746
<b>Faces the open</b>	<b>-0.585</b>	<b>0.296</b>	<b>-1.978</b>	<b>0.048</b>	<b>0.557</b>	<b>0.305–0.976</b>
Other	-0.267	0.336	-0.794	0.427	0.766	0.390–1.465
<b>RAISED (Not raised)</b>						
Raised	<b>0.364</b>	<b>0.178</b>	<b>2.053</b>	<b>0.040</b>	<b>1.440</b>	<b>1.023–2.054</b>
<b>FRONT BACK ACCESS (No front-to-back access)</b>						
Front-to-back access	<b>0.470</b>	<b>0.143</b>	<b>3.277</b>	<b>0.001</b>	<b>1.599</b>	<b>1.206–2.116</b>
<b>OTHER NESTS (No alternative nesting sites used)</b>						
Alternative nesting sites used	<b>0.768</b>	<b>0.136</b>	<b>5.650</b>	<b>&lt;0.001</b>	<b>2.156</b>	<b>1.655–2.821</b>
<b>POND (No garden pond)</b>						
Pond	<b>-0.368</b>	<b>0.141</b>	<b>-2.602</b>	<b>0.009</b>	<b>0.692</b>	<b>0.525–0.914</b>
<b>GOOD HAB</b>	<b>-0.012</b>	<b>0.004</b>	<b>-2.982</b>	<b>0.003</b>	<b>0.988</b>	<b>0.980–0.996</b>
<b>BEDDING (None provided)</b>						
One type	<b>0.914</b>	<b>0.182</b>	<b>5.008</b>	<b>&lt;0.001</b>	<b>2.493</b>	<b>1.740–3.560</b>
Both types	<b>1.457</b>	<b>0.268</b>	<b>5.431</b>	<b>&lt;0.001</b>	<b>4.293</b>	<b>2.560–7.347</b>
<b>HEDGEHOG FOOD (None provided)</b>						
Scattered in varying locations	0.803	0.510	1.574	0.115	2.233	0.865–6.583
<0.5 m from nest box	<b>0.881</b>	<b>0.237</b>	<b>3.720</b>	<b>&lt;0.001</b>	<b>2.414</b>	<b>1.523–3.857</b>
0.5–5 m from nest box	<b>1.463</b>	<b>0.185</b>	<b>7.903</b>	<b>&lt;0.001</b>	<b>4.317</b>	<b>3.004–6.209</b>
5.1–10 m from nest box	<b>1.133</b>	<b>0.313</b>	<b>3.621</b>	<b>&lt;0.001</b>	<b>3.105</b>	<b>1.708–5.849</b>
>10 m from nest box	<b>1.233</b>	<b>0.243</b>	<b>5.082</b>	<b>&lt;0.001</b>	<b>3.433</b>	<b>2.145–5.563</b>
<b>BADGERFOX (Not sighted)</b>						
Sighted	-0.159	0.135	-1.177	0.239	0.853	0.655–1.111
<b>DOGS (Absent)</b>						
Present	-0.224	0.152	-1.471	0.141	0.799	0.594–1.081

(continued on next page)

Table 2 (continued)

(b) Breeding nests ( $N = 1,104$ ). Hosmer and Lemeshow Test: $\chi^2_8 = 8.621$ , $p = 0.375$ ; Nagelkerke $R^2 = 0.230$ .						
Variable	Estimate	SE	<i>z</i> value	<i>p</i>	OR	95% CI
(Intercept)	-3.325	0.422	-7.873	<0.001	0.036	0.015–0.080
<b>MONTHS INSTALLED</b>	<b>0.017</b>	<b>0.002</b>	<b>7.908</b>	<b>&lt;0.001</b>	<b>1.017</b>	<b>1.013–1.021</b>
TYPE (Purchased)						
Homemade	0.267	0.153	1.746	0.081	1.306	0.967–1.762
<b>SHELTERED (Not in sheltered location)</b>						
<b>In a sheltered location</b>	<b>0.570</b>	<b>0.228</b>	<b>2.498</b>	<b>0.013</b>	<b>1.768</b>	<b>1.144–2.805</b>
<b>FRONT BACK ACCESS (No front-to-back access for hedgehogs)</b>						
<b>Front-to-back access</b>	<b>0.462</b>	<b>0.177</b>	<b>2.606</b>	<b>0.009</b>	<b>1.587</b>	<b>1.127–2.259</b>
<b>OTHER NESTS (No alternative nesting sites used)</b>						
<b>Alternative nesting sites used</b>	<b>0.863</b>	<b>0.152</b>	<b>5.692</b>	<b>&lt;0.001</b>	<b>2.369</b>	<b>1.764–3.196</b>
<b>POND (No garden pond)</b>						
<b>Pond</b>	<b>-0.667</b>	<b>0.165</b>	<b>-4.041</b>	<b>&lt;0.001</b>	<b>0.513</b>	<b>0.370–0.707</b>
BEDDING (None provided)						
One type	-0.067	0.229	-0.291	0.771	0.936	0.602–1.480
Both types	-0.229	0.286	-0.804	0.422	0.795	0.455–1.395
<b>HEDGEHOG FOOD (None provided)</b>						
Scattered in varying locations	0.992	0.552	1.797	0.072	2.696	0.877–7.810
<0.5 m from nest box	-0.054	0.386	-0.140	0.889	0.947	0.440–2.017
<b>0.5–5 m from nest box</b>	<b>0.976</b>	<b>0.280</b>	<b>3.485</b>	<b>&lt;0.001</b>	<b>2.653</b>	<b>1.563–4.705</b>
5.1–10 m from nest box	0.719	0.403	1.784	0.074	2.053	0.926–4.531
<b>&gt;10 m from nest box</b>	<b>1.141</b>	<b>0.321</b>	<b>3.556</b>	<b>&lt;0.001</b>	<b>3.131</b>	<b>1.691–5.978</b>
BADGERFOX (Not sighted)						
Sighted	-0.096	0.149	-0.645	0.519	0.908	0.678–1.216
DOGS (Absent)						
Present	-0.323	0.182	-1.776	0.076	0.724	0.504–1.029
(c) Winter day nests ( $N = 1,300$ ). Hosmer and Lemeshow Test: $\chi^2_8 = 10.681$ , $p = 0.220$ ; Nagelkerke $R^2 = 0.240$ .						
Variable	Estimate	SE	<i>z</i> value	<i>p</i>	OR	95% CI
(Intercept)	-1.976	0.516	-3.832	<0.001	0.139	0.050–0.381
<b>MONTHS INSTALLED</b>	<b>0.014</b>	<b>0.003</b>	<b>5.442</b>	<b>&lt;0.001</b>	<b>1.014</b>	<b>1.009–1.019</b>
TYPE (Purchased)						
<b>Homemade</b>	<b>0.483</b>	<b>0.137</b>	<b>3.515</b>	<b>&lt;0.001</b>	<b>1.621</b>	<b>1.240–2.125</b>
<b>HARD STANDING (Not on hardstanding)</b>						
<b>On hardstanding</b>	<b>0.468</b>	<b>0.184</b>	<b>2.547</b>	<b>0.011</b>	<b>1.597</b>	<b>1.119–2.302</b>
<b>SHELTERED (Not in sheltered location)</b>						
<b>In a sheltered location</b>	<b>0.495</b>	<b>0.175</b>	<b>2.821</b>	<b>0.005</b>	<b>1.640</b>	<b>1.163–2.314</b>
<b>DISTANCE BUILDING (<math>\geq 5</math> m from a building)</b>						
<5 m from a building	0.216	0.148	1.463	0.144	1.241	0.930–1.662
<b>FACING (Entrance faces wall/fence)</b>						
Parallel to wall/fence	-0.077	0.285	-0.270	0.787	0.926	0.523–1.605
Faces shrubs/plantings	0.031	0.297	0.104	0.917	1.031	0.570–1.831
<b>Faces the open</b>	<b>-0.590</b>	<b>0.279</b>	<b>-2.112</b>	<b>0.035</b>	<b>0.555</b>	<b>0.317–0.949</b>
Other	0.188	0.323	0.582	0.561	1.207	0.637–2.266

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Table 2 (continued)

