



Policy analysis

Using biological records to infer long-term occupancy trends of mammals in the UK



Frazer G. Coomber^{a,b}, Bethany R. Smith^{a,d}, Tom A. August^c, Colin A. Harrower^c, Gary D. Powney^{c,e}, Fiona Mathews^{a,b,*}

^a Mammal Society, Black Horse Cottage, 33 Milton Abbas, Blandford Forum, Dorset DT11 0BL, UK

^b The University of Sussex, Sussex House, Falmer, Brighton BN1 9RH, UK

^c UK Centre of Ecology and Hydrology, Maclean Building, Crowmarsh Gifford, Wallingford OX10 8BB, UK

^d School of Animal, Rural and Environmental Sciences, Nottingham Trent University, Southwell NG25 0QF, UK

^e Oxford Martin School & School of Geography and the Environment, University of Oxford, OX1 3BD, UK

ARTICLE INFO

Keywords:

Citizen science
Mammals
Occupancy models
Bayesian modelling
Trends
United Kingdom

ABSTRACT

Conservation action is usually triggered by detecting trends in species' population size, geographical range, or occupancy (proportion of sites occupied). Robust estimates of these metrics are often required by policy makers and practitioners, yet many species lack dedicated monitoring schemes. An alternative source of data for trend estimation is provided by biological records, i.e., species presence information. In the UK, there are millions of such records, but biological trend assessments are often hindered by biases caused by the unstructured way in which they are collected. Recent advances in occupancy modelling that account for changes in survey effort and detectability over time mean that robust occupancy trends can now be estimated from these records. By grouping mammal species into survey assemblages — species likely to be recorded at the same time — and applying occupancy models, this study provides estimates of long-term (1970 to 2016) occupancy trends for 37 terrestrial mammal species from the UK. The inter-annual occupancy growth rates for these species ranged from -4.26% to 11.25%. This information was used to classify two species as strongly decreasing, five as decreasing, 12 as no change, 11 as increasing and seven as strongly increasing. Viewing the survey assemblages as a whole, the occupancy growth rates for small mammals were, on average, decreasing (-0.8% SD 1.57), whereas bats and deer (0.9% SD 1.30) were increasing (3.8% SD 3.25; 0.9% SD 1.30 respectively), and mid-sized mammals were stable (-0.3 SD 1.72). These results contribute much-needed information on a number of data deficient species, and provide evidence for prioritising conservation action.

1. Introduction

Assessments of a species' extinction risk, conservation status, and responses to interventions, rely on the detection of trends in parameters such as abundance and distribution (Butchart et al., 2010; Maes et al., 2015). While long-term trends are ideally assessed through systematic monitoring schemes, the logistical and financial demands of such schemes mean that they are restricted to relatively few taxa (Schmeller et al., 2009).

Most mammal species in the UK lack long-term trend data. Where structured surveys exist, their coverage is often limited geographically or temporally (e.g. Barlow et al., 2015; Judge et al., 2014) so trends are

not available for some regions (or countries) or for sufficiently long time-scales. In addition, cross-species comparisons, which are needed to prioritise conservation action, are difficult because different metrics are applied to different taxa (such as distribution: e.g. Crawford, 2010); density and abundance (e.g. Judge et al., 2014); raw count data (e.g. Wright et al., 2014); population indices (e.g. relative abundance and activity e.g. Barlow et al., 2015), and occupancy (the proportion of an area occupied by a species: e.g. McGuire et al., 2014). Finally, methodological issues, including focal species detectability and recorder effort are often not accounted for within the existing surveys (e.g. Aebischer, 2019; Wright et al., 2014): a full assessment of the survey and trend data available for each species of terrestrial mammal in Britain is

* Corresponding author at: Mammal Society, Black Horse Cottage, 33 Milton Abbas, Blandford Forum, Dorset DT11 0BL, UK.

E-mail addresses: science@themammalsociety.org (F.G. Coomber), bethanys935@gmail.com (B.R. Smith), tomaug@ceh.ac.uk (T.A. August), corr@ceh.ac.uk (C.A. Harrower), gawn@ceh.ac.uk (G.D. Powney), F.Mathews@sussex.ac.uk (F. Mathews).

<https://doi.org/10.1016/j.biocon.2021.109362>

Received 25 February 2021; Received in revised form 24 September 2021; Accepted 6 October 2021

Available online 2 November 2021

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provided in Mathews et al. (2018).

The huge repositories of biological records (e.g. eBird, GBIF, iRecord and NBN: Pocock et al., 2015; Sullivan et al., 2009; Telenius, 2011) that have primarily been collected opportunistically by citizen scientists present an opportunity to derive trend metrics to complement those obtained from systematic surveys. These presence-only records provide precise information across large spatial and temporal scales on where, and when, a species was recorded (Powney and Isaac, 2015). However, the majority are collected without standardised protocols, or follow only a semi-structured protocol (e.g. for eBird). They can therefore suffer from biases in temporal and spatial variability in recorder effort (Prendergast et al., 1993), imperfect detection (Chen et al., 2013), and selective recording of species (Szabo et al., 2010), and these factors can hinder trend estimations.

Recently, advanced statistical models have been developed that are capable of estimating species trends from these non-systematic biological records by accounting for the biases inherent in the data collection process (Devarajan et al., 2020; Guillera-Aroita, 2017; Isaac et al., 2014; MacKenzie et al., 2002; Royle and Kéry, 2007). Of the currently available methods, occupancy models (OMs: MacKenzie et al., 2017) display great potential for deducing robust trends from biological records (Isaac et al., 2014). A key output of OMs fitted within a Bayesian framework are species-specific annual occupancy estimates — the proportion of sites occupied by a species — with credible intervals expressing uncertainty. These yearly outputs can be used to create trend indicators for both single, and groups of, species, allowing complex information to be communicated to a wide range of audiences (Hayhow et al., 2019).

Occupancy models require data on whether a species was detected or not at a known date and location, so that detection histories can be computed. Where only detection data are available, non-detections are inferred from the patterns of recording of taxonomically similar or typically recorded together species. For example, if species A, B and C were previously detected together during a site visit, and only species B and C were detected during another visit to the same site within a specified time frame, then the non-detection of species A can be inferred during the second visit (Outhwaite et al., 2019). The technique has previously been applied to several taxa, including birds (Kéry et al., 2010), plants (Chen et al., 2013), and a variety of invertebrates (e.g. moths (Dennis et al., 2019); butterflies (Dennis et al., 2017; van Strien et al., 2013); pollinators (Powney et al., 2019); dragonflies (van Strien et al., 2013), and ants (Outhwaite et al., 2018)). These taxa are typically monitored by separate, but taxa specific, recording schemes in the UK (Outhwaite et al., 2019). British mammal species on the other hand have species-specific survey method recommendations (Battersby and Greenwood, 2004; Macdonald et al., 1998; Toms and Greenwood, 1999). It might therefore be more appropriate to infer non-detections from groups of mammal species likely to be surveyed together (Croft and Smith, 2019), rather than from simple co-occurrence across the entire taxonomic group. For example, small mammals are most frequently surveyed using humane traps, and the non-detection of a deer from the same site on the same day cannot be inferred from a survey that used small mammal trapping; likewise, the non-detection of a mouse cannot be inferred from a deer detection.

To date, studies using OMs on mammalian biological records typically use records from single survey methods, e.g. owl pellets (van Strien et al., 2015) and roadkill (Santos et al., 2018) and therefore tend to sample only particular groups of species. However, there is a need to monitor all species. For example, despite an abundance of biological record data in the UK, the latest review of British mammals found that limited data on species-habitat specific density and occupancy estimates resulted in high uncertainty of conservation trends for many species (for further details on these reliability indices see Mathews et al., 2018). This study developed a method to group mammal species into survey assemblages enabling the inference of non-detections and creation of detection histories from biological records. The OM framework was used

to deduce long-term occupancy trends for mammals in the UK, providing a new approach to identify mammal species of conservation concern.

