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Comparing non-invasive surveying techniques for elusive, nocturnal mammals: a case study of the West European hedgehog (*Erinaceus europaeus*)

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Abstract

Monitoring changes in populations is fundamental for effective management. The West-European hedgehog (*Erinaceus europeaus*) is of conservation concern in the UK because of recent substantial declines. Surveying hedgehogs is, however, problematic because of their nocturnal, cryptic behaviour. We compared the effectiveness of three methods (infra-red thermal camera, specialist search dog, spotlight) for detecting hedgehogs in three different habitats. Significantly more hedgehogs were detected, and at greater distance, using the camera and dog than the spotlight in amenity grassland and pasture; no hedgehogs were detected in woodland. Increasing ground cover reduced detection distances, with most detections (59.6%) associated with bare soil or mown grass; the dog was the only method that detected hedgehogs in vegetation taller than the target species' height. The additional value of surveying with a detection dog is most likely to be realised in areas where badgers (*Meles meles*), an intra-guild predator, are and/or where sufficient ground cover is present; both would allow hedgehogs to forage further from refuge habitats such as hedgerows. Further consideration of the effectiveness of detection dogs for finding hedgehogs in nests, as well as developing techniques for monitoring this species in woodland, is warranted.

Key words: Conservation dog; cryptic species, detection dog; infra-red camera; mammal monitoring; thermal camera

INTRODUCTION

Wildlife management and conservation interventions are becoming increasingly important globally as extensive anthropogenic changes are made to the environment (Vitousek et al. 1997, Millennium Ecosystem Assessment (MEA) 2005, Sutherland 2013, Veach et al. 2017) and biodiversity is threatened (Butchart et al. 2010, Wagler 2013, Tittensor et al. 2014, Ceballos & Ehrlich 2018). The effective development and implementation of conservation and/or management strategies is, in part, dependent upon quantifying the distribution and abundance of populations and how they are changing spatially and/or temporally (Warren et al. 2000, Wilson & Delahay 2001, Grenyer et al. 2006, Schipper et al. 2008).

Methods for estimating temporal and spatial variation in population size and distribution can be broadly split into direct versus indirect methods (Langbein et al. 1999, Wilson & Delahay 2001, Day et al. 2016). Direct methods are associated with counts of live animals themselves, whereas indirect counts are based on counts of “field signs” such as refugia (Waters et al. 2011, Judge et al. 2014), tracks (Alibhai et al. 2017, Williams et al. 2018b), scats (Churchfield et al. 2000, Day et al. 2016, Cortázar-Chinarro et al. 2019, Mwebi et al. 2019) and feeding signs (Redpath et al. 2001, Meek et al. 2012), or e.g. counts of animals killed on roads (Baker et al. 2004, Seiler et al. 2004, Bright et al. 2015) or by hunters (Aebischer et al. 2011, Aebischer 2019). These indirect approaches have tended to be used where direct methods are not possible (e.g. the focal species occupies a habitat where direct observation is not possible), or because they are cheaper (Alibhai et al. 2017). The use of indirect measures is, however, predicated on the assumption that they reflect population size per se or some relative measure of population size, but it is known that they can be associated with a range of confounding factors that make estimates uncertain and interpretation of data difficult (McDonald & Harris 1999, Bright et al. 2015). Converting counts of relative abundance to measures of absolute abundance is particularly problematic.

In addition to counting animals for population monitoring, capturing individuals may also be an important component of scientific studies. For example, radio- and satellite-tracking have revolutionised our understanding of animal movement patterns (Craighead & Craighead 1972, Deutsch et al. 1998, Marzluff et al. 2001,) and the attachment of bio-loggers and animal-mounted video cameras enable scientists to obtain data that would otherwise be impossible to get (Yasuhiko 2004, Ropert-Coudert & Wilson 2005, Loyd et al. 2013, Volpov et al. 2015; Wilmers et al. 2015). Handling animals also enables morphological, physiological, isotopic, reproductive and parasitological data to be collected (Wassenaar & Hobson 2000, Elledge et al. 2008, Telfer et al. 2010, Wikenros et al. 2016), as well as being crucial to the application of techniques such as the use of doubly labelled water for estimating energy consumption (Lifson et al. 1955, Lifson & McClintock 1966, Nagy 2001, Pettett et al. 2017a). Typically, animals are captured using devices such as nets, traps and snares (Flowerdew et al. 2004, Hill & Greenaway 2005, Tyrrell et al. 2009): this is often expensive, time-consuming, and associated with significant animal welfare and legal issues (Putman 1995, Lane & McDonald 2010, Brown et al. 2013). Consequently, the development of novel methods for locating animals that improve welfare standards and enable the collection of robust data is important for designing successful management plans.

The West-European hedgehog (*Erinaceus europeaus,* hereafter ‘hedgehog’) is a species of increasing conservation concern in Britain (Mathews et al. 2018), and elsewhere (Haigh 2011, Van de Poel et al. 2015), because of a substantial decline in recent decades (Holsbeek et al. 1999, Huijser & Bergers 2000, Van de Poel et al. 2015, Hof & Bright 2016, Mathews et al. 2018, Müller 2018 Pettett et al. 2018, Williams et al. 2018a, Wilson & Wembridge 2018). This has been widely attributed to a range of factors, including: a substantial reduction in the extent and quality of hedgerows (Carey et al. 2008, Moorhouse et al. 2014); increased predation and competition pressure from badgers (*Meles meles*) (Young et al. 2006, Judge et al. 2014); direct or indirect impact of roads (Huijser & Bergers 2000, Rondinini & Doncaster 2002) and the extensive use of pesticides (Battersby 2005), which have resulted in direct poisoning (Dowding et al. 2010) or a decline in the abundance and variety of invertebrate prey (Geiger et al. 2010, Hof & Bright 2010). The magnitude of this decline is, however, equivocal because of problems associated with quantifying hedgehog density.

To date, researchers and NGOs have generally relied upon spotlighting, footprint-tunnels, trapping and/or counts of dead animals on roads to either (i) capture hedgehogs (mainly for marking and to attach radio-tracking or GPS-tracking devices) or (ii) estimate relative abundance or hedgehog presence-absence (Young et al. 2006, Poulton & Reeve 2010, Trewby et al. 2014, Pettett et al. 2017a, b, Williams et al. 2018 a, b). However, these approaches have often varied in their efficacy and are associated with factors that may affect their robustness or usefulness. In addition, most studies have relied on a single technique, preventing comparison of the efficacies of different techniques. For example, footprint-tunnels have been used successfully in both urban and rural areas in the UK (Yarnell et al. 2014, Williams et al. 2018a, b) but have had limited success in some other studies (Haigh et al. 2012, Gurnell & Bowen 2016). Similarly, spotlight surveys were the most effective method for locating hedgehogs in Regent's Park, London (Gurnell & Bowen 2016), whereas Poulton and Reeve (2010) dismissed this method for surveying hedgehogs, as when applied, they only detected hedgehogs in 14 of 97 visits across 30 sites in Britain. The latter could, however, have simply reflected low patterns of occupancy at the sites surveyed rather than a limitation of spotlighting per se; this is supported by spotlights and footprint-tunnels providing consistent results across 17 of 19 (89%), 15 of 18 (83%) and 6 of 17 (94%) sites surveyed in spring, summer and autumn, respectively, by Yarnell et al. (2014: authors' unpublished data). Finally, footprint-tunnels do not provide information about hedgehog density, merely recording presence/absence (Yarnell et al. 2014, Williams et al. 2018a), whilst the number of hedgehogs killed on roads may be affected by factors other than just animal density such as road size (Rondinini & Doncaster 2002). Consequently, there is a need to consider novel survey methods that overcome the limitations associated with these current methods, but also to compare their relative efficacy by conducting standardised surveys at the same site(s).

Two methods that could potentially be used to survey hedgehogs more efficiently are infra-red thermal cameras and detection dogs. Infra-red thermal (IRT) cameras display an image of the scene using emitted heat (infra-red radiation) rather than visible light (Cilulko et al. 2013). In the context of surveying for animals, this approach is particularly useful at night when the contrast between the heat of the animal and the surrounding vegetation is large (Sabol & Hudson 1995, Mayle et al. 1999, Butler et al. 2006, Bowen et al. 2019). This overcomes issues associated with using visible light, such as from a spotlight or torch, to detect species that are cryptically camouflaged and those, such as with hedgehogs, which "freeze" or curl up when feeling threatened (Reeve 1994, Nottingham et al. 2019). However, like spotlights, IRT cameras are not as effective in dense vegetation, which blocks the heat signature (Ditchkoff et al. 2005); this is particularly problematic for small species where even short grass may obscure individuals (Boonstra et al. 1994, Karp 2020).

Specially trained dogs have been used for conservation purposes since the 1890s when they were used to locate New Zealand kiwi (*Apreyx* spp.) and kakapo (*Strigops habroptilus*) (Helton 2009). Since these pioneering projects, dogs have been trained to detect the presence of a wide array of biological organisms and associated structures and ejecta, including: plants (Goodwin et al. 2010); large mammal faeces (Vynne et al. 2011, de Oliveira et al. 2012, Arandjelovic et al. 2015); reptiles (Stevenson et al. 2010, Nielsen et al. 2016); nests (Cablk & Heaton 2006, O'Connor et al. 2012); carcasses (Paula et al. 2011, Mathews et al. 2013); and owl pellets (Wasser et al. 2012). Dogs rely on detecting the focal animal/object by scent rather than sight and are able, therefore, to detect these even if they are not in direct line of sight e.g. in vegetation (Leigh & Dominick 2015, Karp 2020), at a greater distance than humans in some instances (Goodwin et al. 2010, de Oliveira et al. 2012). Furthermore, dogs trained to detect particular scents mean that they are better able to discriminate between objects/structures that challenge human observers. For example, dogs were 153% more accurate and 19 times faster at identifying koala (*Phascolarctos cinereus*) scat than experienced human surveyors (Cristescu et al. 2015).

Both IRT cameras and dogs have previously been used to locate hedgehogs. For example, dogs were used in the search for hedgehogs on the island of North Uist in Scotland during a removal programme to protect ground-nesting birds (Scottish Natural Heritage, unpublished); overall, over 1129 searches with dogs were undertaken, although no figure of the number of hedgehogs found during that time is available. Similarly, Warwick (1987) briefly used a dog during initial surveys in North Ronaldsey (Orkney Islands, Scotland) where it effectively found hedgehogs in a familiar area but not elsewhere. Finally, Morris (1988) also mentions success in finding hedgehogs with a dog although this is not described in detail. IRT cameras have been used successfully in Regent's Park, London, UK (Bowen et al. 2019) and forest fragments in Auckland, New Zealand (Nottingham et al. 2019). Conversely, Haigh et al. (2014) concluded that the IRT camera they used was ineffective.