<b>FRONT BACK ACCESS (No front-to-back access for hedgehogs)</b>						
Front-to-back access	<b>0.366</b>	<b>0.150</b>	<b>2.445</b>	<b>0.014</b>	<b>1.441</b>	<b>1.074–1.932</b>
<b>OTHER NESTS (No alternative nesting sites used)</b>						
Alternative nesting sites used	<b>0.560</b>	<b>0.134</b>	<b>4.195</b>	<b>&lt;0.001</b>	<b>1.751</b>	<b>1.349–2.278</b>
POND (No garden pond)						
Pond	−0.232	0.142	−1.626	0.104	0.793	0.600–1.049
GOOD HAB	−0.006	0.004	−1.441	0.150	0.994	0.987–1.002
<b>BEDDING (None provided)</b>						
One type	<b>0.868</b>	<b>0.204</b>	<b>4.261</b>	<b>&lt;0.001</b>	<b>2.383</b>	<b>1.601–3.564</b>
Both types	<b>1.484</b>	<b>0.266</b>	<b>5.585</b>	<b>&lt;0.001</b>	<b>4.412</b>	<b>2.636–7.482</b>
<b>HEDGEHOG FOOD (None provided)</b>						
Scattered in varying locations	0.555	0.498	1.116	0.265	1.742	0.665–4.759
<0.5 m from nest box	<b>0.662</b>	<b>0.267</b>	<b>2.477</b>	<b>0.013</b>	<b>1.938</b>	<b>1.151–3.283</b>
0.5–5 m from nest box	<b>1.065</b>	<b>0.212</b>	<b>5.011</b>	<b>&lt;0.001</b>	<b>2.900</b>	<b>1.916–4.412</b>
5.1–10 m from nest box	<b>0.633</b>	<b>0.306</b>	<b>2.071</b>	<b>0.038</b>	<b>1.883</b>	<b>1.038–4.447</b>
>10 m from nest box	<b>1.251</b>	<b>0.270</b>	<b>4.635</b>	<b>&lt;0.001</b>	<b>3.492</b>	<b>2.069–5.966</b>
BIRD FOOD (None provided)						
Provided	0.201	0.134	1.507	0.132	1.223	0.941–1.589
BADGERFOX (Not sighted)						
Sighted	−0.219	0.133	−1.643	0.100	0.803	0.618–1.043
DOGS (Absent)						
Present	−0.224	0.152	−1.471	0.141	0.799	0.594–1.081
(d) Hibernation nests ( $N = 1,592$ ). Hosmer and Lemeshow Test: $\chi^2_8 = 14.175, p = 0.077$ ; Nagelkerke $R^2 = 0.286$ .						
Variable	Estimate	SE	z value	p	OR	95% CI
(Intercept)	−2.731	0.486	−5.622	<0.001	0.065	0.025–0.168
<b>MONTHS INSTALLED</b>	<b>0.021</b>	<b>0.002</b>	<b>8.820</b>	<b>&lt;0.001</b>	<b>1.021</b>	<b>1.017–1.026</b>
<b>TYPE (Purchased)</b>						
Homemade	<b>0.251</b>	<b>0.121</b>	<b>2.080</b>	<b>0.038</b>	<b>1.285</b>	<b>1.015–1.630</b>
FRONT OR BACK (Front garden)						
Back garden	0.079	0.221	0.357	0.721	1.082	0.700–1.666
<b>HARD STANDING (Not on hardstanding)</b>						
On hardstanding	<b>0.373</b>	<b>0.161</b>	<b>2.316</b>	<b>0.021</b>	<b>1.452</b>	<b>1.061–1.996</b>
SHELTERED (Not in sheltered location)						
In a sheltered location	0.299	0.161	1.862	0.063	1.348	0.984–1.848
<b>DISTANCE BUILDING (<math>\geq 5</math> m from a building)</b>						
<5 m from a building	<b>0.341</b>	<b>0.137</b>	<b>2.500</b>	<b>0.012</b>	<b>1.407</b>	<b>1.078–1.841</b>
<b>FACING (Entrance faces wall/fence)</b>						
Parallel to wall/fence	0.001	0.302	0.003	0.997	1.001	0.541–1.780
Faces shrubs/plantings	−0.043	0.314	−0.138	0.890	0.957	0.507–1.746
Faces the open	<b>−0.585</b>	<b>0.296</b>	<b>−1.978</b>	<b>0.048</b>	<b>0.557</b>	<b>0.305–0.976</b>
Other	−0.267	0.336	−0.794	0.427	0.766	0.390–1.465
<b>ORIENTATION (Entrance faces North)</b>						
East	0.305	0.172	1.776	0.076	1.357	0.969–1.902
South	<b>0.347</b>	<b>0.168</b>	<b>2.065</b>	<b>0.039</b>	<b>1.415</b>	<b>1.018–1.968</b>
West	0.189	0.185	1.020	0.308	1.208	0.840–1.737

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Table 2 (continued)

<b>RAISED (Not raised)</b>						
<b>Raised</b>	<b>0.364</b>	<b>0.178</b>	<b>2.053</b>	<b>0.040</b>	<b>1.440</b>	<b>1.023–2.054</b>
CONNECTED	−0.021	0.045	−0.473	0.636	0.979	0.896–1.070
<b>FRONT BACK ACCESS (No front-to-back access for hedgehogs)</b>						
<b>Front-to-back access</b>	<b>0.496</b>	<b>0.134</b>	<b>3.697</b>	<b>&lt;0.001</b>	<b>1.643</b>	<b>1.263–2.139</b>
<b>OTHER NESTS (No alternative nesting sites used)</b>						
<b>Alternative nesting sites used</b>	<b>0.656</b>	<b>0.118</b>	<b>5.564</b>	<b>&lt;0.001</b>	<b>1.926</b>	<b>1.530–2.428</b>
<b>POND (No garden pond)</b>						
Pond	−0.130	0.125	−1.040	0.299	0.878	0.686–1.122
GOOD HAB	−0.004	0.003	−1.173	0.241	0.996	0.989–1.003
<b>BEDDING (None provided)</b>						
<b>One type</b>	<b>0.720</b>	<b>0.183</b>	<b>3.940</b>	<b>&lt;0.001</b>	<b>2.055</b>	<b>1.440–2.952</b>
<b>Both types</b>	<b>1.107</b>	<b>0.237</b>	<b>4.677</b>	<b>&lt;0.001</b>	<b>3.024</b>	<b>1.909–4.831</b>
<b>HEDGEHOG FOOD (None provided)</b>						
Scattered in varying locations	0.141	0.477	0.295	0.768	1.151	0.449–2.946
<0.5 m from nest box	0.167	0.245	0.684	0.494	1.182	0.732–1.911
<b>0.5–5 m from nest box</b>	<b>0.933</b>	<b>0.188</b>	<b>4.957</b>	<b>&lt;0.001</b>	<b>2.542</b>	<b>1.763–3.690</b>
<b>5.1–10 m from nest box</b>	<b>0.962</b>	<b>0.290</b>	<b>3.319</b>	<b>0.001</b>	<b>2.617</b>	<b>1.489–4.646</b>
<b>&gt;10 m from nest box</b>	<b>1.088</b>	<b>0.237</b>	<b>4.597</b>	<b>&lt;0.001</b>	<b>2.968</b>	<b>1.873–4.739</b>
<b>BIRD FOOD (None provided)</b>						
Provided	−0.102	0.121	−0.843	0.399	0.903	0.712–1.144
<b>BADGERFOX (Not sighted)</b>						
Sighted	−0.133	0.119	−1.112	0.266	0.876	0.693–1.106
<b>DOGS (Absent)</b>						
<b>Present</b>	<b>−0.346</b>	<b>0.140</b>	<b>−2.462</b>	<b>0.014</b>	<b>0.708</b>	<b>0.537–0.932</b>

placing a small stick or piece of straw across the entrance, to determine whether an animal (assumed to be a hedgehog) has entered. Although critically important in the context of ensuring the welfare of the animals involved, this does limit the amount of data available for studies such as this one: we were only able to consider whether nest boxes had ever been used during their ‘lifetime’, rather than the frequency of use.

The majority (88.3%) of hedgehog nest boxes had been installed within the five-year period prior to this survey, implying that there has been a marked increase in recent years in the number of householders providing such refuge structures. In most cases (78.9%), these boxes were deployed after the householder knew that hedgehogs were already visiting their garden implying that personal knowledge of the species’ presence is a particularly strong motivational factor influencing whether householders decide to help hedgehogs in this way. Nevertheless, the subsequent use of these boxes will be dependent on the suitability of their design and placement in the householder’s garden. Consequently, it is important that the factors influencing nest box use for day nesting, breeding and/or hibernating are identified so that householders and conservation practitioners can be advised appropriately to maximise their use.

**Table 3** Summary of explanatory variables considered in GLM analyses that had significant positive (+) or negative (-) influences on the use of nest boxes by hedgehogs for summer day nesting, breeding, winter day nesting and/or hibernation (see Table 2 for detailed breakdown). Single symbol =  $p < 0.05$ , double symbol =  $p < 0.01$ , triple symbol =  $p < 0.001$ .

Variable	Summer	Breeding	Winter	Hibernation
MONTHS INSTALLED	+++	+++	+++	+++
TYPE			+++	+
MATERIAL				
HEIGHT				
WIDTH				
DEPTH				
CAPACITY				
FRONT OR BACK	+			
HARD STANDING	+		+	+
Sheltered	++	+	++	
DISTANCE BUILDING	++			+
FACING	-		-	-
ORIENTATION				+
RAISED	+			+
CONNECTED				
FRONT BACK ACCESS	++	++	+	+++
OTHER NESTS	+++	+++	+++	+++
POND	--	---		
GOOD HAB	--			
BEDDING	+++		+++	+++
HEDGEHOG FOOD	+++	+++	+++	+++
BIRD FOOD				
BADGERFOX				
DOGS				-
URBAN500				
ARABLEDIST				
WOODDIST				
GRASSDIST				

**Notes.**

For variables with >2 categories, the effect refers to the following levels: Facing the open; Orientation to the south; BEDDING provided was natural, artificial or both; HEDGEHOG FOOD provided in any of the possible locations listed in the survey including scattered, <0.5 m, 0.5–5 m, 5.1–10 m and/or >10 m from the nest box.