2. Material and methods

2.1. Data standardisation

Biological records of terrestrial mammals were sourced from a database housed by the Mammal Society (see Crawley et al., 2020). Only records from the UK or the Isle of Man, identified to species level, with date specified to day, and location at a 1 km² spatial scale or finer were included. Records of feral, domestic and vagrant animals were excluded. The time-period under consideration was 1970-2016, except for bats where the start date was set as 2005 to avoid complications resulting from recent species taxonomic revisions (Jones and Barratt, 1999). As OMs require data from multiple sites (MacKenzie et al., 2017), rare mammals — species recorded in <100 sites — were excluded. Similarly, poorly sampled sites (with fewer than 2 years of data) were also excluded.

Each record was assigned to one of 255,306 1 km² referenced Ordinance Survey British National Grid squares (BNG) (hereafter referred to as a 'site'). Where there were multiple records of a species from the same site and date, only one unique record was retained. Sites from Northern Ireland were converted from Irish grid format to BNG.

2.2. Survey assemblages

Mammal species were assigned to survey assemblages based on an adapted CLUSTASPEC analysis (Preston et al., 2011). The CLUSTASPEC algorithm is a two-stage clustering procedure, developed to classify species' distribution patterns, that amalgamates species into clusters based on their co-occurrence within grid squares (Preston et al., 2011). The first stage of the clustering algorithm begins with single species clusters (i.e. the number of clusters equals the number of species) and then amalgamates the most similar clusters in a stepwise manner based on the cosine of the angle between focal and comparison cluster centroids (Legendre and Legendre, 2012). After all single species clusters have been amalgamated the algorithm subsequently removes the smallest cluster, redistributing the associated individual species within that cluster to the remaining clusters, based on the same similarity metric as above. This continues until the desired number of clusters, specified by the user, is reached. The second stage then checks each species against the other available clusters, reassigning, where necessary, species between clusters to those with which they show the highest similarity. This is continued until all species remain stationary.

This method was adapted by assigning species to an assemblage based on their similarity of co-occurrence at the same site on the same day. This was achieved by creating a unique date-site identifier for all available mammalian records and running the CLUSTASPEC algorithm on this dataset in R3.5.2 (R Core Team, 2018). Assemblage assignment was cross-checked for consistency with the published literature on surveying mammals in the UK, e.g. MaMoNet guidelines for survey techniques for mammals in the UK (Barlow et al., 2015; Battersby and Greenwood, 2004; Macdonald et al., 1998; Toms and Greenwood, 1999).

The number of clusters considered for the CLUSTASPEC algorithm was three to ten, but assignment into seven clusters was chosen based on the highest similarity of the species within clusters to the survey groupings documented in the published literature (Table A.1; A.2). Animals usually recorded on their own are unlikely to provide useful inferences of non-detections to other species within an assemblage. Therefore, species within an assigned cluster that were recorded on their own at a given site and date in more than 95% of cases were removed (Fig. 1 and Figs. A.1 to A.5). In addition, species that are typically recorded using a specific survey method, different to that applied to the other species within a cluster, were also removed. Finally, the three bat

CLUSTERS	EXCLUSIONS	ASSEMBLAGES		
Wood mouse Hazel dormouse Bank vole Common shrew Field vole Yellow-necked mouse Water shrew Harvest mouse Pygmy shrew Lesser white-toothed shrew	<div style="display: flex; align-items: center;"> <div style="width: 15px; height: 15px; border: 1px solid black; background: repeating-linear-gradient(45deg, transparent, transparent 2px, black 2px, black 4px);"></div> Survey </div>	small mammals		
Roe deer Red deer Reeves' muntjac deer Fallow deer Sika deer			deer	
Common pipistrelle bat Soprano pipistrelle bat Noctule bat Serotine bat Barbastelle bat Leisler's bat Nathusius' pipistrelle bat			bats	
Brown long-eared bat Natterer's bat Daubenton's bat Lesser horseshoe bat Greater horseshoe bat Greater mouse-eared bat	<div style="display: flex; align-items: center;"> <div style="width: 15px; height: 15px; border: 1px solid black; background: repeating-linear-gradient(45deg, transparent, transparent 2px, black 2px, black 4px);"></div> Rare </div>			
Whiskered bat Bechstein's bat House mouse Brandt's bat Grey long-eared bat Alcathoe bat	<div style="display: flex; align-items: center;"> <div style="width: 15px; height: 15px; border: 1px solid black; background: repeating-linear-gradient(45deg, transparent, transparent 2px, black 2px, black 4px);"></div> Survey </div>			
Grey squirrel European rabbit Red fox European mole European badger Red squirrel European hedgehog Brown hare Brown rat Stoat Weasel Polecat Chinese water deer Pine marten Mountain hare Wild boar Eurasian beaver Wildcat Edible dormouse Common vole	<div style="display: flex; align-items: center;"> <div style="width: 15px; height: 15px; border: 1px solid black; background: repeating-linear-gradient(45deg, transparent, transparent 2px, black 2px, black 4px);"></div> 95% </div>			
European otter Water vole American mink Grey seal Harbour seal Black rat	<div style="display: flex; align-items: center;"> <div style="width: 15px; height: 15px; border: 1px solid black; background: repeating-linear-gradient(45deg, transparent, transparent 2px, black 2px, black 4px);"></div> 95% </div>			mid-sized mammals

Fig. 1. Schematic representation of the inclusion criteria applied to mammal species within the assigned seven clusters and the resulting final four assemblages considered for the modelling process. Species exclusion criteria, indicated using a shaded cross, are: Rare (recorded at <100 sites), 95% (majority list length one i.e. recorded on its own most of the time) and Survey (different survey methods to other species in the same cluster).

analysis because of a low number of species remaining after the inclusion criteria were applied.

In total, 37 mammal species passed these inclusion criteria and were assigned to one of four survey assemblages referred to subsequently as 'small mammals', 'deer', 'bats' and 'mid-sized mammals', broadly reflecting different survey techniques and animal sizes (Fig. 1 and Table 1). All subsequent modelling procedures were conducted separately on the individual assemblages, using only records of species from that assemblage. These detection records were then arranged into detection histories by reorganising records into visits — a unique combination of day and site in the records data — within a closure period (here one calendar year), inferring non-detections of a species by the detection of other species within the survey assemblage.

In total, 445,654 records from 418,496 visits to 61,297 unique sites across the UK were available for modelling (Table 1). The number of records showed a significant increase over time for all survey assemblages except bats, which had a significant decrease in the number of records across the last two years (Fig. A.6). The percentage of sites revisited and the mean number of sites revisited was relatively constant over time for all assemblages (Table A.3). Only the bats survey assemblage displayed a significant change in list length — the number of species within an assemblage recorded at a given site and date — over time. This increase in list length coincides with the increased use of broad-spectrum acoustic recording devices and automatic species identification software, which permits easier detection and identification of a wide range of bat species (Adams et al., 2012; MacSwiney et al., 2008). Although sample sites were distributed across the UK, sampling was not uniform or random: for small mammals and bats, most sites were in England and Wales; for deer, most sites were in England and Scotland; whereas the sites for mid-sized mammals were from across the UK (Fig. 2). In all assemblages, there were very few sites in Northern Ireland compared with the rest of the UK.