The efficacy of these two techniques have not, however, been compared, nor have these techniques been applied in non-urban habitats within Britain. Therefore, in this study, we conducted a pilot project to compare the effectiveness of an IRT camera, a detection dog and spotlighting as methods for locating hedgehogs in a rural landscape. Specifically, we compared: (i) the absolute number of hedgehogs detected by each method in three different habitats (amenity grassland, pasture, woodland); (ii) the mean detection distance of each method in each habitat; and (iii) the effect of vegetative ground cover on detection distance. We then go on to: (iv) discuss our observations of using a detection dog, in controlled conditions for the first time, as a method for locating hedgehogs; and (v) consider the costs and benefits associated with each of the three methods in the context of future studies.

MATERIALS AND METHODS

Data were collected on the Hartpury University and College campus, Gloucestershire, UK (National Grid reference SO785237), a 360ha mixed commercial farm used for agricultural teaching and research. Previous studies had confirmed that hedgehogs were present (Bearman-

Brown et al. 2020). The site was surveyed on 18 separate nights during May-October 2019 following a standardised transect route (approx. 6km long; but see Results) which encompassed three specific habitat types (HABITAT): amenity grassland, pasture and woodland. Surveys were conducted using three different methods (METHOD): spotlighting; infra-red thermal (IRT) camera; and a trained conservation detection dog. All three habitats were surveyed on any given night using a single method; habitats were visited in a random order. Six replicates were performed for each method giving a total of 54 surveys (3 methods * 6 replicates * 3 habitats).

Surveys started approximately one hour after sunset and were conducted on nights with minimal rain and wind as these may have affected hedgehog behaviour and reduced the efficiency of one or more of the survey methods, for example strong winds can affect a dog's ability to locate the target (Jamieson 2019). Two measures of survey effort were recorded within each habitat: survey duration (TIME: maximum 40 minutes) and distance travelled (DISTANCE). Air temperature and humidity were recorded at the start and end of each survey and each time a hedgehog was located.

Spotlight and thermal camera surveying

Spotlight (1 million candle-power Clulite CB2 Clubman, Clulite Engineering Ltd., Petersfield, Hampshire, UK) and infra-red thermal camera (FLIR E53, FLIR Systems UK, West Malling, Kent, UK) surveys were conducted on foot by an experienced hedgehog surveyor (LBB). The surveyor was accompanied by a second person for safety reasons but who was instructed to remain silent throughout; any hedgehogs missed by the surveyor but observed by the safety person were recorded at the end of the surveying (i.e. they were not recorded as a "detection" for the purposes of the current study). The spotlight was not filtered as in some other studies (Pettett et al. 2017a,b).

When using the spotlight or IRT, these were used intermittently with the surveyor walking ten paces then stopping to slowly scan the surrounding area whilst also listening for the sound of hedgehogs foraging or moving through undergrowth; however, no hedgehogs were detected by sound alone. This approach was adopted to minimise the risk of tripping, as the IRT camera may not indicate hazards that have equal thermal properties to the surrounding area. Batteries on both devices were changed after the second survey of the night (after approximately 1.5 hours) . The thermal camera was recently calibrated, and set up according to the following parameters (Bowen et al. 2019): emissivity setting set to a custom setting of 0.95; distance 20m; relative humidity 50%; atmospheric temperature 20°C; and window compensation off.

Dog-team surveying

One male rescue springer spaniel dog was trained to search for, and quietly indicate upon, the scent of hedgehog: training was conducted using hedgehog spines taken from specimens found dead on roads. The dog had previously been trained to detect a range of wildlife odours and worked in a commercial capacity for a consultancy undertaking wildlife surveys. Consequently, he was only available for the current project outside these other commitments. The alert behaviour was to sit near (≥0.5m) the source of the odour and remain there quietly until called away, at which point he received the reward (tennis ball). He was handled by an experienced, trained detection dog handler (LW).

The dog and handler team were despatched on different nights to the human surveyors to ensure the dog was not following the scent of human surveyors. The dog worked on an 8m long line to ensure close control at all times. The handler followed the standardised transect route, but the dog was allowed to lead the handler when an odour was detected. Once the odour trail had been followed to ensure all areas had been covered, the dog-handler team would then return to the point at which they had departed from the transect.

As the primary focus of this study was to determine the reliability of the dog in detecting hedgehogs in a range of habitats, the dog-handler team was followed at a distance of 15-20m by a second surveyor with the thermal camera. This allowed the area to be checked unobtrusively to determine if any hedgehogs had been missed by the dog. The handler was not informed if any hedgehogs had been missed until the surveys had been completed.

The dog team worked for a maximum of three hours per night for welfare reasons, with 40 minutes survey time followed by a 20-minute break. During the break period, the dog’s harness was removed, and he was put in his kennel in a van as a clear indication that it was time to rest. Water was offered at regular intervals during surveying in accordance with environmental temperature and humidity to ensure that his mucous membranes remained moist and that he was working effectively.

Data recording

To minimise disruption to surveying during the current project, a period of prior surveying was undertaken on site using the thermal camera to locate, capture and mark hedgehogs for identification purposes. By doing this, any hedgehog captured during the study could be identified and released quickly; unmarked animals, however, did need more extensive handling as these also needed to be marked for reference.

All hedgehogs detected during the study were captured by hand under licence from Natural England, as the use of dazzling devices such as high-powered spotlights for detecting hedgehogs is restricted under Schedule 6 of the Wildlife and Countryside Act, 1981 (licence number: 2017-31042-SCI-SCI). At their initial capture, all animals were weighed, sexed, given a health check and marked using sections of numbered plastic tubing (Printasleeve Ltd, Crewkerne, Somerset, UK) glued (to five individual spines on the nape of the neck (Reeve et al. 2019). Animals caught for the first time were released at the point of capture within 15 minutes; previously marked animals that had been re-caught were typically released within ≤5 minutes. The time taken to process each animal was excluded from the 40-minute survey period.

The capture location of each hedgehog was recorded using a handheld GPS device (Garmin GPS 60). The height of vegetation in the area immediately surrounding the hedgehog was categorised as: (1) bare ground or mown grass; (2) less than the height of the back of the hedgehog (approx. <15cm); (3) ≤0.5m tall; (4) ≤1m tall; or (5) >1m tall. These categories were condensed to two levels for analysis (low: Category 1; high: Categories 2-5 combined) because of small sample sizes in the latter divisions.

For spotlighting and the IRT camera, detection distance was approximated by pacing as the straight-line distance from the surveyor to the position of the hedgehog when it was first sighted

(Bowen et al. 2019). For the dog team, detection distance was taken as the straight-line distance from the dog to the hedgehog at the point the handler believed (based on extensive work undertaken by the handler with this dog and others in a professional capacity) it was clear the dog had caught the animal's scent e.g. through a noted change in direction, activity level or body position,. This would correspond to the minimum distance at which the dog detected the scent of the hedgehog, as it is not possible to define exactly the point at which the dog initially detected the scent from the target.

Data analysis

Survey effort

As the number of hedgehogs detected by each method may vary in relation to the method itself but also the density of hedgehogs in the different habitats and survey effort, preliminary analyses were conducted to determine whether survey effort was consistent. A general linear model was used to analyse the effects of HABITAT (pasture, amenity, woodland) and METHOD (camera, spotlight, dog) on distance walked in each habitat (DISTANCE): this model included a HABITAT*METHOD interaction term. Both predictor variables were modelled as fixed factors. Data were checked to ensure that they conformed to the underlying assumptions of the test (Grafen & Hails 2002). Data for the duration of surveying (TIME) were not normally distributed, so a Kruskal-Wallis test was used to compare median values across all nine HABITAT-METHOD subgroups.

The relationship between DISTANCE and TIME was analysed using Pearson correlation as these are likely to be inter-related, which can cause problems with multicollinearity in statistical models (Grafen & Hails 2002, Field 2017). Initially, data across all three habitats were compared. A further correlation was conducted for those data from amenity grassland and pasture but excluding woodland as the latter was excluded from the analysis comparing the survey methods since hedgehogs were not detected in woodland by any method (see Results).

Comparison of survey methods

The effect of METHOD, HABITAT, TIME, DISTANCE, air TEMPERATURE and HUMIDITY on the number of hedgehogs detected was analysed using a generalised linear model (GLM) assuming a Poisson error distribution. As no hedgehogs were detected in woodland using any method, these data were both uninformative for evaluating the influence of the covariates and caused under-dispersion; they were, therefore, removed prior to analysis. An initial global model containing all covariates was fitted and then AIC based multi-model selection (Burnham & Anderson 2002) was applied using the *MuMin* package (Barton 2019) in R version 3.3.3 to find the best fitting models; models with ΔAICc values <2 were assumed to have equal support (Burnham & Anderson 2004). The assumptions of the GLM were then tested for the global model and the single best-fitting model, using a goodness-of-fit deviance test and a residual dispersion test for a Poisson error distribution through the *DHARMa* package (Hartig 2017).

Factors affecting detection distance

It was not possible to incorporate METHOD, HABITAT type (amenity grassland, pasture) and ground COVER (low, high) into a single analysis because of e.g. the inherent limitations of the methods themselves and how this influenced sample sizes in different categories (see

Supplementary Figure S1). For example, surveyors are less likely to be able to detect hedgehogs in dense cover using a spotlight or IRT camera because the animal is physically hidden from view, whereas this may not be the case for a detection dog. Therefore, we used a combination of Kruskal-Wallis and Mann-Whitney tests to compare differences in the distance over which hedgehogs were first detected in relation to (a) survey method, (b) ground cover and (c) habitat.

General linear model, Kruskal-Wallis and Mann-Whitney analyses were conducted using Minitab version 19 and SPSS version 25. Data are presented as mean (±SD) or median (±IQR) in accordance with the statistical tests used.

RESULTS

Seventeen hedgehogs were found during surveys, with each hedgehog located a median of 3 times (IQR = 1-3).

Survey effort

Survey DISTANCE was not significantly affected by METHOD (General linear model: $F_{2,45}$ = 0.05, P = 0.952) or the interaction between METHOD*HABITAT ($F_{4,45}$ = 0.99, P = 0.424) but was significantly affected by HABITAT ($F_{2,45}$ = 60.74, P < 0.001). Distance walked was significantly higher in pasture (2.27 ± 0.20 km) than in amenity grassland (1.73 ± 0.19) and woodland (1.67 ± 0.14).

There was also a significant difference in the duration of surveying (TIME) across the nine HABITAT and METHOD subgroups (Kruskal-Wallis test: H = 20.72, DF = 8, P = 0.008). Although there was a lot of overlap between subgroups, this difference was principally due to a longer survey time in pasture where all surveys lasted 40 minutes regardless of survey method, compared to mean survey times of 38.9 (range: 36-40) minutes for amenity grassland and 36.8 (range: 32-40) minutes for woodland.