Collectively, our analyses indicated that there were subtle differences in the factors associated with the use of nest boxes for day nesting, breeding and hibernating, but, overall, these tended to be factors relating to nest box placement, resource provisioning and site-based features, rather than those relating to box design. For all nesting types, the length of time the box had been deployed, the availability of artificial food and the presence of access points for hedgehogs into back gardens from the front significantly increased the likelihood that a nest box had been used. However, both deployment time and artificial food could be associated with a form of reporting bias. For example, householders may have been increasingly more likely to have noticed, by chance, that their box had been



used simply because the box had been in their garden for longer, and those householders who fed hedgehogs, may have been more likely to monitor hedgehog activity in their garden; the latter may also explain the positive association between nest box use and the identification of other nesting sites in the garden. Alternatively, it is known that a range of mammal species exhibit neophobic responses to novel objects in the environment (*Stryjek, Kalinowski & Parsons, 2019*), such that hedgehogs may need to become habituated to a nest box before using it (*sensu Madikiza et al., 2010*).

Conversely, artificial food may represent an attractive resource for hedgehogs in the context of selecting the position of nest sites. Food abundance has been known to influence nest box occupancy by arboreal mammals (*Nakamura-Kojo et al., 2014*) and, for birds, can facilitate greater occupancy of closely spaced refuges when compared to sites where food is less abundant (*Hussel, 2012*). Supplementary food can simultaneously act to increase energy intake and reduce foraging time, such that animals would have more time for nest building (*Smith et al., 2013*). However, patterns of hibernation may be disrupted where anthropogenic food is regularly available (*Gazzard & Baker, 2020*), and the nutritional quality of such food may also be inadequate (*Gimmel, Eulenberger & Liesegang, 2021*). In addition, artificial food often attracts several individuals to the same location, which may increase intra-specific aggression; although this is known to happen at feeding stations, it is not known whether this also extends to artificial refuges. Nonetheless, proximity to a food source may be desirable in those instances where hedgehogs may be reluctant to move far from a nest site, for example, during breeding when vulnerable young are present, and during hibernation when natural food availability is low. Similarly, staying close to a nest site would potentially be important where nest boxes themselves are a limiting resource. Whether this is an issue is, however, equivocal: for example, the householders in this study collectively reported an average of 0.6 other nest sites within their gardens, in locations that are likely to be present in a broad range of other gardens (*e.g.*, in vegetation and compost heaps, as well as underneath woodpiles, sheds and decking). Furthermore, the quantity of urban habitat within 500 m of the garden, and the distance to the nearest area of arable land, woodland or grassland, had no effect on nest box use suggesting that these other habitats are not critically important as potential nesting locations.

One of the major factors thought to affect urban hedgehog populations is patterns of connectivity between neighbouring back gardens but also from an individual householder's front garden to their back garden (*Gazzard et al., 2021; App et al., 2022; Gazzard, Yarnell & Baker, 2022*). In this study, nest box use was not significantly affected by the number of neighbouring back gardens which were accessible to hedgehogs from the respondent's own garden, but front-to-back access was significantly positively correlated with all four patterns of nest box use. Both results could potentially be explained by the fact that most householders put out boxes once they knew hedgehogs were already visiting; consequently, access into the respondent's garden was already possible. Alternatively, front-to-back access could simply be a proxy for houses with larger gardens: in the UK, detached and semi-detached houses are typically associated with larger gardens which permit access down both or one the sides of the house, respectively; terraced houses typically have the smallest sized gardens, and access from the front to the back is not always possible. However,

it has been noted that front-to-back access also significantly decreases the proportion of time hedgehogs spend in back gardens (*Gazzard, Yarnell & Baker, 2022*). Although the underlying reason for this is not known, it could suggest that front gardens contain important resources not present in back gardens, or that this facilitates movement through the landscape (particularly between blocks of houses separated by roads) and perhaps even helps animals avoid one another when foraging. More detailed information is therefore required on how key resources are distributed throughout the urban landscape, but also the patterns of behaviour exhibited by hedgehogs in different types of gardens.

Given the potential vulnerability of animals that are sleeping, hibernating or which have dependent young, hedgehogs would be expected to select locations which reduce the risk of detection by predators (*Evans et al., 2002*), accidental disturbance and which also offer protection from inclement weather conditions; refuges located in sheltered locations are likely to experience reduced exposure to rain, wind and direct sunshine, and may more closely mimic natural nesting locations (*Morris, 2018*). Accordingly, nest boxes in the current study were more likely to have been used by hedgehogs when they were positioned in sheltered locations, such as under shrub cover, and less likely to have been used when entrances faced into the open (*i.e.*, facing towards the middle of the garden); these relationships were generally consistent for all nesting types with the exception of sheltered locations during hibernation and the orientation of the box's entrance during breeding. It may be the case that during breeding and hibernation, the influence of other factors are of greater relative importance, aligning with the specific needs and/or vulnerabilities of hedgehogs at these times.

During the hibernation period, there is a risk that exceptionally low temperatures within nests could trigger thermogenesis (*Malan, 2010*) leading to the utilisation of brown fat stores (*Nedergaard & Cannon, 1990*) which are critical for rapid metabolism during arousals from torpor (*Morris, 2018*). Indeed, in hedgehogs, hibernacula temperatures  $<0^{\circ}\text{C}$  have been associated with increased oxygen consumption and shorter periods of torpor, compared to individuals in nests maintained at temperatures  $>0^{\circ}\text{C}$  (*Soivio, Tähti & Kristoffersson, 1968*). In this study, nest boxes located on hardstanding, within close proximity ( $<5\text{ m}$ ) to buildings and those with entrances oriented to the south were more likely to have been used for hibernation (although summer day nesting was also positively influenced by the former variables). Temperatures of hardstanding and building surfaces tend to be higher than those measured on soil, grass or other green areas due to their greater ability to absorb and retain solar radiation (see *Bowler et al., 2010; Loughner et al., 2012*). Additionally, when entrances are oriented east or south, internal nest temperatures can be warmer than in nest boxes facing other orientations (*Ardia, Pérez & Clotfelter, 2006; Butler, Whitman & Dufty Jr, 2009*). As such, it is possible that the thermal properties of surrounding substrates and ambient sunshine could positively influence temperature profiles within nest boxes during the hibernation period, although this requires verification as well as investigation of how thermal profiles may be affected by the design of the nest box itself.

Hedgehogs were also significantly less likely to have used a nest box for hibernating on sites where the respondent owned a dog. Hibernating animals are presumably less

responsive to predation attempts or disturbances (Boyles *et al.*, 2020) since it takes typically >5 h for hedgehogs to fully arouse from torpor (Morris, 2018). They may therefore seek to hibernate in locations where predators are less likely to occur. The presence of badgers and/or foxes did not, however, have a marked effect on nest box use during hibernation, although it must be noted that badgers do not often leave their setts over winter (Fowler & Racey, 1988), and we were not able to investigate the effect of foxes alone as only a low number of respondents reported having sighted them in their garden. However, it is reasonable to assume that hedgehog boxes are often likely to be sited in gardens where foxes are present, given their agility and widespread distribution in urban areas in the UK (Scott *et al.*, 2014). Similarly, both foxes and badgers are likely to be attracted to gardens where food is put out for hedgehogs by the householder. At the present time, however, there are few data available on the frequency with which hedgehogs, foxes and badgers interact with one another in residential gardens, the manner of these interactions nor the effectiveness of anti-predation features of hedgehog nest boxes such as integral bases, external tunnels or internal partitions (see Bailey & Bonter, 2017).

In this study, we were not able to investigate in detail how the design of nest boxes influenced their use by hedgehogs since many design-related variables had to be excluded due to issues arising from multicollinearity. Of the variables that were included in the analyses, the external dimensions, internal volume and primary construction materials of boxes were not important factors affecting nest box use, whereas the type of nest box and whether it was raised off the ground had significant impacts. First, homemade nest boxes were more likely to have been used than commercially available nest boxes for winter day nesting and hibernation. This could possibly be associated with parameters that were not measured in this study, such as the age, condition, thickness or colour of the materials used to construct homemade boxes. For example, it has been demonstrated that dark-green wooden nest boxes experience greater average daily temperatures when compared to boxes painted with lighter colours (Griffiths *et al.*, 2017); it could be possible that homemade nest boxes were more likely to have been painted in such a way that influenced nest box selection during colder periods. Second, boxes that were raised off the ground were significantly more likely to have been used for summer day nesting and hibernation. However, it is not clear whether the latter was representative of a specific design feature (*i.e.*, legs attached to the base), placement decision (*e.g.*, nest box was elevated on bricks), or even a proxy of such boxes possessing bases (by default, a box raised off the ground would have a solid base). Further investigation is needed to determine any preferences for, and the effects of, various nest box design features.