2.3. The occupancy model (OM)

The OM framework is a hierarchical model consisting of state and observation sub-models. The state sub-model describes the true occupancy state (Z_{it} ; Eq. (1)) at site i in year t and the observation sub-model describes the conditional probability that a species is observed (P_{itv}) given that it is present ($Z_{it} = 1$; Eq. (2)) (MacKenzie et al., 2002; Royle and Kéry, 2007). The state sub-model has a binary response and ψ_{it} is used to denote the probability under a Bernoulli distribution that a site is occupied with probabilities that can vary with year (b_t) and site (u_i) (Eq. (1)). The year effect (b_t) was modelled as a random walk (Eq. (C.1)), imposing an a priori judgement that a site's occupancy probabilities are likely to be similar from one year to the next (Outhwaite et al., 2018). This adaption improves occupancy estimates from low recording intensity data by relaxing the requirement for sites to have data from adjacent years, information needed to calculate colonisation and extinction transition rates.

$$Z_{it} \sim \text{Bernoulli}(\psi_{it}); \text{logit}(\psi_{it}) = \log\left(\frac{\psi_{it}}{1 - \psi_{it}}\right) = b_t + u_i \tag{1}$$

$$Y_{itv} | Z_{it} \sim \text{Bernoulli}(P_{itv}; Z_{it}); \text{logit}(P_{itv}) = \log\left(\frac{P_{itv}}{1 - P_{itv}}\right) = a_t + \delta_1 \cdot \text{DT}2_{itv} + \delta_2 \cdot \text{DT}3_{itv} \tag{2}$$

clusters were combined into one assemblage as individual bat species can be monitored using multiple survey techniques (Barlow et al., 2015). The aquatic mammals cluster was not considered for further

If a site is occupied, then Y_{itv} can be modelled under a Bernoulli distribution to calculate detection probabilities (P_{itv}) per site i , per year t ,

Table 1

The survey assemblage classifications and included species lists with information on the data available for each.

Survey Assemblage	Small mammals (1)	Deer (2)	Bats (3)	Mid-sized mammals (4)
	Bank vole (<i>Myodes glareolus</i>)	Fallow deer (<i>Dama dama</i>)	Barbastelle bat (<i>Barbastella barbastellus</i>)	Brown hare (<i>Lepus europaeus</i>)
	Common shrew (<i>Sorex araneus</i>)	Red deer (<i>Cervus elaphus</i>)	Bechstein's bat (<i>Myotis bechsteinii</i>)	Brown rat (<i>Rattus norvegicus</i>)
	Field vole (<i>Microtus agrestis</i>)	Reeves' muntjac deer (<i>Muntiacus reevesi</i>)	Brandt's bat (<i>Myotis brandtii</i>)	European badger (<i>Meles meles</i>)
	Harvest mouse (<i>Micromys minutus</i>)	Roe deer (<i>Capreolus capreolus</i>)	Brown long-eared bat (<i>Plecotus auritus</i>)	European mole (<i>Talpa europaea</i>)
	Water shrew (<i>Neomys fodiens</i>)	Sika deer (<i>Cervus nippon</i>)	Common pipistrelle bat (<i>Pipistrellus pipistrellus</i>)	European rabbit (<i>Oryctolagus cuniculus</i>)
	Wood mouse (<i>Apodemus sylvaticus</i>)		Daubenton's bat (<i>Myotis daubentonii</i>)	Grey squirrel (<i>Sciurus carolinensis</i>)
	Yellow-necked mouse (<i>Apodemus flavicollis</i>)		Greater horseshoe bat (<i>Rhinolophus ferrumequinum</i>)	Red fox (<i>Vulpes vulpes</i>)
			Grey long-eared bat (<i>Plecotus austriacus</i>)	Stoat (<i>Mustela erminea</i>)
			Leisler's bat (<i>Nyctalus leisleri</i>)	Weasel (<i>Mustela nivalis</i>)
			Lesser horseshoe bat (<i>Rhinolophus hipposideros</i>)	
			Nathusius' pipistrelle bat (<i>Pipistrellus nathusii</i>)	
			Natterer's bat (<i>Myotis nattereri</i>)	
			Noctule bat (<i>Nyctalus noctula</i>)	
			Serotine bat (<i>Eptesicus serotinus</i>)	
			Soprano pipistrelle bat (<i>Pipistrellus pygmaeus</i>)	
			Whiskered bat (<i>Myotis mystacinus</i>)	
No. of Species	7	5	16	9
Total number of records	32,593	126,854	32,548	253,668
Min. records per species	1242	2833	222	10,252
Mean records per species	5116	13,253	759	30,750
Max. records per species	12,010	58,962	14,036	60,144
Total no. of sites	4171	14,432	7704	39,582
Total no. visits	27,193	107,533	40,447	243,323

1. Small shrew and rodent species (weight 3 to 45 g), typically surveyed with live-trapping techniques,
2. Deer species (weight 10 to 180 kg), typically surveyed with camera traps and visually by observers e.g. along transects,
3. Bat species (weight 4 to 30 g), typically surveyed by live-trapping, roost inspections, and acoustics surveys,
4. Mid-sized mammal species (weight 55 g to 12 kg) typically surveyed with camera traps and visually by observers e.g. along transects.

and between visits v (Eq. (2)). The probability of detection has a random year-level effect function (a_t) that accounts for variability in detection over time. In addition, a categorical covariate — day-list length — was included in the observation sub-model to estimate sampling effort and variability in selective reporting (Szabo et al., 2010). A categorical covariate was used owing to the higher mammal species richness in the south of the UK compared with the north (Crawley et al., 2020): using a continuous list length in this scenario would result in higher detections in the south (Outhwaite et al., 2019). The day-list length categories used in this model were: (1) Single species records; (2) Short lists, records of two or three species; and (3) Comprehensive lists, records of more than three species from a site within a day. The effect of the different day-list lengths is denoted as δ_1 and δ_2 (Eq. (2)) and indicates how detectability on these list lengths differ relative to a single species record list (a_t) for short and comprehensive day-lists respectively.

Prior distribution specifications for the unknown parameters to be estimated in the models were assigned to represent a complete lack of a priori knowledge. Most priors were assigned to widely dispersed normal distributions but half-Cauchy hyper-priors, equivalent of a Student's t -distribution with 1 degree of freedom, were assigned to the standard deviation parameters (see Eqs. (C.1) to (C.6) for full prior formulations and Outhwaite et al. (2020) for further information).

The occupancy models were fitted in a Bayesian mode of inference using JAGS (Plummer, 2017) with the package 'R2jags' (Su and Yajima, 2015) and the 'Sparta' package (August et al., 2020a) in R3.5.2 (R Core Team, 2018). Models were fitted for all focal species using 30,000 Monte Carlo Markov Chain (MCMC) iterations with three chains, a thinning

rate of three and a burn in rate of 15,000. This was deemed sufficient to achieve convergence for the estimated parameters across most species and years. Convergence, statistically stable parameter estimation, was measured using \hat{R} , a value that compares the Markov chain within and between variance, quantifying whether the chains are drawing from the same distribution of parameter values (Gelman and Rubin, 1992). An \hat{R} value less than 1.1 indicates that a model has converged and conversely, values greater than 1.1 have failed to converge (Gelman and Hill, 2006). Convergence was also assessed through visual inspection of the MCMC chain trace plots (species-specific examples are presented in Fig. C.1).

The number of occupied sites for a focal species — those with predicted presences ($Z_{it} = 1$) — were summed to calculate the proportion of the total number of sampled sites within an assemblage to give an occupancy value between 0 and 1 in any given year. A value of 1 indicates that every sampled site was occupied by the focal species and a value between 0 and 1 indicates the proportion of the sampled sites that had predicted presences.