Survey duration and distance walked were significantly positively correlated when data from all three habitats were considered (Pearson correlation: r = 0.41, n = 54, P = 0.002), but not when woodland was excluded (r = 0.31, n = 36, P = 0.064).

Comparison of survey methods

Hedgehogs were detected on 47 occasions across the 54 transect surveys (mean (±): 0.87 ± 1.20; range: 0-5). There was a marked difference in the number of animals detected within each habitat (Table 1). Most notably, no hedgehogs were detected by any method in woodlands; 2.6 times as many hedgehogs were detected in amenity grassland versus pasture. On no occasion did the dog fail to detect a hedgehog that was located by the second surveyor following behind with the IRT camera.

Table 1. Number of hedgehogs recorded within each habitat using each survey method. Six transect surveys were conducted in each habitat using each method.

Method	**Habitat**			**Total**	**Mean (±SD)**	**Median [Range]**
	Amenity grassland	**Pasture**	**Woodland**			
Infra-red thermal camera	15	4	0	19	1.06 ± 1.55	0.0 [0-5]
Detection dog	12	8	0	20	1.11 ± 1.02	1.0 [0-3]
Spotlight	7	1	0	8	0.44 ± 0.86	0.0 [0-3]
Total	34	13	0	47	0.87 ± 1.20	0.0 [0-5]
Mean (±SD)	1.89 ± 1.32	0.72 ± 0.89	0.00	0.87 ± 1.20		
Median [Range]	2.0 [0-5]	0.5 [0-3]	0.0 [-]			

Across all models, there were significantly fewer hedgehogs detected in pasture than in amenity grassland (Table 2; Figure 1). In three out of the five top-ranked models, including the best overall model, METHOD of detection was retained, with more hedgehogs detected with the infra-red camera and the dog compared to spotlighting (Table 2; Figure 1). DISTANCE walked and TEMPERATURE were retained in two and one of the best models, respectively, although neither were significant.

Table 2. Estimated regression parameters (± standard error) from the general linear model predicting the number of hedgehogs detected. Reference level for 'Habitat' is amenity grassland; reference level for 'Method' is spotlight. Models presented are those with ΔAICc < 2. Full and conditional model averages are presented beneath. Asterisks denote: * < 0.05, ** < 0.01, *** <0.001.

Intercept	Distance (km)	Habitat (Pasture)	Method (Camera)	Method (Dog)	Start temperature (°C)	df	AICc	ΔAICc
-0.04 (± 0.37)		-0.96** (± 0.33)	0.87* (± 0.42)	0.92* (± 0.42)		32	102.1	0.00
0.66 (± 0.70)		-0.89* (± 0.33)	0.97* (± 0.43)	0.87* (± 0.42)	-0.05 (± 0.04)	31	103.5	1.33
0.64*** (± 0.17)		-0.96** (± 0.32)				34	103.5	1.42
1.47 (± 1.35)	0.84 (± 0.75)	-1.39** (± 0.51)	0.83 (± 0.42)	0.86 (± 0.42)		31	103.6	1.46
-1.29 (± 1.35)	1.10 (± 0.76)	-1.56** (± 0.53)				33	103.9	1.73
-0.22 (± 1.18)	0.30 (± 0.62)	-1.11* (± 0.47)	0.61 (± 0.54)	0.61 (± 0.54)	-0.01 (± 0.03)	Full average		
-0.22 (± 1.18)	0.96 (± 0.77)	-1.10* (± 0.47)	0.88* (± 0.42)	0.89* (± 0.42)	-0.05 (± 0.04)	Conditional average		

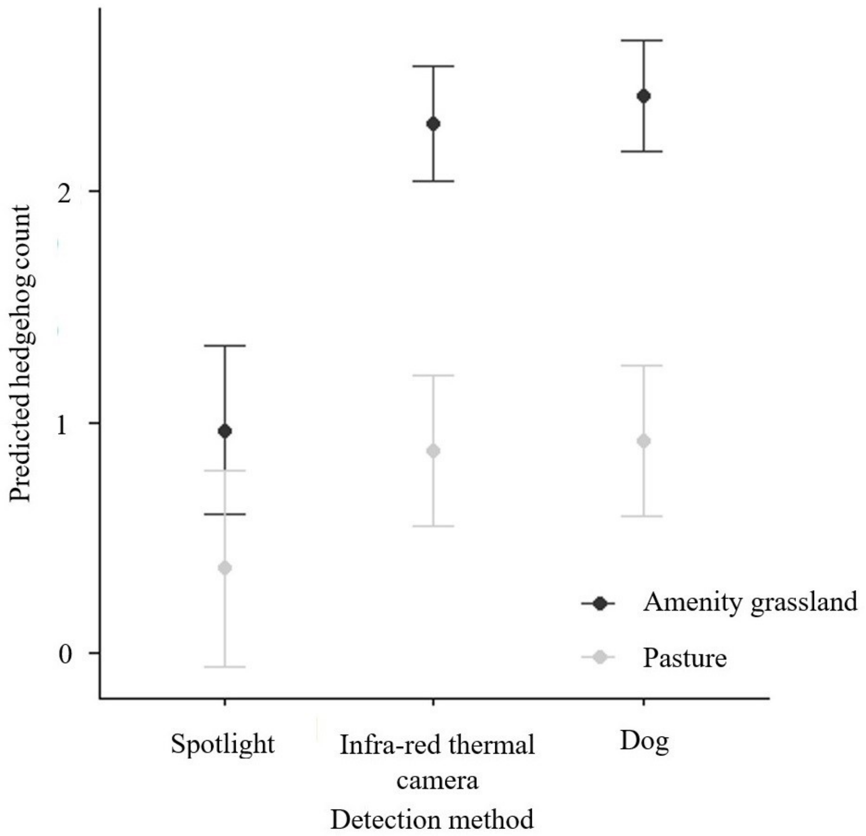


Figure 1. The predicted number (± SE) of hedgehogs detected per transect across HABITAT and METHOD from the single best model (Table 2).

Factors affecting detection distance

On average, the minimum detection distance was significantly greater for the IRT camera compared to the spotlight, with the detection dog intermediate to these two methods (Kruskal-Wallis test: H = 8.21, DF = 3, P = 0.016; Figure 2). However, there was a lot of overlap in the detection distances (Figure 3). Hedgehogs were generally detected by spotlighting at a distance of 1-10m, although one individual was first detected at 20m. Similarly, hedgehogs tended to be detected by the dog within 4-15m, but with two detection events at 25m and 30m; it must be noted, however, that these values are likely to be conservative estimates as the point at which the hedgehog was first detected was sometimes hard to estimate based upon a clear change in the dog's behaviour. Detection distance was most variable using the IRT camera, ranging from 4-50m; this method was associated with the majority of long-distance detections (>15m).

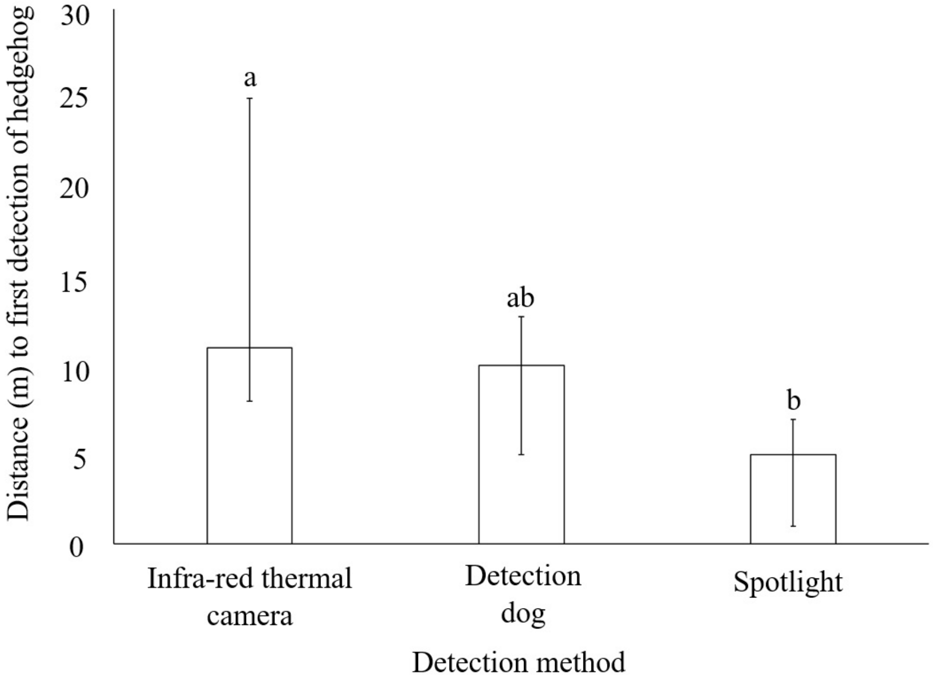


Figure 2. Median (±IQR) distance hedgehogs were first detected using an infra-red thermal camera (N = 19), detection dog (N = 20) or spotlight (N = 8). Data from different habitats and different levels of ground cover combined. Letters denote *post hoc* groupings from a Kruskal-Wallis test.

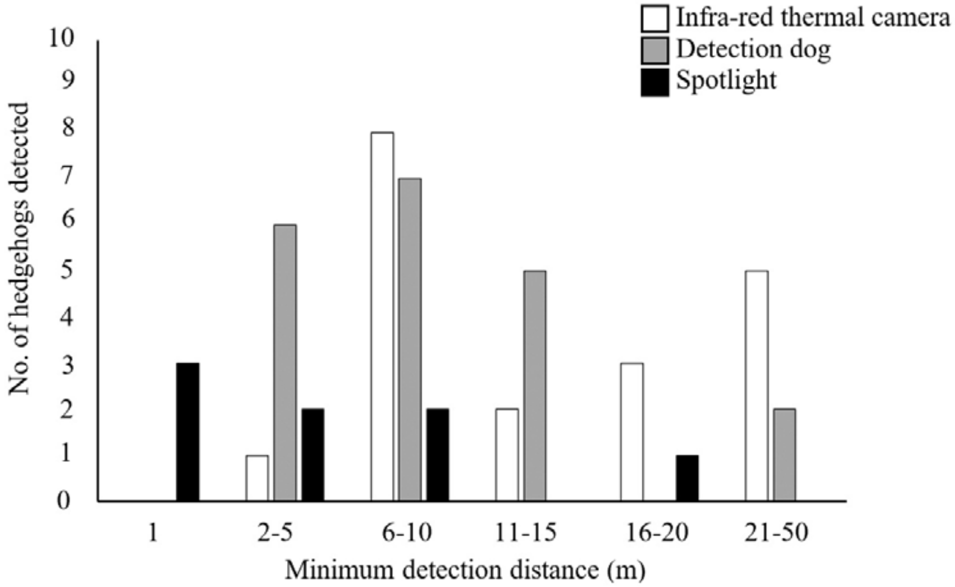
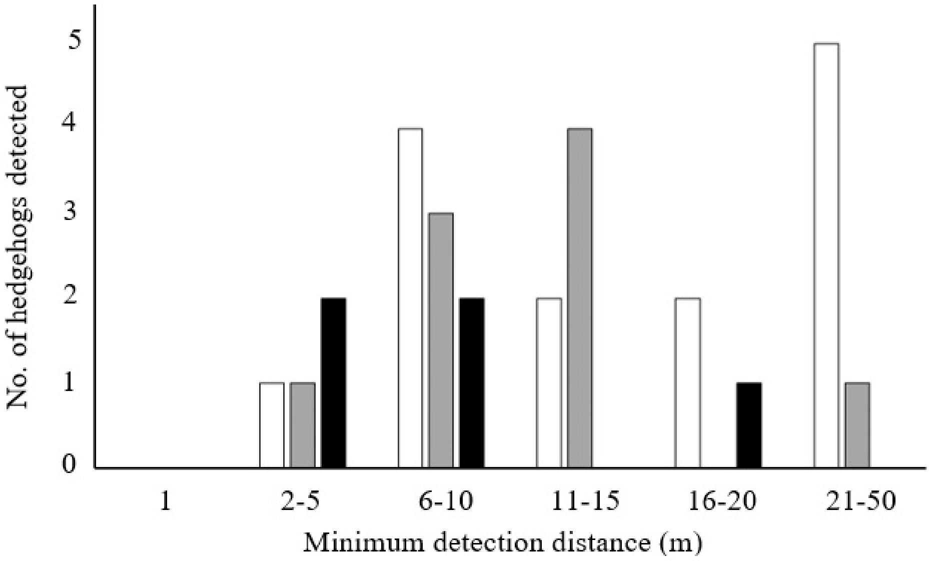