Resources provided by householders strongly influenced nest box use, with the provisioning of bedding and food associated with the largest odds ratios across all models. The provision of bedding materials (*e.g.*, leaves, hay and/or shredded newspaper) within nest boxes significantly positively influenced their use for day and hibernation nesting, but had a (nonsignificant) negative effect in the context of breeding. During reproduction, females with dependent young are particularly sensitive, and mothers may abandon breeding nests and/or kill their young if their nests are disturbed (Morris, 2018). Typically, such disturbance is associated with human activities (*e.g.*, garden maintenance, dog walkers) but

could potentially arise because of intra-specific interactions, although there is no definitive evidence of this. Consequently, it may be that pregnant females consider the presence of bedding material to be an indication of the presence of other hedgehogs, particularly if the box retains the scent of individuals who have visited previously.

In studies of naturally constructed nests, the leaves of broadleaved trees appeared to be preferred, especially as these can be “woven” to create a layered structure which is thought to help maintain the temperature within the nest whilst allowing gaseous transfer (Morris, 2018). Unfortunately, broadleaved trees can often be removed from urban areas in the UK because of, e.g., human safety concerns and the risk posed to buildings (Pauleit, Ennos & Golding, 2005; Andrew & Slater, 2015). In addition, fallen leaves in gardens are often removed by householders for aesthetic reasons. This might consequently be linked to the positive association between nest box use (for summer and winter day nesting, and hibernation) and the active provision of bedding material by humans. However, different nesting materials are likely to vary with respect to their thermal properties (Corrales-Moya et al., 2021), longevity (Hebda, Kandziora & Mitrus, 2017) and/or influence on ectoparasite presence (Reynolds et al., 2019). In addition, some man-made materials may contain toxic compounds that could affect survival (Mukai et al., 2014). Additional research is therefore required to examine which materials are being used by hedgehogs within nest boxes, how this relates to material availability in the wider environment and how nest structure ultimately affects their behaviour and success. Such research would help to identify the most suitable materials which householders should provide, if this was deemed necessary (sensu Slobodník et al., 2017), but also help to determine suitable box cleaning regimes (e.g., Tomás et al., 2007).

## CONCLUSIONS

The use of an online questionnaire survey of householders enabled the rapid collection of a large quantity of information relating to factors affecting nest box use by hedgehogs, but was associated with limitations. First, we were only able to investigate factors associated with whether a box had ever been used, rather than their frequency of use. Second, several variables that were significantly associated with the increased use of boxes could have represented a form of reporting bias whereby respondents who were especially ‘hedgehog-friendly’ may have been more likely to monitor their boxes for hedgehog activity. Whilst acknowledging the limitations of these data, the results indicate moderate to high uptake rates of hedgehog boxes for nesting. Subtle differences in the factors associated with the four patterns of nesting were identified relating to nest box placement, resource provisioning and site-based features; in general terms, householders might be able to improve the likelihood that their nest boxes are used by hedgehogs by placing them under shelter, ensuring that their gardens are sufficiently accessible from the front garden to the back, and providing additional resources such as food and bedding. In some seasons, including over winter, positioning the nest box on hardstanding and/or closer (<5 m) to a building, and ensuring that the box entrance does not face the open, may increase the chances of it being used. The drivers behind such placement ‘preferences’ are, however, unclear, and further research is needed to investigate these factors in more detail.

### Future research recommendations

Although questionnaire surveys represent a mechanism for rapidly collecting large volumes of data, they are susceptible to reporting biases that may exaggerate the importance of hedgehog boxes as nesting sites. Future studies, therefore, need to adopt experimental or quasi-experimental approaches whereby householders are recruited in a more randomised manner. Such studies need to ensure that all householders monitor their boxes continuously so that definitive data on patterns of use can be obtained; this could involve existing technologies, such as commercially available motion-activated cameras, or the development of new approaches such as cameras or other devices mounted inside nest boxes. Furthermore, additional monitoring techniques and/or novel experimental approaches are required to quantify how the internal conditions of boxes are affected by their design and placement, and the relative vulnerability of boxes to other species; choice experiments within gardens would help to identify whether hedgehogs select particular box designs or types of bedding. Finally, the pattern of use of nest boxes must be considered in the context of natural nest site availability, *i.e.*, are nest boxes used more frequently where natural nest sites are limited? Consequently, field studies are required to quantify the frequency of use of artificial refuges relative to other sites, but which also compare the success of hedgehogs in nest boxes *versus* other nesting sites in the context of, for example, over-winter survival rates and reproductive success; ideally, such studies should consider both urban and rural landscapes.

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The authors declare there are no competing interests.

### Author Contributions

- Abigail Gazzard conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Philip J. Baker conceived and designed the experiments, authored or reviewed drafts of the article, and approved the final draft.

### Data Availability

The following information was supplied regarding data availability:

A text copy of the questionnaire and anonymised questionnaire results are available in the [Supplementary Files](#).

### Supplemental Information

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## REFERENCES

- Andrew C, Slater D. 2015.** Why some UK homeowners reduce the size of their front garden trees and the consequences for urban forest benefits as assessed by i-Tree ECO. *The International Journal of Urban Forestry* **36**:197–215.
- Angel S, Parent J, Civco DL, Blei A, Potere D. 2011.** The dimensions of global urban expansion: estimates and projections of all countries, 2000–2050. *Progress in Planning* **75**:53–107 DOI [10.1016/j.progress.2011.04.001](https://doi.org/10.1016/j.progress.2011.04.001).
- App M, Strohbach MW, Schneider A-K, Schröder B. 2022.** Making the case for gardens: estimating the contribution of urban gardens to habitat provision and connectivity based on hedgehogs (*Erinaceus europaeus*). *Landscape and Urban Planning* **220**:104347 DOI [10.1016/j.landurbplan.2021.104347](https://doi.org/10.1016/j.landurbplan.2021.104347).
- Ardia DR, Pérez JH, Clotfelter ED. 2006.** Nest box orientation affects internal temperature and nest site selection by Tree Swallows. *Journal of Field Ornithology* **77**:339–344 DOI [10.1111/j.1557-9263.2006.00064.x](https://doi.org/10.1111/j.1557-9263.2006.00064.x).
- Auslebrook AE, Jones TM, Mulder RA, Lesku JA. 2018.** Impacts of artificial light at night on sleep: a review and prospectus. *Journal of Experimental Zoology –A* **329**:409–418 DOI [10.1002/jez.2189](https://doi.org/10.1002/jez.2189).
- Bailey RL, Bonter DN. 2017.** Predator guards on nest boxes improve nesting success of birds. *Wildlife Society Bulletin* **41**:434–441 DOI [10.1002/wsb.801](https://doi.org/10.1002/wsb.801).
- Baker PJ, Ansell RJ, Dodds PAA, Webber CE, Harris S. 2003.** Factors affecting the distribution of small mammals in an urban area. *Mammal Review* **33**:95–100 DOI [10.1046/j.1365-2907.2003.00003.x](https://doi.org/10.1046/j.1365-2907.2003.00003.x).