To assess whether the model parameterisation is satisfactory to capture the structure of the observed data realistically and to provide support on model fit and the resulting species' trends, diagnostic posterior predictive checks were conducted. These diagnostic checks effectively compare the observed data used to fit the model against a generated dataset of observations, created using samples drawn from the posterior distribution of the model's estimated parameters. Summary statistics were then calculated for both of these datasets using the protocol outlined in Outhwaite et al. (2020). For each species, the proportion of sites with detections, averaged across all years, and the variance



Fig. 2. The distribution of sites used in the occupancy models for the four different survey assemblages of small mammals, deer, bats, and mid-sized mammals. Contains OS data © Crown copyright and database rights (2020).

in the annual mean proportion of detections was calculated and compared.

2.4. Trend indicators

The OM's posterior distribution of annual occupancy estimates, with 95% credible intervals to express uncertainty, are presented graphically for each species. A loess trend line (with 50% smoothing span), showing the smoothed inter-annual occupancy trend is also displayed. The percentage change in occupancy from the first year to the last, with 95% credible intervals, was calculated to present the overall change in occupancy for each species across the time-period. Trend estimates derived from first and last year values may not reflect long-term patterns of change because of fluctuating inter-annual occupancy estimates. Therefore, we also present species-specific average occupancy growth rates, computed across the entire time-period as the arithmetic mean of

the percentage inter-annual change in occupancy (with 95% credible intervals calculated from the posterior distribution). The advantage of using growth rates is that species-specific and assemblage-composite trend indices can be constructed from the same data. The calculations for species-specific and assemblage trends, based on the outputs from the OM, were conducted in the 'BRCindicators' package (August et al., 2020b).

The species-specific growth rates are used to classify species into Alert Categories chosen to align with the UK wild bird population indices and widely used for other taxa (DEFRA, 2018; Marchant et al., 1997):

1. Strong increase – an average annual occupancy growth rate greater than or equal to +2.81%, equivalent to a doubling of occupancy over a 25-year period,

Table 2

Summary of the species-specific occupancy average annual growth rates with their associated Alert Categories and confidence of trend direction as the percentage of iterations. The occupancy change is the percentage change from the start to end year with their significance. The lower and upper credible intervals are presented in brackets.

Species	Occupancy average growth rates (%)	Alert Category*	Percentage confidence in growth rate change direction	Occupancy change	Occupancy change significance	
small mammals	Bank vole	-1.16 (-44.99 – 74.83)	decrease	51	-0.33 (-0.98 - 0.54)	
	Common shrew	-1.45 (-43.46 – 73.52)	decrease	52	-0.30 (-0.75 - 0.28)	
	Field vole	-1.42 (-39.72 – 56.37)	decrease	<50	-0.50 (-1.05 - 0.09)	
	Harvest mouse	-2.82 (-31.84 – 37.86)	strong decrease	55	-2.10 (-3.16 - -0.97)	***
	Water shrew	-1.18 (-23.92 – 29.44)	decrease	54	-0.81 (-1.73 - 0.03)	
	Wood mouse	1.01 (-27.56 – 39.20)	no change	<50	0.39 (0.13 – 1.00)	***
	Yellow-necked mouse	1.72 (-35.63 – 58.97)	increase	54	1.52 (-0.11 - 3.37)	
deer	Fallow deer	0.01 (-21.45 – 26.80)	no change	<50	0.01 (-0.68 - 0.69)	
	Red deer	-0.64 (-32.36 – 37.89)	no change	51	-0.43 (-1.17 - 0.45)	
	Reeves' muntjac deer	1.73 (-20.33 – 28.70)	increase	57	1.41 (0.70 - 2.18)	***
	Roe deer	0.99 (-18.48 – 24.99)	no change	54	0.32 (0.04 - 0.67)	***
	Sika deer	2.60 (-31.64 – 55.36)	increase	56	2.55 (-0.07 - 5.52)	
bats	Barbastelle bat	4.66 (-24.69 – 49.83)	strong increase	60	3.96 (-0.55 - 9.39)	
	Bechstein's bat	-0.59 (-41.60 – 66.30)	no change	<50	-0.50 (-6.85 - 6.26)	
	Brandt's bat	0.97 (-36.62 – 61.69)	no change	52	0.89 (-5.28 - 7.72)	
	Brown long-eared bat	1.57 (-10.77 – 16.78)	increase	58	0.80 (-0.30 - 1.98)	
	Common pipistrelle bat	2.26 (-9.62 – 15.89)	increase	65	0.84 (0.17 - 1.63)	***
	Daubenton's bat	2.35 (-11.82 – 17.36)	increase	65	1.72 (0.28 - 3.36)	***
	Greater horseshoe bat	2.70 (-24.80 – 41.38)	increase	55	2.43 (-1.34 - 6.43)	
	Grey long-eared bat	2.17 (-32.89 – 58.27)	increase	55	2.24 (-5.26 - 11.09)	
	Leisler's bat	2.90 (-24.73 – 42.05)	strong increase	58	2.51 (-2.12 - 8.26)	
	Lesser horseshoe bat	3.15 (-12.06 – 27.06)	strong increase	60	2.55 (0.72 - 4.72)	***
	Nathusius' pipistrelle	10.36 (-32.38 – 84.57)	strong increase	56	8.52 (1.50 - 16.23)	***
	Natterer's bat	3.61 (-16.91 – 37.34)	strong increase	56	2.76 (0.25 - 5.56)	***
	Noctule bat	7.59 (-21.49 – 42.99)	strong increase	71	2.88 (1.25 - 4.55)	***
	Serotine bat	2.77 (-21.56 – 35.97)	increase	58	1.94 (-0.69 - 4.46)	
	Soprano pipistrelle bat	11.25 (-15.65 – 63.53)	strong increase	62	3.73 (2.59 - 4.84)	***
Whiskered bat	2.45 (-40.70 – 64.64)	increase	56	2.00 (-4.03 - 7.48)		
mid-sized mammals	Brown hare	-0.09 (-29.93 – 53.26)	no change	52	-0.01 (-0.56 – 0.61)	
	Brown rat	1.11 (-45.04 – 77.39)	no change	<50	0.80 (-0.45 – 2.26)	
	European badger	1.4 (-34.81 – 60.75)	increase	53	0.85 (0.28 – 1.49)	***
	European mole	0.42 (-40.25 – 58.59)	no change	<50	0.20 (-0.43 – 0.94)	
	European rabbit	-0.73 (-38.28 – 68.10)	no change	53	-0.25 (-0.66 – 0.22)	
	Grey squirrel	0.52 (-45.64 – 112.82)	no change	<50	0.25 (-0.43 – 1.01)	
	Red fox	0.51 (-30.56 – 50.56)	no change	<50	0.25 (-0.37 – 0.94)	
	Stoat	-1.3 (-30.26 – 36.76)	decrease	53	-1.03 (-1.79 - -0.30)	***
	Weasel	-4.26 (-32.03 – 33.59)	strong decrease	59	-2.63 (-3.31 - -1.94)	***

‡ Baseline year is 1970 for non-bat species; and 2005 for bats.

*Alert category based on BTO (DEFRA, 2018; Marchant et al., 1997).

2. Increase – an average annual occupancy growth rate greater than or equal to +1.16% and less than +2.81%,
3. No change – an average annual occupancy growth rate greater than or equal to -1.14% and less than +1.16%,
4. Decrease – an average annual occupancy growth rate greater than or equal to -2.73% and less than -1.14%,
5. Strong decrease – an average annual occupancy growth change less than -2.73%, equivalent to occupancy halving over a 25-year period.