Figure 3. Pattern of minimum detection distance (m) in relation to survey method: infra-red thermal camera (N = 19), detection dog (N = 20) and spotlight (N = 8). Data from different habitats and different levels of ground cover combined.

Most detections (n = 28) were associated with low ground cover (bare ground or mown grass): hedgehogs tended to be detected using the spotlight, dog and IRT camera at distances of 5-10m, 5-15m and 8-30m, respectively (Figure 4a). In comparison, spotlights were only able to detect hedgehogs in higher vegetation at very short distances (1m) whereas the detection distances for both the IRT camera and dog were much higher (6-18m and 4-25m, respectively; Figure 4b). The dog was the only method that detected hedgehogs in vegetation greater than the height of the hedgehog (Categories 3-5; n = 4). Given these patterns, the median detection distance was significantly greater in low ground cover (Mann-Whitney test: U = 120.50, n = 47, P = 0.002; Figure 5).

(a) Low ground cover



(b) High ground cover

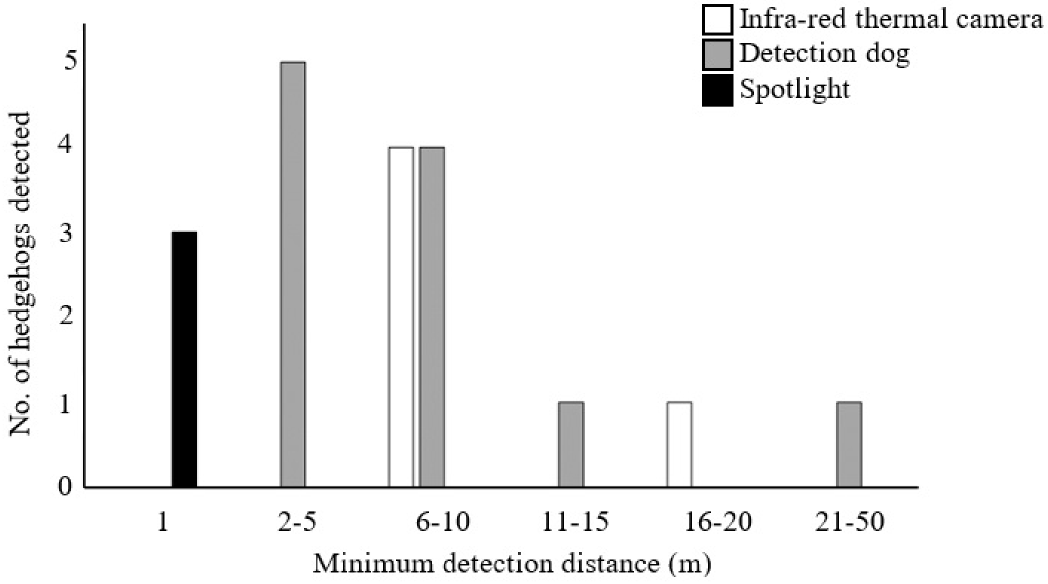


Figure 4. Pattern of minimum detection distance (m) in relation to survey method in (a) low (N = 28) and (b) high (N = 19) ground cover. Data from different habitats combined.

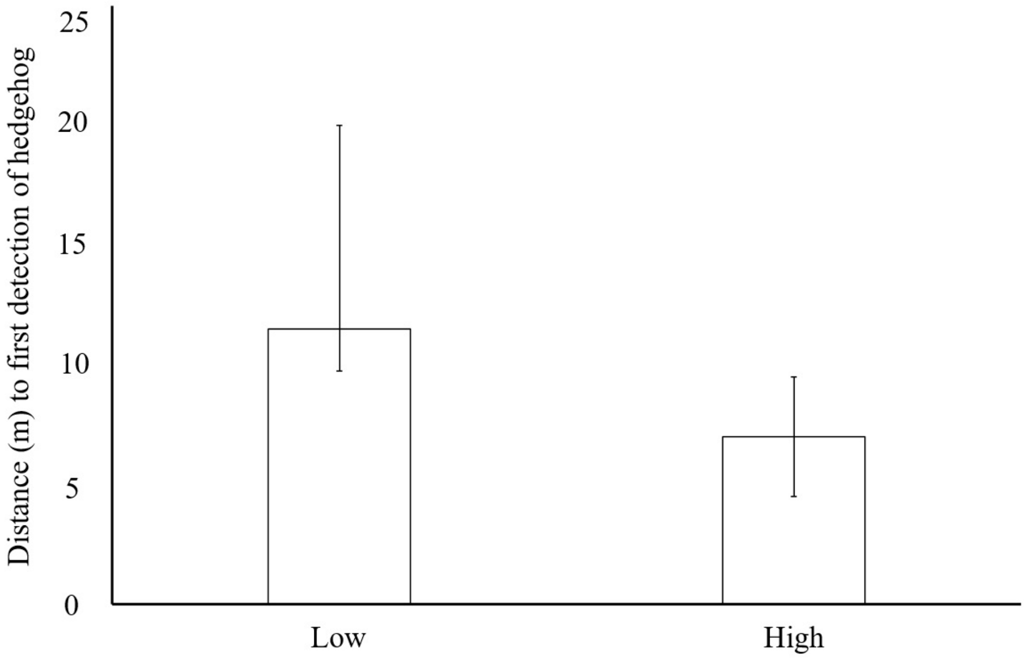


Figure 5. Median (±IQR) detection distance of hedgehogs in low and high vegetation (see text for details). Data from different methods and habitats combined.

DISCUSSION

This pilot study is the first to compare the efficacy of an infra-red thermal camera, a detection dog and spotlighting as methods for locating hedgehogs in three common rural habitats in Britain: amenity grassland, pasture and woodland. A single dog was used in this study so that we could e.g. determine the ability of the dog to access locations where hedgehogs were likely to be detected. In addition, the dog used in this study is part of a commercial organisation run by the handler. As training of detection dogs is time consuming, and there are time constraints with availability, sample sizes were relatively low but were able to identify significant differences between the three methods used. As such, this study should be considered as a proof of concept, but with the recommendation that further research is required.

To standardise survey effort, surveyors walked the same transect route in each habitat, trying to walk at a consistent speed for a maximum of 40 minutes. In addition to affecting survey effort, differences in walking speed in different habitats could affect the amount of noise made by surveyors, thereby affecting the number of animals detected; this is particularly true for hedgehogs which generally tend to freeze or curl into a ball when they feel threatened, although some individuals will actively run away (Reeve 1994, Morris 2018).

However, significant differences were evident for both the distance walked and survey duration within each of the three habitats. Distance walked during surveying was significantly higher in pasture (mean: 2.27 km) than in both amenity grassland (1.73 km) and woodland (1.67 km), whereas survey duration was lower in woodlands (mean: 36.8 minutes) compared to amenity grassland (38.9 minutes) and pasture (40.0 minutes). Consequently, surveyor speed was markedly greater in pasture (3.4 kmh^{-1}) than in the other habitats (amenity grassland: 2.7 kmh^{-1}; woodland: 2.7 kmh^{-1}). At one level, these data indicate the need to record both measures of survey effort in these sorts of studies, but also those where a single technique is used to derive an estimate of the relative abundance of hedgehogs. Standardising survey distance and time may be particularly important in large-scale surveys involving volunteers, where surveyor skill may be a particular issue for cryptic species such as the hedgehog. To date, however, survey effort has not typically been recorded in hedgehog studies in the UK and/or incorporated into the resultant statistical analyses (e.g. Young et al. 2006, Poulton & Reeve 2010, Trewby et al. 2014, Bowen et al. 2019). In this study, distance walked but not survey time was retained in two of the five best-ranked models investigating factors associated with the number of hedgehogs detected (Table 2). Hedgehogs were frequently located repeatedly throughout all survey methods, with a median of three encounters over all surveys. As is typical of hedgehog behaviour (Haigh et al. 2009, Hof & Bright 2010b), individuals were repeatedly located in the same areas, although home range was not quantified in this study as insufficient data were collected.

Approximately twice as many hedgehogs were located, on average, using the IRT camera and detection dog than spotlighting in both amenity grassland and pasture (Figure 1). In addition, the minimum detection distance was greater for the IRT camera (median: 11m) and, to a lesser degree, the detection dog (10m) than the spotlight (5m: Figure 2). These distances for the IRT camera and spotlight are markedly lower than those reported by Bowen *et al.* (2019) from their study in Regent's Park London. In that study, the thermal camera detected hedgehogs at a mean distance of 30.0m, but with a maximum distance of 200m; comparable figures for the torch used were a mean and maximum of 12.0m and 50m, respectively.

Drawing specific comparisons between studies is, however, difficult. For example, in addition to differences associated with the make and model of the thermal camera and torch used in different studies, and the number of surveyors applying each method at any given time (e.g. Bowen *et al.* (2019) utilised 3-4 surveyors for torch surveys compared to one person for their IRT camera), it is also necessary to consider differences in hedgehog density, habitat structure and the wider landscape. One major difference between our study and Bowen *et al.*'s (2019) study is the potential impact of the presence of badgers: these are absent from Regent's Park but are present at Hartpury. Many previous studies have documented changes in the density (Young et al. 2006, Hubert et al. 2011, Trewby et al. 2014, Van de Poel et al. 2015) and movement behaviour (Hof et al. 2012, Pettett et al. 2017b) of hedgehogs in the presence versus absence of badgers. Notably, hedgehogs tend to remain in closer proximity to areas of cover where badgers are present, which would tend to have the effect of reducing detection distances because animals would be less likely to be in open habitats a long way from protective vegetation.