- Baker PJ, Harris S. 2007.** Urban mammals: what does the future hold? An analysis of the factors affecting patterns of use of residential gardens in Great Britain. *Mammal Review* **37**:297–315.
- Battin J. 2004.** When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology* **18**:1482–1491 DOI [10.1111/j.1523-1739.2004.00417.x](https://doi.org/10.1111/j.1523-1739.2004.00417.x).
- BBC. 2014.** Give hedgehogs a home. Available at [https://www.bbc.co.uk/breathingplaces/hedgehog\\_home/](https://www.bbc.co.uk/breathingplaces/hedgehog_home/) (accessed on 03 October 2021).
- Bearman-Brown LE, Baker PJ, Scott D, Uzal A, Evans L, Yarnell RW. 2020.** Over-winter survival and nest site selection of the West European hedgehog (*Erinaceus europaeus*) in arable dominated landscapes. *Animals* **10**:1449 DOI [10.3390/ani10091449](https://doi.org/10.3390/ani10091449).
- Berthier K, Leippert F, Fumagalli L, Arlettaz R. 2012.** Massive nest-box supplementation boosts fecundity, survival and even immigration without altering mating and reproductive behaviour in a rapidly recovered bird population. *PLOS ONE* **7**:e36028 DOI [10.1371/journal.pone.0036028](https://doi.org/10.1371/journal.pone.0036028).
- Beyer GL, Goldingay RL. 2006.** The value of nest boxes in the research and management of Australian hollow-using arboreal marsupials. *Wildlife Research* **33**:161–174 DOI [10.1071/WR04109](https://doi.org/10.1071/WR04109).
- Bleu J, Agostini S, Biard C. 2017.** Nest-box temperature affects clutch size, incubation initiation, and nestling health in great tits. *Behavioral Ecology* **28**:793–802 DOI [10.1093/beheco/ax039](https://doi.org/10.1093/beheco/ax039).
- Bolton M, Medeiros R, Hothersall B, Campos A. 2004.** The use of artificial breeding chambers as a conservation measure for cavity-nesting procellariiform seabirds: a case study of the Madeiran storm petrel (*Oceanodroma castro*). *Biological Conservation* **116**:73–80 DOI [10.1016/S0006-3207\(03\)00178-2](https://doi.org/10.1016/S0006-3207(03)00178-2).
- Bowler DE, Buyung-Ali L, Knight TM, Pullin AS. 2010.** Urban greening to cool towns and cities: a systematic review of the empirical evidence. *Landscape and Urban Planning* **97**:147–155 DOI [10.1016/j.landurbplan.2010.05.006](https://doi.org/10.1016/j.landurbplan.2010.05.006).
- Boyles JG, Johnson JS, Blomberg A, Lilley TM. 2020.** Optimal hibernation theory. *Mammal Review* **50**:91–100 DOI [10.1111/mam.12181](https://doi.org/10.1111/mam.12181).
- Brady MJ, Risch TS, Dobson FS. 2000.** Availability of nest sites does not limit population size of southern flying squirrels. *Canadian Journal of Zoology* **78**:1144–1149 DOI [10.1139/z00-048](https://doi.org/10.1139/z00-048).
- Brazill-Boast J, Pryke SR, Griffith SC. 2013.** Provisioning habitat with custom-designed nest-boxes increases reproductive success in an endangered finch. *Austral Ecology* **38**:405–412 DOI [10.1111/j.1442-9993.2012.02424.x](https://doi.org/10.1111/j.1442-9993.2012.02424.x).
- British Hedgehog Preservation Society. 2021.** Hedgehog homes. Available at <https://www.britishhedgehogs.org.uk/hedgehog-homes/> (accessed on 07 December 2021).
- British Hedgehog Preservation Society. 2022.** Gardening with hedgehogs. Available at <https://www.britishhedgehogs.org.uk/gardening-with-hedgehogs/> (accessed on 03 May 2022).
- Burnham KP, Anderson DR. 1998.** *Model selection and inference*. 2nd edition. New York: Springer-Verlag.

- Butler MW, Whitman BA, Dufty Jr AM. 2009.** Nest box temperature and hatching success of American kestrels varies with nest box orientation. *The Wilson Journal of Ornithology* 121:778–782 DOI [10.1676/08-124.1](https://doi.org/10.1676/08-124.1).
- Catry I, Franco AMA, Rocha P, Alcazar R, Reis S, Cordeiro A, Ventim R, Teodósio J, Moreira F. 2013.** Foraging habitat quality constrains effectiveness of artificial nest-site provisioning in reversing population declines in a colonial cavity nester. *PLOS ONE* 8:e58320 DOI [10.1371/journal.pone.0058320](https://doi.org/10.1371/journal.pone.0058320).
- Chace JF, Walsh JJ. 2006.** Urban effects on native avifauna: a review. *Landscape and Urban Planning* 74:46–69 DOI [10.1016/j.landurbplan.2004.08.007](https://doi.org/10.1016/j.landurbplan.2004.08.007).
- Corrales-Moya J, Barrantes G, Chacón-Madriral E, Sandoval L. 2021.** Human waste used as nesting material affects nest cooling in the clay-colored thrush. *Environmental Pollution* 284:117539 DOI [10.1016/j.envpol.2021.117539](https://doi.org/10.1016/j.envpol.2021.117539).
- Cowan MA, Callan MN, Watson MJ, Watson DM, Doherty TS, Michael DR, Dunlop JA, Turner JM, Moore HA, Watchorn DJ, Nimmo DG. 2021.** Artificial refuges for wildlife conservation: what is the state of the science? *Biological Reviews* 96:2735–2754 DOI [10.1111/brv.12776](https://doi.org/10.1111/brv.12776).
- Cowan MA, Dunlop JA, Turner JM, Moore HA, Nimmo DG. 2020.** Artificial refuges to combat habitat loss for an endangered marsupial predator: how do they measure up? *Conservation Science and Practice* 2:204.
- Davies ZG, Fuller RA, Loram A, Irvine KN, Sims V, Gaston KJ. 2009.** A national scale inventory of resource provision for biodiversity within domestic gardens. *Biological Conservation* 142:761–771 DOI [10.1016/j.biocon.2008.12.016](https://doi.org/10.1016/j.biocon.2008.12.016).
- Davison WB, Bollinger E. 2000.** Predation rates on real and artificial nests of grassland birds. *Ornithology* 117:147–153 DOI [10.1093/auk/117.1.147](https://doi.org/10.1093/auk/117.1.147).
- Deanesly R. 1934.** The reproductive processes of certain mammals, Part 6: the reproductive cycle of the female hedgehog. *Philosophical Transactions of the Royal Society B* 233:239–276.
- Demeyrier V, Lambrechts MM, Perret P, Grégoire A. 2016.** Experimental demonstration of an ecological trap for a wild bird in a human-transformed environment. *Animal Behaviour* 118:181–190 DOI [10.1016/j.anbehav.2016.06.007](https://doi.org/10.1016/j.anbehav.2016.06.007).
- Doncaster CP, Rondinini C, Johnson PCD. 2001.** Field test for environmental correlates of dispersal in hedgehogs, *Erinaceus europaeus*. *Journal of Animal Ecology* 70:33–46.
- Dowding CV, Harris S, Poulton S, Baker PJ. 2010.** Nocturnal ranging behaviour of urban hedgehogs, *Erinaceus europaeus*, in relation to risk and reward. *Animal Behaviour* 80:13–21 DOI [10.1016/j.anbehav.2010.04.007](https://doi.org/10.1016/j.anbehav.2010.04.007).
- Dowler Burroughes N, Dowler J, Burroughes G. 2021.** Admission and survival trends in hedgehogs admitted to RSPCA wildlife rehabilitation centres. *Proceedings of the Zoological Society* 74:198–204 DOI [10.1007/s12595-021-00363-9](https://doi.org/10.1007/s12595-021-00363-9).
- Dulisz B, Stawicka AM, Knozowski P, Diserens TA, Nowakowski JJ. 2022.** Effectiveness of using nest boxes as a form of bird protection after building modernization. *Biodiversity and Conservation* 31:277–294 DOI [10.1007/s10531-021-02334-0](https://doi.org/10.1007/s10531-021-02334-0).



- Evans MR, Lank DB, Boyd S, Cooke F. 2002. A comparison of the characteristics and fate of Barrow's goldeneye and bufflehead nests in nest boxes and natural cavities. *The Condor* **104**:610–619 DOI [10.1093/condor/104.3.610](https://doi.org/10.1093/condor/104.3.610).
- Finch D, Smith BR, Marshall C, Coomber FG, Kubasiewicz LM, Anderson M, Wright PGR, Mathews F. 2020. Effects of artificial light at night (ALAN) on European hedgehog activity at supplementary feeding stations. *Animals* **10**:768 DOI [10.3390/ani10050768](https://doi.org/10.3390/ani10050768).
- Fischer J, Lindenmayer DB. 2007. Landscape modification and habitat fragmentation: a synthesis. *Global Ecology and Biogeography* **16**:265–280 DOI [10.1111/j.1466-8238.2007.00287.x](https://doi.org/10.1111/j.1466-8238.2007.00287.x).
- Fowler PA, Racey PA. 1988. Overwintering strategies of the badger, *Meles meles*, at 57°N. *Journal of Zoology* **214**:635–651 DOI [10.1111/j.1469-7998.1988.tb03763.x](https://doi.org/10.1111/j.1469-7998.1988.tb03763.x).
- Fox J, Monette G. 1992. Generalized collinearity diagnostics. *Journal of the American Statistical Association* **87**:178–183 DOI [10.1080/01621459.1992.10475190](https://doi.org/10.1080/01621459.1992.10475190).
- Franco AMA, Marques JT, Sutherland WJ. 2005. Is nest-site availability limiting Lesser Kestrel populations? A multiple scale approach. *Ibis* **147**:657–666 DOI [10.1111/j.1474-919x.2005.00437.x](https://doi.org/10.1111/j.1474-919x.2005.00437.x).
- Gaston KJ, Smith RM, Thompson K, Warren PH. 2005. Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. *Biodiversity & Conservation* **14**:395–413 DOI [10.1007/s10531-004-6066-x](https://doi.org/10.1007/s10531-004-6066-x).
- Gazzard A, Baker PJ. 2020. Patterns of feeding by householders affect activity of hedgehogs (*Erinaceus europaeus*) during the hibernation period. *Animals* **10**:1344 DOI [10.3390/ani10081344](https://doi.org/10.3390/ani10081344).
- Gazzard A, Boushall A, Brand E, Baker PJ. 2021. An assessment of a conservation strategy to increase garden connectivity for hedgehogs that requires cooperation between immediate neighbours: a barrier too far? *PLOS ONE* **16**:e0259537 DOI [10.1371/journal.pone.0259537](https://doi.org/10.1371/journal.pone.0259537).
- Gazzard A, Yarnell RW, Baker PJ. 2022. Fine-scale habitat selection of a small mammalian urban adapter: the West European hedgehog (*Erinaceus europaeus*). *Mammalian Biology* In Press DOI [10.1007/s42991-022-00251-5](https://doi.org/10.1007/s42991-022-00251-5).
- Gimmel A, Eulenberger U, Liesegang A. 2021. Feeding the European hedgehog (*Erinaceus europaeus* L.)—risks of commercial diets for wildlife. *Animal Physiology and Animal Nutrition* **105**:91–96 DOI [10.1111/jpn.13561](https://doi.org/10.1111/jpn.13561).
- Goldingay RL, Rohweder D, Taylor B. 2020. Nest box contentions: are nest boxes used by the species they target? *Ecological Management & Restoration* **21**:115–122 DOI [10.1111/emr.12408](https://doi.org/10.1111/emr.12408).
- Goldingay RL, Ruegger NN, Grimson MJ, Taylor BD. 2015. Specific nest box designs can improve habitat restoration for cavity-dependent arboreal mammals. *Restoration Ecology* **23**:482–490 DOI [10.1111/rec.12208](https://doi.org/10.1111/rec.12208).
- Gortat T, Barkowska M, Gryczynska-Siemiakowska A, Pieniazek A, Kozakiewicz A, Kozakiewicz M. 2014. The effects of urbanization—small mammal communities in a gradient of human pressure in Warsaw city, Poland. *Polish Journal of Ecology* **62**:163–172 DOI [10.3161/104.062.0115](https://doi.org/10.3161/104.062.0115).