Finally, composite indicators, based on the survey assemblage combined species-specific average growth rates, and their uncertainty, were computed. A baseline index value of 100 was set for the first year (1970 or, for bats, 2005). This composite indicator was considered significant if the baseline value (100) did not fall between its credible

intervals. The growth rate and occupancy change trends can be considered significant if the value '0', i.e. no change in occupancy, did not fall between their lower and upper credible intervals. The use of the word significant is not based on the typical frequentist definition. Instead, significance is used to highlight notable changes, for example we are 95% confident an assemblage has declined if the baseline value is above the upper 95% credible interval.

3. Results

3.1. Summary statistics

Occupancy models were produced for the four survey assemblages: small mammals, bats, deer and mid-sized mammals (Table 1). Each

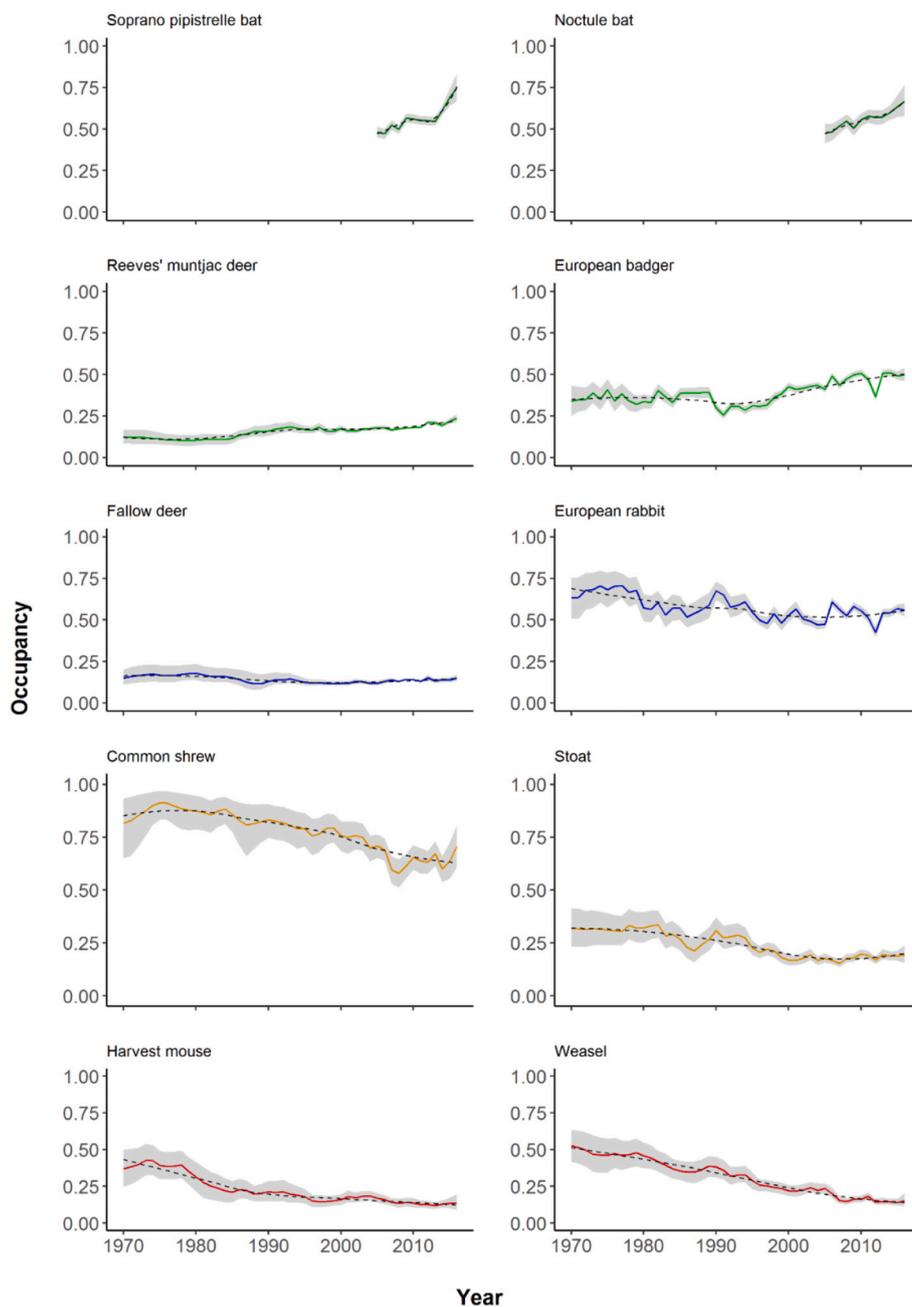


Fig. 3. Species-specific occupancy trend examples for the five different Alert Categories. Top row – strong increase, second row – increase, third row – no change, fourth row – decrease, and bottom row – strong decrease. The solid line represents the mean occupancy for that year and the shaded area indicates the 95% credible intervals for each occupancy estimate. The overall trend is represented by the smoothed trend loess line (dashed line).

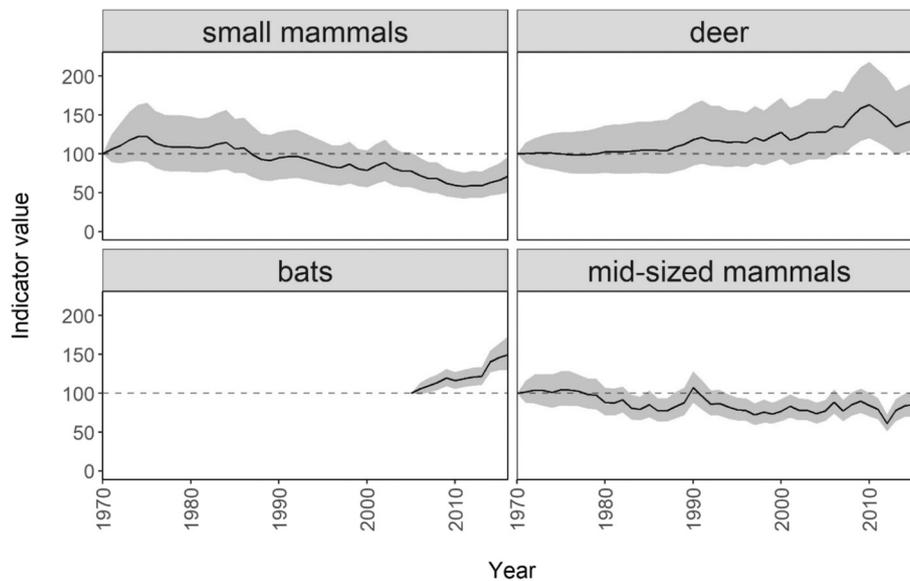


Fig. 4. The composite indicator trends (black line) and credible intervals (shaded regions) for the four survey assemblages. The reference index is set to 100 and the reference year is 1970 except for bats where it is 2005. Indicator trends can be considered significant if the reference index is beyond the limits of the credible intervals.

model successfully converged, with \hat{R} values less than 1.1 and standard deviations less than 0.2, for all species in all years with only one exception, the weasel (*Mustela nivalis*), where there was not full convergence for several earlier year estimates (1972-1982, 1987-1989, and 1991-1993). The estimated detection probabilities for each species and their associated day-list lengths were also sufficiently high, with narrow credible intervals (Fig. B.1). Each species-specific trend can therefore be interpreted as displaying informative occupancy estimates across all years, with the possible exception of early-year estimates for the weasel. Furthermore, the posterior predictive check diagnostic for mean proportion of sites with detections and variance across years indicated that the model parameterisation predicted the observed data very closely, with nearly all observed values from both summary statistics falling within the credible intervals of the posterior predictive interval (Fig. C.2). However, it should be noted that some species do display large credible intervals.