None of the three methods detected any hedgehogs in woodland. This could indicate an inability of all three methods to work effectively in very cluttered habitats, or that woods are not a favoured habitat for hedgehogs at this time of the year. Although the data are limited, there is some evidence that supports the latter hypothesis. For example, woodlands were the least selected habitat in a radio-tracking study of hedgehogs in arable landscapes (Pettett et al. 2017b) and were not identified as a factor significantly affecting patterns of hedgehog occupancy in a national survey of England and Wales (Williams et al. 2018a). As outlined above, one possible factor affecting the use of woodlands is the likelihood of encountering badgers, which favour woodlands and plantations as habitats for their setts (Wilson et al. 1997). This aspect of hedgehog ecology requires urgent attention as two previous national estimates of the total number of hedgehogs in Britain (Harris et al. 1995, Mathews et al. 2018) have both relied upon an estimate of 40 hedgehogs/km^2 for broadleaved woodland, with this single habitat harbouring 37% of the national population.

Detection distances were, however, significantly affected by the amount of ground cover. In fact, we had to merge all categories of ground cover other than bare ground or mown grass (59.6% of all detection events) for analysis because of the small number of detections in categories where even small amounts of grass were present. Not surprisingly, therefore, the median detection distance was significantly higher (11.5m) at the lowest level of ground cover (recorded as bare ground or mown grass) compared to more vegetated areas (7.0m). In the presence of vegetative cover, the detection dog out-performed the other two methods, accounting for 11 of 19 (57.9%) detections, and was the only method where hedgehogs were detected when they were surrounded by vegetation taller than they were.

Performance of the detection dog

As biological organisms, detection dogs are potentially susceptible to a range of limitations not evident with other forms of survey “equipment” including fatigue, distraction and potential risk to the focal animals themselves. In this study, we therefore adapted the surveying protocol to minimise some of these issues. For example, we ensured that the dog had a 20-minute rest period after each habitat had been surveyed and did not work for more than three hours each night. In addition, as the detection of animals by scent can be affected by environmental conditions, leading to inconsistencies in detection ability (Gutzwiller 1990, Cablk et al. 2008), we only surveyed when the air temperature was above ~10^{o}C (mean 15.4^{o}C; range 9.3-24.1^{o}C) and conditions were dry at the start of the night’s survey (humidity: mean 68.3%; range 39.8-99.9%). Humidity was not significant in the analysis of factors affecting the numbers of hedgehogs detected, but air temperature at the start of surveying was retained in one of the five top-ranking models: in that model, air temperature was negatively related to the number of hedgehogs located but the parameter was not significant (Table 2). This partly corroborates the observation of Pettett et al. (2017a) that hedgehogs were more likely to be further from cover in colder temperatures.

Whilst in many instances, dogs have been used to detect scats (e.g. Smith et al., 2005, Long et al., 2007, Vynne et al., 2011) or carcasses (e.g. Paula et al., 2011, Alasaad et al., 2012, Mathews et al., 2013), the use of a dog to locate and approach live (potentially) prey animals poses additional challenges. These include the potential for the dog to injure the animal, for the animal to injure itself in attempts to escape, and/or for the transmission of disease. In this context, both the selection of a dog with a low prey drive and rigorous training is critical (Karp 2020). In this study, the dog never approached a hedgehog closer than approximately 0.5m as trained, and never attempted to pursue any other animal encountered during surveying (e.g. rabbits *Oryctolagus cunniculus*). Upon approach by the dog, all hedgehogs demonstrated a freeze or curl response suggesting the risk of injury to the hedgehogs was low, as attempts to escape were not evident; all animals also demonstrated the same responses when spotlights were used, as has been previously reported (Bowen et al. 2019). However, a flee response was observed on two occasions when using the IRT camera; in both cases, the animals were already only a short distance from cover.

To further ensure the safety of the hedgehogs and the dog itself, the dog remained on a long line as recommended by Mathews et al., (2013). However, previous authors have suggested that allowing a dog to search freely allows for more natural movement and search patterns for the target (de Oliveira et al., 2012, Glen et al., 2018, Thomas et al., 2020) and dogs have been found to be more effective off-lead in controlled trials searching for scats (Cristescu et al. 2015); the use of dogs to find live, nocturnal animals at night has also been recently reported (Karp 2020). Therefore, future studies could examine whether the use of an unrestricted dog could further increase hedgehog detection rates; this could be particularly important in habitats, such as woodlands, where the presence of the surveyor may impede the dog's movement. However, it must be noted that on no occasion did the dog in this study fail to detect a hedgehog that was also detected by the second surveyor carrying the IRT camera, such that detection reliability in both amenity grassland and pasture was not negatively impacted by being restrained.

The dog in this study was used to detect free-roaming hedgehogs. However, the ability to detect hedgehogs in their nests could offer both scientific and practical benefits. For example, they could facilitate studies investigating the use of different habitats as sites for summer nests and winter hibernacula (Morris 1973, Reeve & Morris 1985); they may be especially helpful in helping obtain data from smaller individuals that cannot be fitted with radio-tags on welfare grounds, but which may be more vulnerable to variation in food availability (sensu Rasmussen et al. 2019). Nesting hedgehogs are also vulnerable to a range of human activities including mowing, bonfires and the clearance of land for development (Reeve 1994, Reeve & Huijser 1999, Rasmussen et al. 2019). In these contexts, detection dogs offer one possible means of locating nesting animals which could then be moved out of harm's way; currently no option exists to do this.

Cost-benefit comparisons

Both the IRT camera and the detection dog enabled surveyors to detect more hedgehogs and at greater distances than spotlighting, and the IRT camera detected more hedgehogs at greater distances than the dog in areas of low ground cover, but this was reversed in areas of high ground cover. As such, thermal cameras and detection dogs both offer distinct advantages over spotlighting in terms of both capturing hedgehogs and for surveying and monitoring populations, but also some disadvantages including price and practicability. For example, the IRT camera and spotlight models (including battery packs) used in this study retailed at a cost of approximately £4600 and £270, respectively. In comparison, the detection dog cost £470 a night (£350 fee, £80 transport and £40 accommodation) to hire. These figures translate to a unit-cost of £242, £34 and £141 per hedgehog detected, respectively, although the cost of both the IRT camera and the spotlight are fixed, such that the financial reward of purchasing these devices would increase each time they are used; this is not the case for the detection dog.

However, the added value of the camera and the dog are the additional number of animals that would be detected per unit effort. From a scientific perspective, these extra detection events would lead to more robust data, including increased statistical power (Mayle et al. 1999). Unfortunately, quantifying the magnitude of this added value from the current study is complicated because of how the data were collected: because the focus of the study was to compare the ability of the three methods to detect live hedgehogs, and especially because the IRT camera is dependent on identifying body heat, we had to collect data on live hedgehogs in real time. It was not possible to use all three methods simultaneously as having three sets of surveyors in the field in the same place would increase levels of disturbance on hedgehog behaviour and there would be difficulties in maintaining the independence of observations. Consequently, we used one technique each night, which meant that the distribution of hedgehogs was not consistent across each night of surveying. The increased detection distance associated with the camera and dog would not be of benefit if they simply detected hedgehogs that would otherwise have been detected by the spotlight in due course e.g. they were in front of the surveyor on the general trajectory of the transect and would remain stationary. The increased detection range of the camera and dog would be an advantage if hedgehogs sought cover at the sound of an approaching surveyor; there are currently no data on whether this is a problem or not, and thus the application of such techniques discussed here support future investigation.

Furthermore, data from radio-tracking studies suggest that, in areas where badgers are present, hedgehogs are typically in close proximity to refuge habitats such as hedgerows. For example, (Hof et al. 2012) recorded mean distances to cover of 8m at sites with badgers versus 28m at sites without badgers. Similarly, Pettett et al. (2017a) recorded that hedgehogs were, on average, 13m and 7m closer to hedgerows and buildings, respectively, when badgers were present. In the context of, for example, a citizen-science project to estimate hedgehog abundance across a large spatial scale (sensu Williams et al. 2018b), surveyors would likely be instructed to follow hedgerows and other linear habitats because of the increased likelihood of detecting hedgehogs, but also to avoid damaging crops or disturbing livestock. In these circumstances, spotlight searches may represent a cheap and effective method for surveying hedgehogs, although surveyors would need to be licensed in accordance with the Wildlife and Countryside Act which is unlikely to be granted to novice surveyors. Conversely, a licence is not required for IRT cameras and the IRT camera provides a mechanism for detecting and following hedgehogs at a distance without the risk of the disturbance associated with the use of a spotlight, thus providing a less invasive means of surveying.

However, hedgehogs are also known to forage further from refuge habitats if badgers are absent and if other cover is available. For example, the mean distance to cover increased from 4m to 42m in Hof & Bright's (2012) study, and from 12m when arable crops were less than 50cm tall, to 38m when they were >1m tall. In these circumstances, the IRT camera and dog would be advantageous, e.g. being able to locate hedgehogs much further into a pasture field even where a transect follows the field margin. A detection dog, in particular, would be able to locate hedgehogs in taller vegetation than an IRT camera or spotlight, which would help extend the amount of time surveys could be conducted throughout the year as vegetation grows; although, it is questionable whether farmers would allow surveyors to approach hedgehogs in arable fields if this was likely to damage the crop.

The current availability of just a single commercial “hedgehog dog” is a limitation for the widespread use of this approach in future studies, especially for extensive studies where multiple sites need to be surveyed within a single field-season. However, having demonstrated that dogs can be successfully trained to locate active hedgehogs, further individuals may become available in due course. It is important to acknowledge that performance can vary between dogs and handlers (Cablk & Heaton, 2006, Jamieson *et al.*, 2017, DeMatteo *et al.*, 2019), and even one dog's performance may change with different handlers (Jamieson et al. 2018). As such, this dog/handler variation would need to be incorporated into the design of future studies.

Conclusion

Spotlights have conventionally been used to locate hedgehogs for tagging and marking and to estimate relative abundance. In this study, however, significantly more hedgehogs were detected using an infra-red thermal camera and a detection dog, and at greater distances, in amenity grassland and pasture. Nevertheless, the benefits of an IRT camera and dog for surveying hedgehog populations are likely to be dependent on the typical pattern of hedgehog foraging behaviour. One factor known to significantly affect the distance hedgehogs range from cover is the presence / absence of badgers: in the presence of badgers, IRT cameras and dogs may offer limited benefits as hedgehogs are likely to stay close to cover, within the typical detection range of a spotlight; in the absence of badgers, IRT cameras and dogs may enable hedgehogs to be detected at much greater distances from transect lines.