- Griffiths SR, Rowland JA, Briscoe NJ, Lentini PE, Handasyde KA, Lumsden LF, Robert KA. 2017.** Surface reflectance drives nest box temperature profiles and thermal suitability for target wildlife. *PLOS ONE* **12**(5):e0176951 DOI [10.1371/journal.pone.0176951](https://doi.org/10.1371/journal.pone.0176951).
- Grol PFE, Voûte AM, Verboom B. 2011.** The influence of a Christmas market on hibernating bats in a man-made limestone cave. *Lutra* **54**:69–88.
- Grunst ML, Grunst AS, Pinxten R, Eens M. 2021.** Variable and consistent traffic noise negatively affect the sleep behavior of a free-living songbird. *Science of the Total Environment* **778**:146338 DOI [10.1016/j.scitotenv.2021.146338](https://doi.org/10.1016/j.scitotenv.2021.146338).
- Gryz J, Jaworski T, Krauze-Gryz D. 2021.** Target species and other residents—an experiment with nest boxes for red squirrels in central Poland. *Diversity* **13**:277 DOI [10.3390/d13060277](https://doi.org/10.3390/d13060277).
- Guillemette CU, Fletcher QE, Boutin S, Hodges RM, McAdam AG, Humphries MM. 2008.** Lactating red squirrels experiencing high heat load occupy less insulated nests. *Biology Letters* **5**:166–168.
- Haigh A. 2011.** The ecology of the European hedgehog (*Erinaceus europaeus*) in rural Ireland. PhD thesis, University College Cork.
- Haigh A, Butler F, O’Riordan RM. 2012a.** Intra- and interhabitat differences in hedgehog distribution and potential prey availability. *Mammalia* **76**:261–268.
- Haigh A, O’Riordan RM, Butler F. 2012b.** Nesting behaviour and seasonal body mass changes in a rural Irish population of the Western hedgehog (*Erinaceus europaeus*). *Mammal Research* **57**:321–331.
- Hale R, Swearer SE. 2016.** Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B* **283**:20152647 DOI [10.1098/rspb.2015.2647](https://doi.org/10.1098/rspb.2015.2647).
- Hebda GA, Kandziora A, Mitrus S. 2017.** Decomposition of nest material in tree holes and nest-boxes occupied by European starlings *Sturnus vulgaris*: an experimental study. *Acta Ornithologica* **52**:119–125 DOI [10.3161/00016454AO2017.52.1.011](https://doi.org/10.3161/00016454AO2017.52.1.011).
- Hedgehog Street. 2021.** Hedgehog-friendly garden features. Available at <https://www.hedgehogstreet.org/help-hedgehogs/helpful-garden-features/> (accessed on 03 October 2021).
- Heeb P, Kölliker M, Richner H. 2000.** Bird-ectoparasite interactions, nest humidity, and ectoparasite community structure. *Ecology* **81**:958–968.
- Hodges RJ, Seabrook C. 2016.** Use of artificial refuges by the northern viper *Vipera berus* - 1. Seasonal and life stage variations on chalk downland. *The Herpetological Bulletin* **137**:6–12.
- Hoeh JPS, Bakken GS, Mitchell WA, O’Keefe JM. 2018.** In artificial roost comparison, bats show preference for rocket box style. *PLOS ONE* **13**(10):e0205701 DOI [10.1371/journal.pone.0205701](https://doi.org/10.1371/journal.pone.0205701).
- Hof AR, Bright PW. 2009.** The value of green spaces in built-up areas for western hedgehogs. *Lutra* **52**:69–82.
- Hof AR, Bright PW. 2010.** The value of agri-environment schemes for macro-invertebrate feeders: hedgehogs on arable farms in Britain. *Animal Conservation* **13**:467–473 DOI [10.1111/j.1469-1795.2010.00359.x](https://doi.org/10.1111/j.1469-1795.2010.00359.x).

- Hof AR, Snellenberg J, Bright PW. 2012.** Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. *Animal Behaviour* **4**:1099–1106.
- Hosmer DW, Lemeshow S. 1980.** Goodness of fit tests for the multiple logistic regression model. *Communications in Statistics –Theory and Methods* **9**:1043–1069 DOI [10.1080/03610928008827941](https://doi.org/10.1080/03610928008827941).
- Hubert P, Julliard R, Biagiatti S, Poulle M-L. 2011.** Ecological factors driving the higher hedgehog (*Erinaceus europaeus*) density in an urban area compared to the adjacent rural area. *Landscape and Urban Planning* **103**:34–43 DOI [10.1016/j.landurbplan.2011.05.010](https://doi.org/10.1016/j.landurbplan.2011.05.010).
- Humphries MM, Thomas DW, Speakman JR. 2002.** Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* **418**:313–316 DOI [10.1038/nature00828](https://doi.org/10.1038/nature00828).
- Hussel DJT. 2012.** The influence of food abundance on nest-box occupancy and territory size in the tree swallow, a species that does not defend a feeding territory. *Ornithological Applications* **114**:595–605 DOI [10.1525/cond.2012.100231](https://doi.org/10.1525/cond.2012.100231).
- Jackson DL. 2000.** Guidance on the interpretation of the Biodiversity Broad Habitat Classification (terrestrial and freshwater types): definitions and the relationship with other classifications. JNCC Report 307, Peterborough..
- Jackson DB. 2006.** The breeding biology of introduced hedgehogs (*Erinaceus europaeus*) on a Scottish Island: lessons for population control and bird conservation. *Journal of Zoology* **268**:303–314 DOI [10.1111/j.1469-7998.2005.00035.x](https://doi.org/10.1111/j.1469-7998.2005.00035.x).
- Jackson DB, Green RE. 2000.** The importance of the introduced hedgehog (*Erinaceus europaeus*) as a predator of the eggs of waders (*Charadrii*) on machair in South Uist, Scotland. *Biological Conservation* **93**:333–348 DOI [10.1016/S0006-3207\(99\)00135-4](https://doi.org/10.1016/S0006-3207(99)00135-4).
- Jensen AB. 2004.** Overwintering of European hedgehogs *Erinaceus europaeus* in a Danish rural area. *Acta Theriologica* **49**:145–155 DOI [10.1007/BF03192516](https://doi.org/10.1007/BF03192516).
- Jiménez-Valverde A, Lobo JM, Hortal J. 2009.** The effect of prevalence and its interaction with sample size on the reliability of species distribution models. *Community Ecology* **10**:196–205 DOI [10.1556/ComEc.10.2009.2.9](https://doi.org/10.1556/ComEc.10.2009.2.9).
- Juškaitis R. 2005.** The influence of high nestbox density on the common dormouse *Muscardinus avellanarius* population. *Acta Theriologica* **50**:43–50 DOI [10.1007/BF03192617](https://doi.org/10.1007/BF03192617).
- Kaneko Y, Newman C, Buesching CD, Macdonald DW. 2010.** Variations in badger (*Meles meles*) sett microclimate: differential cub survival between main and subsidiary setts, with implications for artificial sett construction. *International Journal of Ecology* **2010**:859586 DOI [10.1155/2010/859586](https://doi.org/10.1155/2010/859586).
- Kristiansson H. 1981.** Young production of European hedgehog in Sweden and Britain. *Acta Theriologica* **26**:504–507 DOI [10.4098/AT.arch.81-45](https://doi.org/10.4098/AT.arch.81-45).
- Larson ER, Eastwood JR, Buchanan KL, Bennett ATD, Berg ML. 2015.** How does nest box temperature affect nestling growth rate and breeding success in a parrot? *Emu* **115**:247–255 DOI [10.1071/MU14081](https://doi.org/10.1071/MU14081).