3.2. Species-specific inter-annual occupancy

Overall, 30% of the 37 mammal species analysed had a negative occupancy growth rate and overall occupancy change, indicating that between 1970 and 2016 (2005 to 2016 for bats) their occupancy decreased from year to year on average with lower occupancy at the end of the time-period. Using the occupancy growth rates and the threshold values of the proposed Alert Categories, seven species were classified as strongly increasing, 11 as increasing, 12 as no change, five as decreasing and two as strongly decreasing (Table 2). Note that it is possible for a species to have a negative growth rate but not be classified as decreasing if the magnitude of the change is below the Alert Category threshold. The 95% credible intervals of the annual average growth rates all spanned 0, indicating that no growth rates were significant. Two trend examples from each Alert Category are shown in Fig. 3; and trends, along with detection probability graphs, for all species are presented in Fig. B.1. The overall occupancy change for each species was highly correlated to the growth rate ($r = 0.91$), but based on this change three species were found to have significantly decreased and 11 significantly increased in occupancy (Table 2).

3.3. Survey assemblage composite trends

The survey assemblage composite indicator, calculated using the combined inter-annual growth rates from the species within each assemblage, and the species' trends within each assemblage display distinctive assemblage-specific patterns (Fig. 4). The small mammals assemblage shows a consistently declining index from 1975 to 2016 (Fig. 4). Five species within this assemblage were classified as decreasing, or strongly decreasing for the harvest mouse (*Micromys minutus*), with a mean growth rate across all species within this assemblage having the largest percentage decrease of any assemblage (-0.8%, SD 1.57: Table 2). The deer assemblage index began with little change between 1970 and 1987, but began increasing after this point, except for 2011 to 2013 (Fig. 4). Although most species within the deer assemblage were classified as no change, the mean growth rate across all species was positive (0.9%, SD 1.30: Table 2). The bats assemblage index increased consistently between 2005 and 2016 (Fig. 4), with 15 of the 16 species having positive growth rates, and all except two species being categorised as increasing or strongly increasing. On average, the species within the bats assemblage had the highest assemblage mean growth rate (3.8%, SD 3.25: Table 2). The mid-sized mammals index remained relatively constant from 1970 to 1977 but decreased to a relatively consistent index after this time (Fig. 4). The species growth rates in this assemblage are more varied, with five species displaying increasing and four species decreasing growth rates (Fig. 4). However, despite the mean growth rate across all species in this assemblage being slightly negative -0.3% (SD 1.72: Table 2), most species (67%) are classified as no change. The stoat (*Mustela erminea*) and weasel are the only species in this assemblage to have sufficiently large declines in average growth rates to be classified as decreasing, and strongly decreasing, respectively. The European badger (*Meles meles*) is classified as increasing (Table 2).

4. Discussion

This study estimates trends in occupancy for 37 (66%) of the 58 UK terrestrial mammal species, using unstructured data largely collected by citizen scientists. International obligations and domestic policies mean that monitoring trends in wildlife populations is required for a variety of purposes. For example, there are periodic reporting requirements for key species listed on the appendices of the EU Habitats Directive (92/

43/EEC), and Red Lists (which are used in a variety of ways, including assessment of progress against Convention on Biological Diversity Targets) require the identification of species at risk from extinction. Yet the difficulty and expense of systematic recording schemes for mammals means that they are relatively uncommon. Only 12 of the 26 terrestrial mammal species on the British Priority Species Indicator have abundance indices and previously, none had occupancy or distribution indices (Eaton et al., 2015). Similarly, a recent review of British mammals found a high proportion (43%) of conservation trends to be unreliable, with 61% of species lacking information on occupancy estimates (Mathews et al., 2018). The results of this study, therefore, have added much needed information on a number of data deficient species for policy, conservation and management practitioners.

Using Alert Categories applied to birds in the UK (DEFRA, 2018; Marchant et al., 1997), 19% of the modelled species were categorised as decreasing, 32% as stable and 49% as increasing. While there is debate about whether decline alone should be sufficient to classify species as being at risk of extinction regardless of censured population size (under Criterion A of the IUCN Red List, IUCN, 2017) (e.g. Godfrey and Godley, 2008), early intervention triggered by the detection of such trends is generally likely to be beneficial. For British mammals, this work indicates consistent patterns of decline for all small mammals excluding the wood mouse (*Apodemus sylvaticus*) suggesting that conservation action is required. The scale of the decline observed for the weasel is sufficient to change its classification from Least Concern (a judgement based largely on an unchanging extent of occurrence) to Vulnerable on the GB Regional Red List (Mathews et al., 2018). This assessment is unaffected by the model's lack of convergence for this species in the early time period because the assessment considers only 10 years or 3 generations, whichever is the longer.

The combination of modelling framework, survey assemblage grouping, and record inclusion criteria used in this study is a rigorous method to deduce trends from biological records. It attempts to account for detectability, selective recording, and changes in survey effort. The models had convergent \hat{R} values, narrow credible intervals for estimated annual occupancy and sufficiently high detection probabilities, suggesting that the outputs are internally robust (Outhwaite et al., 2018). However, as with any statistical modelling exercise, it is important to check model assumptions, fit, and predictions (Devarajan et al., 2020). The posterior predictive check diagnostic indicates that the proportion of sites and the inter-annual variability generally fits the observed data well. Most species' mean predictions lie close to the observed for both summary statistics, and nearly all species observed values fall within the predicted credible intervals, although there are some species for which these intervals are quite large. Furthermore, comparisons between trends derived from systematic and non-systematic schemes represent an additional diagnostic to validate the estimated OM results (van Strien et al., 2013). It is important to acknowledge that the outcome measures used in different schemes vary (for example, extent of occurrence, abundance or, as here, occupancy), and while there is consensus that these indices are related (e.g. Borregaard and Rahbek, 2010), the relationships between them can be complex and take multiple forms (e.g. Dallas et al., 2017; Gaston, 1996). Nevertheless, congruence in the findings from different schemes lends weight to the view that they reflect the underlying conservation status of populations (MacKenzie and Reardon, 2013).

The modelled results on occupancy trends for bat species align with those from the UK's Bat Conservation Trust's National Bat Monitoring Programme (Barlow et al., 2015; BCT, 2019). Their roost counts (which provide an index of abundance) and field surveys (which are most analogous to this study as the index is based on modelled occurrence (Kamp et al., 2016)) indicate that all bat species with sufficient data have been stable or increased since 1999. Similarly, the Deer Distribution Survey found that all six deer species found in the UK had increasing occupancy at 10 km grid square resolution between 1972 and 2002; an

order and direction of change that closely matched this study (Ward, 2005). For the European badger, the estimated increase in occupancy (1.4%) is broadly in agreement with estimates of change in abundance (2.6%, 95% CI 2.2-2.9% between 1985 and 2013) (Judge et al., 2014; Wilson et al., 1997), with occupancy typically expected to increase more slowly than population size (Holt et al., 2002). It can therefore be concluded that the results of this study are validated for a number of species from other types of surveys. In addition, this provides evidence that the OM results for species with previously unknown occupancy trends, due to a lack of systematic surveys, are likely to be reliable.