No hedgehogs were detected in woodland by any method. This could indicate that all three methods are not suitable for surveying in this habitat or that hedgehogs typically avoid woodlands during the summer and autumn. Future studies, therefore, need to determine whether woodlands are an important habitat for hedgehogs and, if so, identify a suitable method for surveying them. In this context, detection dogs may be suitable as they were the only method in this study to detect hedgehogs in vegetation greater than the height of a hedgehog.

This study has demonstrated that detection dogs can be trained to successfully and safely locate free-ranging hedgehogs, with a performance comparable to, or greater than, current technologies, although they are associated with markedly higher costs. Further consideration should, therefore, be given to improving this technique e.g. by comparing the effectiveness when the dog is not confined to a leash; this may be particularly true for habitats with high ground cover. Additional attention should also be focused on investigating the effectiveness of detecting hedgehogs when they are in summer and/or winter nests, as this may have applied benefits for this declining species.

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References

Aebischer N.J. 2019: Fifty-year trends in UK hunting bags of birds and mammals, and calibrated estimation of national bag size, using GWCT's National Gamebag Census. Eur. J. Wildl. Res. 65: 64.

Aebischer N.J. Davey P.D. & Kingdon N.G. 2011: National Gamebag Census: Mammal Trends to 2009. Game & Wildlife Conservation Trust. Fordingbridge, Hampshire.

Alasaad S. Permunian R. Gakuya F. Mutinda M. Soriguer R.C. & Rossi L. 2012: Sarcoptic-mange detector dogs used to identify infected animals during outbreaks in wildlife. BMC Vet. Res. 8.

Alibhai S. Jewell Z. & Evans J. 2017: The challenge of monitoring elusive large carnivores: An accurate and cost-effective tool to identify and sex pumas (Puma concolor) from footprints. PLoS One 12: e0172065.

Arandjelovic M. Bergl R.A. Ikfuingei R. Jameson C. Parker M. & Vigilant L. 2015: Detection dog efficacy for collecting faecal samples from the critically endangered Cross River gorilla (Gorilla gorilla diehli) for genetic censusing. R. Soc. Open Sci. 2: 140423.

Baker P.J. Harris S. Robertson C.P.J. Saunders G. & White P.C.L. 2004: Is it possible to monitor mammal population changes from counts of road traffic casualties? An analysis using Bristol's red foxes Vulpes vulpes as an example. Mamm. Rev. 34: 115–130.

Barton K. 2019: Package "MuMIn" R Package version 1(6). Available at: https://cran.r-project.org/web/packages/MuMIn/index.html

Battersby J. 2005: UK mammals: Species status and population trends. JNCC/Tracking Mammals Partnership. Peterborough, UK.

Bearman-Brown, L.E., Baker, P.J., Scott, D., Uzal, A., Evans, L., & Yarnell, R.W. 2020: Over-winter survival and nest site selection of the west-European hedgehog (*Erinaceus europaeus*) in arable dominated landscapes. *Animals 10: 1449.*

Boonstra R. Krebs C.J. Boutin S. & Eadie J.M. 1994: Finding Mammals Using Far-Infrared Thermal Imaging. J. Mammal. 75: 1063–1068.

Bowen C. Reeve N.J. Pettinger T. & Gurnell J. 2019: An evaluation of thermal infrared cameras for surveying hedgehogs in parkland habitats. Mammalia 84: 12–14.

Bright P.W. Balmforth Z. & Macpherson J.L. 2015: The effects of changes in traffic flow on mammal road kill counts. Appl. Ecol. Environ. Res. 13: 171–179.

Brown D.D. Kays R. Wikelski M. Wilson R. & Klimley A. 2013: Observing the unwatchable through acceleration logging of animal behavior. Anim. Biotelemetry 1.

Burnham K.P. & Anderson D.R. 2002: Model selection and multi-model inference: A practical information-theoretic approach. Springer-Verlag. New York.

Burnham K.P. & Anderson D.R. 2004: Multimodel inference: Understanding AIC and BIC in model selection. Sociol. Methods Res. 33: 261–304.

Butchart S.H.M. Walpole M. Collen B. Strien A. van. Scharlemann J.P.W. Almond R.E.A. Baillie J.E.M. Bomhard B. Brown C. Bruno J. Carpenter K.E. Carr G.M. Chanson J. Chenery A.M. Csirke J. Davidson N.C. Dentener F. Foster M. Galli A. Galloway J.N. Genovesi P. Gregory R.D. Hockings M. Kapos V. Lamarque J.F. Leverington F. Loh J. McGeoch M.A. McRae L. Minasyan A. Morcillo M.H. Oldfield T.E.E. Pauly D. Quader S. Revenga C. Sauer J.R. Skolnik B. Spear D. Stanwell-Smith D. Stuart S.N. Symes A. Tierney M. Tyrrell T.D. Vié J.C. & Watson R. 2010: Global Biodiversity: Indicators of recent declines. Science (80-.). 328: 1164–1169.

Butler D.A. Ballard W.B. Haskell S.P. & Wallace M.C. 2006: Limitations of thermal infrared imaging for locating neonatal deer in semiarid shrub communities. Wildl. Soc. Bull. 34: 1458–1462.

Cablk M.E. & Heaton J.S. 2006: Accuracy and reliability of dogs in surveying for desert tortoise (Gopherus agassizii). Ecol. Appl. 16: 1926–1935.

Cablk M.E. Sagebiel J.C. Heaton J.S. & Valentin C. 2008: Olfaction-based detection distance: a quantitative analysis of how far away dogs recognize tortoise odor and follow it to source. Sensors 8: 2208–2222.

Carey P.D. Wallis S.M. Emmett B. Maskell L.C. Murphy J. Norton L.R. Simpson I.C. & Smart S.M. 2008: Countryside Survey: UK Headline Messages from 2007. Centre for Ecology & Hydrology. Wallingford, UK. 32 pp.

Ceballos G. & Ehrlich P.R. 2018: The misunderstood sixth mass extinction. Science (80-.). 360: 1080–1081.

Churchfield S. Barber J. & Quinn C. 2000: A new survey method for Water Shrews (Neomys fodiens) using baited tubes. Mamm. Rev. 30: 249–254.

Cilulko J. Janiszewski P. Bogdaszewski M. & Szczygielska E. 2013: Infrared thermal imaging in studies of wild animals. Eur. J. Wildl. Res. 59: 17–23.

Cortázar-Chinarro M. Halvarsson P. & Virgós E. 2019: Sign surveys for red fox (Vulpes vulpes) censuses: evaluating different sources of variation in scat detectability. Mammal Res. 64: 183–190.

Craighead F.C. & Craighead J.J. 1972: Grizzly bear prehibernation and denning activities as determined by radiotracking. Wildl. Monogr. 32: 3–35.

Cristescu R.H. Foley E. Markula A. Jackson G. Jones D. & Frère C. 2015: Accuracy and efficiency of detection dogs: A powerful new tool for koala conservation and management. Sci. Rep. 5: 1–6.

Day C.C. Westover M.D. Hall L.K. Larsen R.T. & McMillan B.R. 2016: Comparing direct and indirect methods to estimate detection rates and site use of a cryptic semi-aquatic carnivore. Ecol. Indic. 66: 230–234.

DeMatteo K.E. Davenport B. & Wilson L.E. 2019: Back to the basics with conservation detection dogs: fundamentals for success. Wildlife Biol. 2019: 1–9.

Deutsch C.J. Bonde R.K. & Reid J.P. 1998: Radio-tracking manatees from land and space: tag design, implementation, and lessons learned from long-term study. Mar. Technol. Soc. J. 32: 18–29.

Ditchkoff S.S. Raglin J.B. Smith J.M. & Collier B.A. 2005: Capture of white-tailed deer fawns using thermal imaging technology. Wildl. Soc. Bull. 33: 1164–1168.

Dowding C.V. Shore R.F. Worgan A. Baker P.J. & Harris S. 2010: Accumulation of anticoagulant rodenticides in a non-target insectivore, the European hedgehog (Erinaceus europaeus). Environ. Pollut. 158: 161–166.

Elledge A.E. Allen L.R. Carlsson B.L. Wilton A.N. & Leung L.K.P. 2008: An evaluation of genetic analyses, skull morphology and visual appearance for assessing dingo purity: Implications for dingo conservation. Wildl. Res. 35: 812–820.

Field A. 2017: Discovering Statistics Using IBM SPSS Statistics. SAGE Publications Ltd. London, UK.

Flowerdew J.R. Shore R.F. Poulton S.M.C. & Sparks T.H. 2004: Live trapping to monitor small mammals in Britain. Mamm. Rev. 34: 31–50.

Geiger F. Bengtsson J. Berendse F. Weisser W.W. Emmerson M. Morales M.B. Ceryngier P. Liira J. Tscharntke T. Winqvist C. Eggers S. Bommarco R. Pärt T. Bretagnolle V. Plantegenest M. Clement L.W. Dennis C. Palmer C. Oñate J.J. Guerrero I. Hawro V. Aavik T. Thies C. Flohre A. Hänke S. Fischer C. Goedhart P.W. & Inchausti P. 2010: Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. Basic Appl. Ecol. 11: 97–105.

Glen A.S. Russell J.C. Veltman C.J. & Fewster R.M. 2018: I smell a rat! Estimating effective sweep width for searches using wildlife-detector dogs. Wildl. Res. 45: 500–504.

Goodwin K.M. Engel R.E. & Weaver D.K. 2010: Trained dogs outperform human surveyors in the detection of rare Spotted Knapweed (Centaurea stoebe). Invasive Plant Sci. Manag. 3: 113–121.

Grafen A. & Hails R. 2002: Modern Statistics for the Life Sciences. Oxford University Press. Oxford, UK.

Grenyer R. Orme C.D.L. Jackson S.F. Thomas G.H. Davies R.G. Davies T.J. Jones K.E. Olson V.A. Ridgely R.S. Rasmussen P.C. Ding T.S. Bennett P.M. Blackburn T.M. Gaston K.J. Gittleman J.L. & Owens I.P.F. 2006: Global distribution and conservation of rare and threatened vertebrates. Nature 444: 93–96.

Gurnell J. & Bowen C. 2016: A Study of Hedgehogs in The Regent's Park Year 3. London, UK. 1-53 pp.

Gutzwiller K.J. 1990: Minimizing dog-induced biases in game bird research. Wildl. Soc. Bull. 18: 351–356.

Haigh A. 2011: The Ecology of the European hedgehog (Erinaceus europaeus) in rural Ireland. PhD Thesis, Univ. Coll. Cork.

Haigh A. Butler F. & O'Riordan R.M. 2009: Habitat use by the European hedgehog (Erinaceus europaeus L., 1758) in an Irish rural landscape. Irish Nat. J.: 36–45.