- Larson ER, Eastwood JR, Buchanan KL, Bennett ATD, Berg ML. 2018.** Nest box design for a changing climate: the value of improved insulation. *Ecological Management & Restoration* **19**:39–48 DOI [10.1111/emr.12292](https://doi.org/10.1111/emr.12292).
- Latham D, Knowles M. 2008.** Assessing the use of artificial hibernacula by great crested newts *Triturus cristatus* and other amphibians for habitat enhancement, Northumberland, England. *Conservation Evidence* **5**:74–79.
- Le Roux DS, Ikin K, Lindenmayer DB, Bistricher G, Manning AD, Gibbons P. 2016.** Effects of entrance size, tree size and landscape context on nest box occupancy: considerations for management and biodiversity offsets. *Forest Ecology and Management* **366**:135–142 DOI [10.1016/j.foreco.2016.02.017](https://doi.org/10.1016/j.foreco.2016.02.017).
- Libois E, Gimenez O, Oro D, Mínguez E, Pradel R, Sanz-Aguilar A. 2012.** Nest boxes: a successful management tool for the conservation of an endangered seabird. *Biological Conservation* **155**:39–43 DOI [10.1016/j.biocon.2012.05.020](https://doi.org/10.1016/j.biocon.2012.05.020).
- Łopucki R, Kitowski I. 2017.** How small cities affect the biodiversity of ground-dwelling mammals and the relevance of this knowledge in planning urban land expansion in terms of urban wildlife. *Urban Ecosystems* **20**:933–943 DOI [10.1007/s11252-016-0637-y](https://doi.org/10.1007/s11252-016-0637-y).
- Loram A, Tratalos J, Warren PH, Gaston KJ. 2007.** Urban domestic gardens (X): the extent & structure of the resource in five major cities. *Landscape Ecology* **22**:601–615 DOI [10.1007/s10980-006-9051-9](https://doi.org/10.1007/s10980-006-9051-9).
- Loughner CP, Allen DJ, Zhang D-L, Pickering KE, Dickerson RR, Landry L. 2012.** Roles of urban tree canopy and buildings in urban heat island effects: parameterization and preliminary results. *Journal of Applied Meteorology and Climatology* **51**:1775–1793 DOI [10.1175/JAMC-D-11-0228.1](https://doi.org/10.1175/JAMC-D-11-0228.1).
- Madikiza ZJK, Betolino S, Baxter RM, Do Linh San E. 2010.** Nest box use by woodland dormice (*Graphiurus murinus*): the influence of life cycle and nest box placement. *European Journal of Wildlife Research* **56**:735–743 DOI [10.1007/s10344-010-0369-x](https://doi.org/10.1007/s10344-010-0369-x).
- Mainwaring MC. 2011.** The use of nestboxes by roosting birds during the non-breeding season: a review of the costs and benefits. *Ardea* **99**:167–176 DOI [10.5253/078.099.0206](https://doi.org/10.5253/078.099.0206).
- Malan A. 2010.** Is the torpor-arousal cycle of hibernation controlled by a non-temperature-compensated circadian clock? *Journal of Biological Rhythms* **25**:166–175 DOI [10.1177/0748730410368621](https://doi.org/10.1177/0748730410368621).
- Mänd R, Tilgar V, Lõhmus A, Leivits A. 2005.** Providing nest boxes for hole-nesting birds –Does habitat matter? *Biodiversity & Conservation* **14**:1823–1840 DOI [10.1007/s10531-004-1039-7](https://doi.org/10.1007/s10531-004-1039-7).
- Martin JK, Martin AA. 2007.** Resource distribution influences mating system in the bobuck (*Trichosurus cunninghami*: Marsupialia). *Behavioral Ecology* **154**:227–236.
- Mathews F, Harrower C. 2020.** *IUCN –compliant red list for britain’s terrestrial mammals. assessment by the mammal society under contract to natural England, natural resources wales and scottish natural heritage*. Peterborough: Natural England.
- Mathews F, Kubasiewicz L, Gurnell J, Harrower C, McDonald R, Shore R. 2018.** A Review of the Population and Conservation Status of British Mammals. A Report by

- the Mammal Society under Contract to Natural England, Natural Resources Wales and Scottish Natural Heritage. Natural England, Peterborough.
- McComb LB, Lentini PE, Harley DKP, Lumsden LF, Eyre AC, Briscoe NJ. 2021.** Climate and behaviour influence thermal suitability of artificial hollows for a critically endangered mammal. *Animal Conservation* Epub ahead of print 2021 24 October DOI 10.1111/acv.12750.
- Moorhouse TP, Palmer SCF, Travis JM, Macdonald DW. 2014.** Hugging the hedges: might agri-environment manipulations affect landscape permeability for hedgehogs? *Biological Conservation* 176:109–116 DOI 10.1016/j.biocon.2014.05.015.
- Morris P. 1972.** Winter nests of the hedgehog (*Erinaceus europaeus* L.). *Oecologia* 11:299–313.
- Morris P. 1977.** Pre-weaning mortality in the hedgehog (*Erinaceus europaeus*). *Journal of Zoology* 182:162–164 DOI 10.1111/j.1469-7998.1977.tb04150.x.
- Morris P. 2018.** *Hedgehog*. London: The New Naturalist Library, HarperCollins Publishers.
- Morton RD, Marston CG, O’Neil AW, Rowland CS. 2020.** Land Cover Map 2017 (land parcels, GB). Wallingford: NERC Environmental Information Data Centre DOI 10.5285/b77ce981-d038-4774-a620-f50da5dd3d31.
- Mukai M, Woods LW, Stump S, Ebel Jr JG, Levitt AS, Frey MW, Smith J, Uzal FA, Poppenga RH, Puschner B. 2014.** Detection of diisocyanates in nesting material associated with mortality in pigeon chicks. *Journal of Veterinary Diagnostic Investigation* 26:327–333 DOI 10.1177/1040638713520543.
- Nagelkerke NJD. 1991.** A note on a general definition of the coefficient of determination. *Biometrika* 78:691–692 DOI 10.1093/biomet/78.3.691.
- Nakamura-Kojo Y, Kojo N, Ootsuka T, Minami M, Tamate HB. 2014.** Influence of tree resources on nest box use by the Japanese dormouse *Glirulus japonicus*. *Mammal Study* 39:17–26 DOI 10.3106/041.039.0104.
- Nedergaard J, Cannon B. 1990.** Mammalian hibernation. *Philosophical Transactions of the Royal Society B* 326:669–686.
- Office for National Statistics. 2020.** Explore access to gardens (and their typical size) in your neighbourhood. Available at <https://www.ons.gov.uk/economy/environmentalaccounts/articles/oneineightbritishhouseholdshasnogarden/2020-05-14#gardens> (accessed on 18 April 2022).
- Pauleit S, Ennos R, Golding Y. 2005.** Modeling the environmental impacts of urban land use and land cover change—a study in Merseyside, UK. *Landscape and Urban Planning* 71:295–310 DOI 10.1016/S0169-2046(04)00083-0.
- Pettett CE, Moorhouse TP, Johnson PJ, Macdonald DW. 2017.** Factors affecting hedgehog (*Erinaceus europaeus*) attraction to rural villages in arable landscapes. *European Journal of Wildlife Research* 63:54 DOI 10.1007/s10344-017-1113-6.
- Pretzsch I, Dausmann KH. 2012.** Impact of climatic variation on the hibernation physiology of *Muscardinus avellanarius*, Chapter 8. In: Ruf T, Bieber C, Arnold W, Millesi E, eds. *Living in a seasonal world*. Berlin: Springer.