A potential limiting factor in this study is that all biological records were used without incorporating monitoring method (for example, bat detector) as a covariate in the model, a variable known to be linked to a species' detectability. Failure to account for these differences in detectability could potentially lead to incorrect conclusions. A study that used an OM framework on red snapper (*Lutjanus campechanus*) found that detectability for camera trapping methods was twice that of chevron fish traps and was an important model predictor (Coggins et al., 2014). Similarly, mammal detectability in Australia was also found to be highly dependent on the monitoring method used (Einoder et al., 2018). In this study, all records were used without accounting for different survey methods because this information was lacking for a large proportion of them. The division into survey assemblages may help to alleviate this issue, as it could be assumed that species within an assemblage are likely to be surveyed together. However, it must be understood that co-occurrence could potentially arise from different observers in the same site and may not represent the same survey methods in all cases. This information should be considered when interpreting these results, and efforts should be made to collect information on survey methods in the future. For example, acoustic bat detectors have advanced in recent years with microphone types and their unique frequency responses resulting in differences between detectability of different bat species (Adams et al., 2012), with consequent effects on bat trend analyses (Barlow et al., 2015). In addition, season (phenology), landscape variables (e.g. elevation), biological demographics and local abundance have all been shown to affect a species' detectability (Chen et al., 2013; Einoder et al., 2018; Li, 2018; Rossman et al., 2016; Royle and Nichols, 2003; Zipkin et al., 2017).

To ensure that the inferred occupancy estimates using unstructured biological data are accurate, these data must meet the modelling framework assumptions (MacKenzie et al., 2017). The use of serial recording loggers, such as static bat detectors or camera traps, may actually lead to model violations of replicate observation independence (Wright et al., 2016), creating temporally replicated 'snapshot' visits over successive days. Furthermore, the sampling sites used in this study were not randomly or systematically selected and spatial correlation, caused by clustering of sample sites, could potentially lead to an overestimation of precision (McNew and Handel, 2015). Species misidentification can also lead to false positives — a record of a species at a site where it is in fact absent — and, within an OM framework, can lead to an overestimation of occupancy (Guillera-Arroita, 2017). The biological records used in this study were subject to automatic and expert verification procedures (August et al., 2015), hence the issue of false positives should be minimal. However, there is still the possibility that some species, especially cryptic species like whiskered (*Myotis mystacinus*) and Brandt's (*Myotis brandtii*) bats, may have been misidentified. Moreover, around a third of the species considered were excluded from analysis because accurate detection histories could not be computed. This issue arose because these species were usually recorded alone, either because of survey technique e.g. dedicated European otter (*Lutra lutra*) surveys, or because of particular public interest in a single species, e.g. the European hedgehog (*Erinaceus europaeus*).

Most assessments of trends in conservation status depend on comparison of snapshot assessments taken at two time points, often separated by many years. For example, the recent British Mammal Atlas compares distributions in 1960-1992 with those in 2000-2016 (Crawley

et al., 2020); population reviews typically operate on a 20-year time window (Harris et al., 1995; Mathews et al., 2018); and data intensive systematic surveys are often performed infrequently e.g. 10 years for the National Otter Survey (Crawford, 2010). Clearly, such approaches create a decadal time lag for detection of changes, with consequences for the effectiveness of interventions. In contrast, continual recording and analysis of unstructured data and the presentation of inter-annual changes can highlight changes shortly after they occur. For example, the effects of disease outbreaks such as the 1992 (Moss et al., 2002) and 2010 (Westcott and Choudhury, 2015) Rabbit Haemorrhagic Disease outbreaks are indicated by a corresponding decrease in occupancy of European rabbits (*Oryctolagus cuniculus*) shortly after these dates (Fig. 3).

Presentation of continuous inter-annual changes can also help overcome the problem of selecting an appropriate baseline, and means that trends can be calculated using a range of start and end points or 'moving windows' (see Goodwin et al., 2017 for example; IUCN, 2017). If a starting year has a relatively high abundance (or equivalently, selecting sites for repeated survey on the basis of having high abundance) erroneous inferences of declines may be estimated as repeat surveys will tend to produce estimates closer to the mean (e.g. Fournier et al., 2019). Conversely, starting monitoring when a population is already depressed will under-estimate extents of declines (the so-called 'shifting-baseline' effect; Soga and Gaston, 2017). Readers are able to assess the effects of altering baseline years for the species in this project through the interactive resource provided online (<https://mammalsociety.shinyapps.io/OccupancyTrends/>).

Although OMs represent a robust method for determining species trends from biological records (Isaac et al., 2014), and enable consistent analyses to be undertaken across multiple species, they still have less power at deducing trends compared with systematic surveys (Kamp et al., 2016). Therefore, the scale of changes, and the numbers of species affected, may be underestimated. This is important for some species, including the stoat, weasel, harvest mouse, bank vole (*Myodes glareolus*), common shrew (*Sorex araneus*), field vole (*Microtus agrestis*) and water shrew (*Neomys fodiens*), which were all found to be decreasing, three of which have displayed a significant decrease in occupancy since 1970. This decrease is likely to be a true biological decrease, but all of these species lack any systematic monitoring schemes. Using OMs and a novel clustering algorithm — to refine non-detection inference — on unstructured citizen science records offers an opportunity to highlight species, which are not subject to systematic surveys, where resources for conservation and monitoring actions are most urgently needed.

5. Conclusion

Occupancy models represent one of the most robust methods to deduce trends from unstructured biological records. Using OMs and a novel systematic method for inferring non-detections of mammal species, this study estimates the first long-term occupancy trends for a large proportion of terrestrial mammal species in the UK, many of which had no previously reported trends. These estimates are validated through comparisons with other survey approaches, where available. This study increases the information on mammal conservation status available to practitioners and policy makers; it provides support to previously reported trends and surveys, it estimates 14 new species trends previously unavailable, and it provides evidence to assist the prioritisation of species for conservation action.

Declaration of competing interest

We declare that this manuscript is all original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal *Biological Conservation*. No part of the research has been published in any form elsewhere, unless it is fully acknowledged in the manuscript. The manuscript is not being considered for

publication elsewhere while it is being considered for publication in the journal *Biological Conservation*. Any research in the paper not carried out by the authors is fully acknowledged in the manuscript. All sources of funding are acknowledged in the manuscript, and authors have declared any direct financial benefits that could result from publication. All appropriate ethics and other approvals were obtained for the research.

Acknowledgements

We thank all the individual recorders, verifiers, mammal groups and universities who have helped over the decades to collect biological records of mammals. We are also grateful to the staff of the UK Centre for Ecology and Hydrology, particularly Jack Hatfield who helped to run the models on the UKCEH high performance-computing cluster and Nick Isaac for introducing the SPARTA package and help with model validation. Finally, we thank Paul Jerem, Patrick Wright, Charlotte Le Marquand and Lucy Wills for helpful discussions and comments.

Funding

This work was supported by the Natural Environment Research Council [grant number NE/S006486/1].

Data archiving statement

The data and the mathematical code for the models used in the study will be archived on the University of Sussex's figshare repository (<https://sussex.figshare.com/>).

CRediT Authorship contribution statement

Tom August: Conceptualization (Support); Methodology (Support); Software (Equal); Writing – Review and Editing (Equal). **Frazer Coomber:** Conceptualization (Lead); Formal Analysis (Lead); Methodology (Lead); Visualization (Equal); Writing – original draft (Lead); Review and Editing (Equal). **Colin Harrower:** Conceptualization (Support); Methodology (Support); Software (Equal); Review and Editing (Equal). **Fiona Mathews:** Funding Acquisition (Lead); Project Administration (Lead); Supervision (Lead); Writing – original draft (Support); Review and Editing (Equal). **Gary Powney:** Conceptualization (Support); Methodology (Support); Software (Equal); Review and Editing (Equal). **Bethany Smith:** Visualization (Lead); Writing – original draft (Equal); Review and Editing (Equal).

Appendix A

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2021.109362>.