Haigh A. Butler F. & O'Riordan R.M. 2012: An investigation into the techniques for detecting hedgehogs in a rural landscape. J. Negat. Results Ecol. Evol. Biol. 9: 15–26.

Haigh A. Kelly M. Butler F. & O'Riordan R.M. 2014: Non-invasive methods of separating hedgehog (Erinaceus europaeus) age classes and an investigation into the age structure of road kill. Acta Theriol. (Warsz). 59: 165–171.

Harris S. Morris P.A. Wray S. & Yalden D.W. 1995: A Review of British Mammals: Population Estimates and Conservation Status of British Mammals Other Than Cetaceans. JNCC. Peterborough, UK.

Hartig F. 2017: DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. Available at:
https://cran.r-project.org/web/packages/DHARMa/vignettes/DHARMa.html

Helton W.S. (ed). 2009: Canine ergonomics: The Science of Working Dogs. CRC Press. Boca Raton, FL:

Hill D.A. & Greenaway F. 2005: Effectiveness of an acoustic lure for surveying bats in British woodlands. Mamm. Rev. 35: 116–122.

Hof A.R. & Bright P.W. 2010a: The impact of grassy field margins on macro-invertebrate abundance in adjacent arable fields. Agric. Ecosyst. Environ. 139: 280–283.

Hof A.R. & Bright P.W. 2010b: The value of agri-environment schemes for macro-invertebrate feeders: Hedgehogs on arable farms in Britain. Anim. Conserv. 13: 467–473.

Hof A.R. & Bright P.W. 2012: Factors affecting hedgehog presence on farmland as assessed by a questionnaire survey. Acta Theriol. (Warsz). 57: 79–88.

Hof A.R. & Bright P.W. 2016: Quantifying the long-term decline of the West European hedgehog in England by subsampling citizen-science datasets. Eur. J. Wildl. Res. 62: 407–413.

Hof A.R. Snellenberg J. & Bright P.W. 2012: Food or fear? Predation risk mediates edge refuging in an insectivorous mammal. Anim. Behav. 83: 1099–1106.

Holsbeek L. Rodts J. & Muyldermans S. 1999: Hedgehog and other animal traffic victims in Belgium: Results of a countrywide survey. Lutra 42: 111–119.

Hubert P. Julliard R. Biagianti S. & Poulle M.L. 2011: Ecological factors driving the higher hedgehog (Erinaceus europeaus) density in an urban area compared to the adjacent rural area. Landsc. Urban Plan. 103: 34–43.

Huijser M.P. & Bergers P.J.M. 2000: The effect of roads and traffic on hedgehog (Erinaceus europaeus) populations. Biol. Conserv. 95: 6–9.

Jamieson L.T. 2019: Improving wildlife detection dog team selection and training. The University of Queensland. 144 pp.

Jamieson L.T.J.L.T.J. Baxter G.S.G.S. & Murray P.J.P.J. 2017: Identifying suitable detection dogs. Appl. Anim. Behav. Sci. 195: 1–7.

Jamieson L.T. Baxter G.S. & Murray P.J. 2018: You are not my handler! impact of changing handlers on dogs' behaviours and detection performance. Animals 8.

Judge J. Wilson G.J. Macarthur R. Delahay R.J. & McDonald R.A. 2014: Density and abundance of badger social groups in England and Wales in 2011-2013. Sci. Rep. 4: 3809.

Karp D. 2020: Detecting small and cryptic animals by combining thermography and a wildlife detection dog. Sci. Rep. 10: 14–17.

Lane J.M. & McDonald R.A. 2010: Welfare and "best practice" in field studies of wildlife. In:UFAW Handb. Care Manag. Lab. Other Res. Anim. Hubrecht RC & Kirkwood J. eds., pp. 92–106. John Wiley & Sons, Ltd. London, UK.

Langbein J. Hutchings M.R. Harris S. Stoate C. Tapper S.C. & Wray S. 1999: Techniques for assessing the abundance of Brown Hares Lepus europaeus. Mamm. Rev. 29: 93–116.

Leigh K.A. & Dominick M. 2015: An assessment of the effects of habitat structure on the scat finding performance of a wildlife detection dog. Methods Ecol. Evol. 6: 745–752.

Lifson N. Gordon G.B. & McClintock R. 1955: Measurement of total carbon dioxide production by means of D2O18 1. J. Appl. Physiol. 7: 704–710.

Lifson N. & McClintock R. 1966: Theory of use of the turnover rates of body water for measuring energy and material balance. J. Theor. Biol. 12: 46–74.

Long R.A. Donovan T.M. Mackay P. Zielinski W.J. & Buzas J.S. 2007: Effectiveness of scat detection dogs for detecting forest carnivores. J. Wildl. Manage. 71: 2007–2017.

Loyd K.A.T. Hernandez S.M. Carroll J.P. Abernathy K.J. & Marshall G.J. 2013: Quantifying free-roaming domestic cat predation using animal-borne video cameras. Biol. Conserv. 160: 183–189.

Marzluff J.M. Knick S.T. & Millspaugh J.J. 2001: High-Tech Behavioral Ecology: Modeling the Distribution of Animal Activities to Better Understand Wildlife Space Use and Resource Selection. In:Radio Track. Anim. Popul. Millspaugh JJ & Marzluff JM. eds., pp. 309–326. Academic Press. London, UK.

Mathews F. Kubasiewicz L.M. Gurnell J. Harrower C.A. McDonald R.A. & Shore R.F. 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, UK.

Mathews F. Swindells M. Goodhead R. August T.A. Hardman P. Linton D.M. & Hosken D.J. 2013: Effectiveness of search dogs compared with human observers in locating bat carcasses at wind-turbine sites: a blinded randomized trial. Wildl. Soc. Bull. 37: 34–40.

Mayle B.A. Peace A.J. & Gill R.M.A. 1999: How Many Deer? A Field Guide to Estimating Deer Population Size. Forestry Commission. Edinburgh, UK.

McDonald R.A. & Harris S. 1999: The use of trapping records to monitor populations of stoats Mustela erminea and weasels M. nivalis: The importance of trapping effort. J. Appl. Ecol.

36: 679–688.

Meek W.R. Burman P.J. Sparks T.H. Nowakowski M. & Burman N.J. 2012: The use of Barn Owl Tyto alba pellets to assess population change in small mammals. Bird Study 59: 166–174.

Millennium Ecosystem Assessment (MEA). 2005: Millennium ecosystem assessment: ecosystems and human well-being. Island Press. Washington, DC.

Moorhouse T.P. Palmer S.C.F. Travis J.M.J. & Macdonald D.W. 2014: Hugging the hedges: Might agri-environment manipulations affect landscape permeability for hedgehogs? Biol. Conserv. 176: 109–116.

Morris P.A. 1973: Winter nests of the hedgehog (Erinaceus europaeus L.). Oecologia 11: 299–313.

Morris P.A. 1988: A study of home range and movements in the hedgehog (Erinaceus europaeus). J. Zool. 214: 433–449.

Morris P.A. 2018: Hedgehog. HarperCollins. London.

Müller F. 2018: Langzeit-monitoring der Strassenverkehrsopfer beim Igel (Erinaceus europaeus L.) zur Indikation von Populationsdichte veränderungen entlang zweier Teststrecken im Landkreis Fulda. Beiträge zur Naturkd. Osthessen 54: 21–26.

Mwebi O. Nguta E. Onduso V. Nyakundi B. Jiang X.L. & Kioko E. 2019: Small mammal diversity of Mt. Kenya based on carnivore fecal and surface bone remains. Zool. Res. 40: 61–69.

Nagy K.A. 2001: Food requirements of wild animals: predictive equations for free-living mammals, reptiles, and birds. Nutr. Abstr. Rev. Ser. B 71: 21R–31R.

Nielsen T.P. Jackson G. & Bull C.M. 2016: A nose for lizards; can a detection dog locate the endangered pygmy bluetongue lizard (Tiliqua adelaidensis)? Trans. R. Soc. South Aust. 140: 234–243.

Nottingham C.M. Glen A.S. & Stanley M.C. 2019: Snacks in the city: The diet of hedgehogs in Auckland urban forest fragments. N. Z. J. Ecol. 43.

O'Connor S. Park K.J. & Goulson D. 2012: Humans versus dogs; A comparison of methods for the detection of bumble bee nests. J. Apic. Res. 51: 204–211.

Oliveira M.L. de. Norris D. Ramírez J.F.M. Peres P.H.F. Galetti M. & Duarte J.M.B. 2012: Dogs can detect scat samples more efficiently than humans: An experiment in a continuous Atlantic Forest remnant. Zoologia 29: 183–186.

Paula J. Leal M.C. Silva M.J. Mascarenhas R. Costa H. & Mascarenhas M. 2011: Dogs as a tool to improve bird-strike mortality estimates at wind farms. J. Nat. Conserv. 19: 202–208.

Pettett C.E. Johnson P.J. Moorhouse T.P. Hambly C. Speakman J.R. & Macdonald D.W. 2017a: Daily energy expenditure in the face of predation: Hedgehog energetics in rural landscapes. J. Exp. Biol. 220: 460–468.

Pettett C.E. Johnson P.J. Moorhouse T.P. & Macdonald D.W. 2018: National predictors of hedgehog Erinaceus europaeus distribution and decline in Britain. Mamm. Rev. 48: 1–6.

Pettett C.E. Moorhouse T.P. Johnson P.J. & Macdonald D.W. 2017b: Factors affecting hedgehog (Erinaceus europaeus) attraction to rural villages in arable landscapes. Eur. J. Wildl. Res. 63: 54.

Poel J.L. Van de. Dekker J. & Langevelde F.V. 2015: Dutch hedgehogs Erinaceus europaeus are nowadays mainly found in urban areas, possibly due to the negative effects of badgers Meles meles. Wildlife Biol. 21: 51–55.

Poulton S.M.C. & Reeve N.J. 2010: A pilot study of a method to monitor hedgehogs (Erinaceus europaeus). Mammal Notes Autumn: 1–4.

Putman R.J. 1995: Ethical considerations and animal welfare in ecological field studies. Biodivers. Conserv. 4: 903–915.

Rasmussen S.L. Berg T.B. Dabelsteen T. & Jones O.R. 2019: The ecology of suburban juvenile European hedgehogs (Erinaceus europaeus) in Denmark. Ecol. Evol. 9: 13174–13187.

Redpath S. Clarke R. Madders M. & Thirgood S.J. 2001: Assessing raptor diet: comparing pellets, prey remains, and observational data at Hen Harrier nests. Condor 103: 184–188.

Reeve N.J. 1994: Hedgehogs. T & AD Poyser Ltd. London, UK.

Reeve N.J. Bowen C. & Gurnell J. 2019: An improved identification marking method for hedgehogs. Mammal Commun. 5: 1–5.