- Rasmussen SL, Berg TB, Dabelsteen T, Jones OR. 2019. The ecology of suburban juvenile European hedgehogs (*Erinaceus europaeus*) in Denmark. *Ecology and Evolution* 9:13174–13187 DOI 10.1002/ece3.5764.
- Rast W, Barthel LMF, Berger A. 2019. Music festival makes hedgehogs move: how individuals cope behaviorally in response to human-induced stressors. *Animals* 9:455 DOI 10.3390/ani9070455.
- Rautio A, Valtonen A, Auttila M, Kunnasranta M. 2014. Nesting patterns of European hedgehogs (*Erinaceus europaeus*) under Northern conditions. *Mammal Research* 59:173–181.
- Reeve N. 1994. *Hedgehogs*. London: Academic Press.
- Reeve N, Morris P. 1985. Construction and use of summer nests by the hedgehog (*Erinaceus europaeus*). *Mammalia* 49:187–194.
- Reynolds SJ, Ibáñez Álamo JD, Sumasgutner P, Mainwaring MC. 2019. Urbanisation and nest building in birds: a review of threats and opportunities. *Journal of Ornithology* 160:841–860 DOI 10.1007/s10336-019-01657-8.
- Riber AB. 2006. Habitat use and behaviour of European hedgehog *Erinaceus europaeus* in a Danish rural area. *Acta Theriologica* 51:363–371 DOI 10.1007/BF03195183.
- Rondinini C, Doncaster C. 2002. Roads as barriers to movement for hedgehogs. *Functional Ecology* 16:504–509 DOI 10.1046/j.1365-2435.2002.00651.x.
- Roos S, Johnston A, Noble D. 2012. UK Hedgehog datasets and their potential for long-term monitoring. BTO Research Report 598.
- Rueegger N. 2017. Artificial tree hollow creation for cavity-using wildlife –Trialling an alternative method to that of nest boxes. *Forest Ecology and Management* 405:404–412 DOI 10.1016/j.foreco.2017.09.062.
- Rueegger NN, Goldingay RL, Brookes LO. 2013. Does nest box design influence use by the eastern pygmy-possum? *Australian Journal of Zoology* 60:371–380.
- Salas-Eljatib C, Fuentes-Ramirez A, Gregoire TG, Altamirano A, Yaitul V. 2018. A study on the effects of unbalanced data when fitting logistic regression models in ecology. *Ecological Indicators* 85:502–508 DOI 10.1016/j.ecolind.2017.10.030.
- Schaus J, Uzal A, Gentle LK, Baker PJ, Bearman-Brown L, Bullion S, Gazzard A, Lockwood H, North A, Reader T, Scott DM, Sutherland CS, Yarnell RW. 2020. Application of the Random Encounter Model in citizen science projects to monitor animal densities. *Remote Sensing in Ecology and Conservation* 6:514–528 DOI 10.1002/rse2.153.
- Schaus Calderón J. 2021. Responses of the European hedgehog to urbanisation: impact on population dynamics, animal movement and habitat selection. PhD thesis, Nottingham Trent University.
- Scott DM, Berg MJ, Tolhurst BA, Chauvenet ALM, Smith GC, Neaves K, Lockhead J, Baker PJ. 2014. Changes in the distribution of red foxes (*Vulpes vulpes*) in urban areas in Great Britain: findings and limitations of a media-driven nationwide survey. *PLOS ONE* 9:e99059 DOI 10.1371/journal.pone.0099059.

- Shanahan DF, Strohbach MW, Warren PS, Fuller RA. 2014.** The challenges of urban living. In: Gil D, Brumm H, eds. *Avian urban ecology: behavioural and physiological adaptations*. Oxford: Oxford University Press.
- Shaw RF, Christman K, Crookes R, Gillbert CN, Osborne JL. 2021.** Effect of height and colour of bee bricks on nesting occupancy of bees and wasps in SW England. *Conservation Evidence Journal* 18:10–17 DOI 10.52201/CEJ18KMBE7709.
- Slobodník R, Tulis FF, Chavko J, Lengyel J. 2017.** Monitoring of colonies and provisioning of rooks with nest material as a potential tool for stabilizing colonies and increasing nesting opportunities in the countryside. Project report. *Slovak Raptor Journal* 11:43–50 DOI 10.1515/srj-2017-0004.
- Smith JA, Harrison TJE, Martin GR, Reynolds SJ. 2013.** Feathering the nest: food supplementation influences nest construction by Blue (*Cyanistes caeruleus*) and Great Tits (*Parus major*). *Avian Biology Research* 6:18–25 DOI 10.3184/175815512X13530764553094.
- Soivio A, Tähti H, Kristoffersson R. 1968.** Studies on the periodicity of hibernation in the hedgehog (*Erinaceus europaeus* L.) III. Hibernation in a constant ambient temperature of -5 °C. *Annales Zoologici Fennici* 5:224–226.
- Stone C. 2020.** The best hedgehog houses –how to choose? Available at <https://homeandroost.co.uk/blog/the-best-hedgehog-houses-how-to-choose/> (accessed on 07 December 2021).
- Stryjek R, Kalinowski A, Parsons MH. 2019.** Unbiased sampling for rodents and other small mammals: how to overcome neophobia through use of an electronic-triggered live trap—a preliminary test. *Frontiers in Ecology and Evolution* 7:11 DOI 10.3389/fevo.2019.00011.
- The Wildlife Trusts. 2021.** How to build a hedgehog home. Available at <https://www.wildlifetrusts.org/actions/how-build-hedgehog-home> (accessed on 05 October 2021).
- Tomás G, Merino S, Moreno J, Morales J. 2007.** Consequences of nest reuse for parasite burden and female health and condition in blue tits, *Cyanistes caeruleus*. *Animal Behaviour* 73:805–814 DOI 10.1016/j.anbehav.2006.06.016.
- Trewby ID, Young R, McDonald RA, Wilson GJ, Davison J, Walker N, Robertson A, Doncaster CP, Delahay RJ. 2014.** Impacts of removing badgers on localised counts of hedgehogs. *PLOS ONE* 9:e95477 DOI 10.1371/journal.pone.0095477.
- Van de Poel JL, Dekker J, Van Langevelde F. 2015.** Dutch hedgehogs *Erinaceus europaeus* are nowadays mainly found in urban areas, possibly due to the negative effects of badgers *Meles meles*. *Wildlife Biology* 21:51–55 DOI 10.2981/wlb.00072.
- van der Vinne V, Simons MJP, Reimert I, Gerkema MP. 2014.** Temporal niche switching and reduced nest attendance in response to heat dissipation limits in lactating common voles (*Microtus arvalis*). *Physiology & Behavior* 128:295–302 DOI 10.1016/j.physbeh.2014.01.019.
- Walhovd H. 1984.** The breeding habits of the European hedgehog (*Erinaceus europaeus* L.) in Denmark. *Zeitschrift Für Säugetierkunde* 49:269–277.
- Williams B, Baker PJ, Thomas E, Wilson G, Judge J, Yarnell RW. 2018a.** Reduced occupancy of hedgehogs (*Erinaceus europaeus*) in rural England and Wales: the

- influence of habitat and an asymmetric intraguild predator. *Scientific Reports* **8**:12156 DOI [10.1038/s41598-018-30130-4](https://doi.org/10.1038/s41598-018-30130-4).
- Williams B, Mann N, Neumann JL, Yarnell RW, Baker PJ. 2018b.** A prickly problem: developing a volunteer-friendly tool for monitoring populations of a terrestrial urban mammal, the West European hedgehog (*Erinaceus europaeus*). *Urban Ecosystems* **21**:1075–1086 DOI [10.1007/s11252-018-0795-1](https://doi.org/10.1007/s11252-018-0795-1).
- Williams RL, Goodenough AE, Hart AG, Stafford R. 2013.** Using long-term volunteer records to examine dormouse (*Muscardinus avellanarius*) nestbox selection. *PLOS ONE* **8**:e67986 DOI [10.1371/journal.pone.0067986](https://doi.org/10.1371/journal.pone.0067986).
- Williams RL, Stafford R, Goodenough AE. 2015.** Biodiversity in urban gardens: assessing the accuracy of citizen science data on garden hedgehogs. *Urban Ecosystems* **18**:819–833 DOI [10.1007/s11252-014-0431-7](https://doi.org/10.1007/s11252-014-0431-7).
- Wright PGR, Coomber FG, Bellamy CC, Perkins SE, Mathews F. 2020.** Predicting hedgehog mortality risks on British roads using habitat suitability modelling. *PeerJ* **7**:e8154 DOI [10.7717/peerj.8154](https://doi.org/10.7717/peerj.8154).
- Wu S, Liang Z, Li S. 2019.** Relationships between urban development level and urban vegetation states: a global perspective. *Urban Forestry & Urban Greening* **38**:215–222 DOI [10.1016/j.ufug.2018.12.010](https://doi.org/10.1016/j.ufug.2018.12.010).
- Yarnell RW, Pettett CE. 2020.** Beneficial land management for hedgehogs (*Erinaceus europaeus*) in the United Kingdom. *Animals* **10**:1566 DOI [10.3390/ani10091566](https://doi.org/10.3390/ani10091566).
- Yarnell RW, Surgery J, Grogan A, Thompson R, Davies K, Kimbrough C, Scott DM. 2019.** Should rehabilitated hedgehogs be released in winter? A comparison of survival, nest use and weight change in wild and rescued animals. *European Journal of Wildlife Research* **65**:6 DOI [10.1007/s10344-018-1244-4](https://doi.org/10.1007/s10344-018-1244-4).
- Young RP, Davison J, Trewby ID, Wilson GJ, Delahay RJ, Doncaster CP. 2006.** Abundance of hedgehogs (*Erinaceus europaeus*) in relation to the density and distribution of badgers (*Meles meles*). *Journal of Zoology* **269**:349–356 DOI [10.1111/j.1469-7998.2006.00078.x](https://doi.org/10.1111/j.1469-7998.2006.00078.x).
- Zuur AF, Ieno EN, Elphick CS. 2010.** A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* **1**:3–14 DOI [10.1111/j.2041-210X.2009.00001.x](https://doi.org/10.1111/j.2041-210X.2009.00001.x).