Reeve N.J. & Huijser M.P. 1999: Mortality factors affecting wild hedgehogs: a study of records from wildlife rescue centres. Lutra 42: 7–24.

Reeve N.J. & Morris P.A. 1985: Construction and use of summer nests by the hedgehog. Mammalia 49: 187–194.

Rondinini C. & Doncaster C.P. 2002: Roads as barriers to movement for hedgehogs. Funct. Ecol. 16: 504–509.

Ropert-Coudert Y. & Wilson R.P. 2005: Trends and perspectives in animal-attached remote sensing. Front. Ecol. Environ. 3: 437–444.

Sabol B.M. & Hudson M.K. 1995: Technique Using Thermal Infrared-Imaging for Estimating Populations of Gray Bats. J. Mammal. 76: 1242–1248.

Schipper J. Chanson J.S. Chiozza F. Cox N.A. Hoffmann M. Katariya V. Lamoreux J. Rodrigues A.S.L. Stuart S.N. Temple H.J. Baillie J. Boitani L. Lacher T.E. Mittermeier R.A. Smith A.T. Absolon D. Aguiar J.M. Amori G. Bakkour N. Baldi R. Berridge R.J. Bielby J. Black P.A. Blanc J.J. Brooks T.M. Burton J.A. Butynski T.M. Catullo G. Chapman R. Cokeliss Z. Collen B. Conroy J. Cooke J.G. Fonseca G.A.B. Da. Derocher A.E. Dublin H.T. Duckworth J.W. Emmons L. Emslie R.H. Festa-Bianchet M. Foster M. Foster S. Garshelis D.L. Gates C. Gimenez-Dixon M. Gonzalez S. Gonzalez-Maya J.F. Good T.C. Hammerson G. Hammond P.S. Happold D. Happold M. Hare J. Harris R.B. Hawkins C.E. Haywood M. Heaney L.R. Hedges S. Helgen K.M. Hilton-Taylor C. Hussain S.A. Ishii N. Jefferson T.A. Jenkins R.K.B. Johnston C.H. Keith M. Kingdon J. Knox D.H. Kovacs K.M. Langhammer P. Leus K. Lewison R. Lichtenstein G. Lowry L.F. Macavoy Z. Mace G.M. Mallon D.P. Masi M. McKnight M.W. Medellín R.A. Medici P. Mills G. Moehlman P.D. Molur S. Mora A. Nowell K. Oates J.F. Olech W. Oliver W.R.L. Oprea M. Patterson B.D. Perrin W.F. Polidoro B.A. Pollock C. Powel A. Protas Y. Racey P. Ragle J. Ramani P. Rathbun G. Reeves R.R. Reilly S.B. Reynolds J.E. Rondinini C. Rosell-Ambal R.G. Rulli M. Rylands A.B. Savini S. Schank C.J. Sechrest W. Self-Sullivan C. Shoemaker A. Sillero-Zubiri C. Silva N. De. Smith D.E. Srinivasulu C. Stephenson P.J. Strien N. Van. Talukdar B.K. Taylor B.L. Timmins R. Tirira D.G. Tognelli M.F. Tsytsulina K. Veiga L.M. Vié J.C. Williamson E.A. Wyatt S.A. Xie Y. & Young B.E. 2008: The status of the world’s land and marine mammals: Diversity, threat, and knowledge. Science (80-.). 322: 225–230.

Seiler A. Helldin J.-O. & Seiler C. 2004: Road mortality in Swedish mammals: results of a drivers’ questionnaire. Wildlife Biol. 10: 225–233.

Smith D.A. Ralls K. Cypher B.L. & Maldonado J.E. 2005: Assessment of scat-detection dog surveys to determine kit fox distribution. Wildl. Soc. Bull. 33: 897–904.

Stevenson D.J. Ravenscoft K.R. Zappalorti R.T. Ravenscroft M.D. Weigley S.W. & Jenkins C.L. 2010: Using a wildlife detector dog for locating Eastern Indigo snakes (Drymarchon couperi). Herpetol. Rev. 41: 2006.

Sutherland W.J., ed. 2013: Ecological Census Techniques: A Handbook. Cambridge University Press. Cambridge, UK.

Telfer S. Lambin X. Birtles R. Beldomenico P. Burthe S. Paterson S. & Begon M. 2010: Species interactions in a parasite community drive infection risk in a wildlife population. Science (80-.). 330: 243–246.

Thomas M.L. Baker L. Beattie J.R. & Baker A.M. 2020: Determining the efficacy of camera traps, live capture traps, and detection dogs for locating cryptic small mammal species. Ecol. Evol. 10: 1054–1068.

Tittensor D.P. Walpole M. Hill S.L.L. Boyce D.G. Britten G.L. Burgess N.D. Butchart S.H.M. Leadley P.W. Regan E.C. Alkemade R. Baumung R. Bellard C. Bouwman L. Bowles-Newark N.J. Chenery A.M. Cheung W.W.L. Christensen V. Cooper H.D. Crowther A.R. Dixon M.J.R. Galli A. Gaveau V. Gregory R.D. Gutierrez N.L. Hirsch T.L. Höft R. Januchowski-Hartley S.R. Karmann M. Krug C.B. Leverington F.J. Loh J. Lojenga R.K. Malsch K. Marques A. Morgan D.H.W. Mumby P.J. Newbold T. Noonan-Mooney K. Pagad S.N. Parks B.C. Pereira H.M. Robertson T. Rondinini C. Santini L. Scharlemann J.P.W. Schindler S. Sumaila U.R. Teh L.S.L. Kolck J. Van. Visconti P. & Ye Y. 2014: A mid-term analysis of progress toward international biodiversity targets. Science (80-.). 346: 241–244.

Trewby I.D. Young R.P. McDonald R.A. Wilson G.J. Davison J. Walker N. Robertson P.A. Doncaster C.P. & Delahay R.J. 2014: Impacts of removing badgers on localised counts of hedgehogs. PLoS One 9: 2–5.

Tyrrell C.L. Christy M.T. Rodda G.H. Yackel Adams A.A. Ellingson A.R. Savidge J.A. Dean-Bradley K. & Bischof R. 2009: Evaluation of trap capture in a geographically closed population of brown treesnakes on Guam. J. Appl. Ecol. 46: 128–135.

Veach V. Moilanen A. & Minin E. Di. 2017: Threats from urban expansion, agricultural transformation and forest loss on global conservation priority areas. PLoS One 12: 1–14.

Vitousek P.M. Mooney H.A. Lubchenco J. & Melillo J.M. 1997: Human domination of Earth’s ecosystems. Science (80-.). 277: 494–499.

Volpov B.L. Hoskins A.J. Battaile B.C. Viviant M. Wheatley K.E. Marshall G. Abernathy K. & Arnould J.P.Y. 2015: Identification of prey captures in Australian fur seals (Arctocephalus pusillus doriferus) using head-mounted accelerometers: Field validation with animal-borne video cameras. PLoS One 10: 1–19.

Vynne C. Skalski J.R. Machado R.B. Groom M.J. Jacamo A.T.A. Marinho-Filho J. Neto M.B.R. Pomilla C. Silveira L. Smith H. & Wasser S.K. 2011: Effectiveness of Scat-Detection Dogs in Determining Species Presence in a Tropical Savanna Landscape. Conserv. Biol. 25: 154–162.

Wagler R. 2013: Incorporating the current sixth great mass extinction theme into evolution education, science education, and environmental education research and standards. Evol. Educ. Outreach 6: 1–5.

Warren M.L. Burr B.M. Walsh S.J. Bart H.L. Cashner R.C. Etnier D.A. Freeman B.J. Kuhajda B.R. Mayden R.L. Robison H.W. Ross S.T. & Starnes W.C. 2000: Diversity, Distribution, and Conservation Status of the Native Freshwater Fishes of the Southern United States. Fisheries 25: 7–31.

Warwick H. 1987: Population ecology of the hedgehogs (Erinaceus europeaus) of north Ronaldsey, Orkney. Leicester Polytechnic.

Wassenaar L.I. & Hobson K.A. 2000: Stable-carbon and hydrogen isotope ratios reveal breeding origins of red-winged blackbirds. Ecol. Appl. 10: 911–916.

Wasser S.K. Hayward L.S. Hartman J. Booth R.K. Broms K. Berg J. Seely E. Lewis L. & Smith H. 2012: Using detection dogs to conduct simultaneous surveys of northern spotted (Strix occidentalis caurina) and barred owls (Strix varia). PLoS One 7: e42892.

Waters J. O'Connor S. Park K.J. & Goulson D. 2011: Testing a detection dog to locate bumblebee colonies and estimate nest density. Apidologie 42: 200–205.

Wikenros C. Balogh G. Sand H. Nicholson K.L. & Månsson J. 2016: Mobility of moose—comparing the effects of wolf predation risk, reproductive status, and seasonality. Ecol. Evol. 6: 8870–8880.

Williams B.M. Baker P.J. Thomas E. Wilson G.J. Judge J. & Yarnell R.W. 2018a: Reduced occupancy of hedgehogs (Erinaceus europaeus) in rural England and Wales: The influence of habitat and an asymmetric intra-guild predator. Sci. Rep. 8: 12156.

Williams B.M. Mann N. Neumann J.L. Yarnell R.W. & Baker P.J. 2018b: A prickly problem: Developing a volunteer-friendly tool for monitoring populations of a terrestrial urban mammal, the West European hedgehog (Erinaceus europaeus). Urban Ecosyst. 21: 1075–1086.

Wilmers C.C. Nickel B. Bryce C.M. Smith J.A. Wheat R.E. Yovovich V. & Hebblewhite M. 2015: The golden age of bio-logging: How animal-borne sensors are advancing the frontiers of ecology. Ecology 96: 1741–1753.

Wilson G.J. & Delahay R.J. 2001: Using Field Signs and Observation. Wildl. Res. 28: 151–164.

Wilson G. Harris S. & McLaren G. 1997: Changes in the British badger population, 1988 to 1997. People's Trust for Endangered Species. London, UK. 143 pp.

Wilson E. & Wembridge D. 2018: State of Britain's Hedgehogs, 2018. People's Trust for Endangered Species. London, UK.

Yarnell R.W. Pacheco M. Williams B.M. Neumann J.L. Rymer D.J. & Baker P.J. 2014: Using occupancy analysis to validate the use of footprint tunnels as a method for monitoring the hedgehog Erinaceus europaeus. Mamm. Rev. 44: 234–238.

Yasuhiko N. 2004: New steps in bio-logging science. Mem. Natl. Inst. Polar Res. Spec. issue 58: 50–57.

Young R.P. Davison J. Trewby I.D. Wilson G.J. Delahay R.J. & Doncaster C.P. 2006: Abundance of hedgehogs (Erinaceus europaeus) in relation to the density and distribution of badgers (Meles meles). J. Zool. 269: 349–356.