References

- Adams, A.M., Jantzen, M.K., Hamilton, R.M., Fenton, M.B., Freckleton, R., 2012. Do you hear what I hear? Implications of detector selection for acoustic monitoring of bats. *Methods Ecol. Evol.* 3, 992–998.
- 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, 13.
- August, T., Powney, G.D., Outhwaite, C.L., Harrower, C.A., Hill, M., Hatfield, J., Mancinini, F., Isaac, N.J., 2020a. Sparta: trend analysis for unstructured data. <https://github.com/biologicalrecordscentre/sparta>.
- August, T., Powney, G.D., Outhwaite, C.L., Hatfield, J., Logie, M., Freeman, S., Isaac, N.J., 2020b. BRC indicators: creating multispecies biodiversity indicators. <https://github.com/BiologicalRecordsCentre/BRCIndicators>.
- August, T., Harvey, M., Lightfoot, P., Kilby, D., Papadopoulos, T., Jepson, P., 2015. Emerging technologies for biological recording [in special issue: Fifty years of the biological records centre]. *Biol. J. Linn. Soc.* 115 (3), 731–749.
- Barlow, K.E., Briggs, P.A., Haysom, K.A., Hutson, A.M., Lechiara, N.L., Racey, P.A., et al., 2015. Citizen science reveals trends in bat populations: the National Bat Monitoring Programme in Great Britain. *Biol. Conserv.* 182, 14–26.

- Battersby, J.E., Greenwood, J.J.D., 2004. Monitoring terrestrial mammals in the UK: past, present and future, using lessons from the bird world. *Mammal Rev.* 34 (1), 3–29.
- BCT, 2019. The National Bat Monitoring Programme Annual Report 2018. Bat Conservation Trust, London.
- Borregaard, M.K., Rahbek, C., 2010. Causality of the relationship between geographic distribution and species abundance. *Q. Rev. Biol.* 85 (1), 3–25.
- Butchart, S.H., Walpole, M., Collen, B., van Strien, A.J., Scharlemann, J.P., Almond, R.E., et al., 2010. Global biodiversity: indicators of recent declines. *Science* 328, 1164–1168.
- Chen, G., Kéry, M., Plattner, M., Ma, K., Gardner, B., Zuidema, P., 2013. Imperfect detection is the rule rather than the exception in plant distribution studies. *J. Ecol.* 101, 183–191.
- Coggins Jr., L.G., Bachelier, N.M., Gwinn, D.C., 2014. Occupancy models for monitoring marine fish: a bayesian hierarchical approach to model imperfect detection with a novel gear combination. *PLoS One* 9 (9), e108302.
- Crawford, A., 2010. Fifth otter survey of England 2009–2010. Environment Agency, Bristol.
- Crawley, D., Coomber, F.G., Kubasiewicz, L.M., Harrower, C.A., Evans, P.G.H., Waggit, J., et al., 2020. Atlas of the Mammals of Great Britain and Northern Ireland. Pelagic Publishing, Exeter.
- Croft, S., Smith, G.C., 2019. In: Structuring the unstructured: estimating species-specific absence from multi-species presence data to inform pseudo-absence selection in species distribution models. *BioRxiv*, p. 15.
- Dallas, T., Decker, R.R., Hastings, A., 2017. Species are not most abundant in the centre of their geographic range or climatic niche. *Ecol. Lett.* 20, 1526–1533.
- DEFRA, 2018. Wild Bird Populations in the UK, 1970 to 2017.
- Dennis, E.B., Morgan, B.J., Freeman, S.N., Ridot, M.S., Brereton, T.M., Fox, R., et al., 2017. Efficient occupancy model-fitting for extensive citizen-science data. *PLoS One* 12, e0174433.
- Dennis, E.B., Brereton, T.M., Morgan, B.J.T., Fox, R., Shortall, C.R., Prescott, T., et al., 2019. Trends and indicators for quantifying moth abundance and occupancy in Scotland. *J. Insect Conserv.* 23, 369–380.
- Devarajan, K., Morelli, T.L., Tenan, S., 2020. Multi-species occupancy models: review, roadmap, and recommendations. *Ecography* 43, 1–13.
- Eaton, M.A., Burns, F., Isaac, N.J.B., Gregory, R.D., August, T.A., Barlow, K.E., et al., 2015. The priority species indicator: measuring the trends in threatened species in the UK. *Biodiversity* 16, 108–119.
- Einoder, L.D., Southwell, D.M., Lahoz-Monfort, J.J., Gillespie, G.R., Fisher, A., Wintle, B. A., 2018. Occupancy and detectability modelling of vertebrates in northern Australia using multiple sampling methods. *PLoS One* 13, e0203304.
- Fournier, A.M.V., White, E.R., Heard, S.B., 2019. Site-selection bias and apparent population declines in long-term studies. *Conserv. Biol.* 33, 1370–1379.
- Gaston, K.J., 1996. The multiple forms of the interspecific abundance-distribution relationship. *Oikos* 76, 211–220.
- Gelman, A., Hill, J., 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge.
- Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. *Stat. Sci.* 7, 457–511.
- Godfrey, M.H., Godley, B.J., 2008. Seeing past the red: flawed IUCN global listings for sea turtles. *Endanger. Species Res.* 6, 155–159.
- Goodwin, C.E.D., Hodgson, D.J., Al-Fulaij, N., Bailey, S., Langton, S., McDonald, R.A., 2017. Voluntary recording scheme reveals ongoing decline in the United Kingdom hazel dormouse *Muscardinus avellanarius* population. *Mamm. Rev.* 47, 183–197.
- Guillera-Arroita, G., 2017. Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. *Ecography* 40, 281–295.
- Harris, S., Morris, P., Wray, S., Yalden, D., 1995. A review of british mammals: population estimates and conservation status of British mammals other than cetaceans. JNCC.
- Hayhow, D.B., Eaton, M.A., Stanbury, A.J., Burns, F., Kirby, W.B., Bailey, N., et al., 2019. The State of Nature 2019. The State of Nature partnership.
- Holt, A.R., Gaston, K.J., He, F., 2002. Occupancy-abundance relationships and spatial distribution: a review. *Basic Appl. Ecol.* 3, 1–13.
- Isaac, N.J.B., van Strien, A.J., August, T.A., de Zeeuw, M.P., Roy, D.B., Anderson, B., 2014. Statistics for citizen science: extracting signals of change from noisy ecological data. *Methods Ecol. Evol.* 5, 1052–1060.
- IUCN, 2017. Guidelines for using the IUCN red list categories and criteria. Prepared by the Standards and Petitions Subcommittee.
- Jones, G., Barratt, E.M., 1999. *Vespertilio pipistrellus schreber, 1774 and V. pygmaeus leach, 1825 (currently Pipistrellus pipistrellus and P. pygmaeus; mammalia, Chiroptera): proposed designation of neotypes.* *Bull. Zool. Nomencl.* 56 (3), 182–186.
- 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.
- Kamp, J., Oppel, S., Heldbjerg, H., Nyegaard, T., Donald, P.F., Schröder, B., 2016. Unstructured citizen science data fail to detect long-term population declines of common birds in Denmark. *Divers. Distrib.* 22, 1024–1035.
- Kéry, M., Royle, J.A., Schmid, H., Schaub, M., Volet, B., Haffiger, G., et al., 2010. Site-occupancy distribution modeling to correct population-trend estimates derived from opportunistic observations. *Conserv. Biol.* 24 (5), 1388–1397.
- Legendre, P., Legendre, L., 2012. Numerical Ecology. Elsevier.
- Li, S., 2018. Analysis of biological record data: improvements of the occupancy-detection models. *bioRxiv*.
- Macdonald, D.W., Mace, G.M., Rushton, S., 1998. Proposals for future monitoring of British mammals. Dept. of the Environment, Transport and the Regions.
- MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, J.A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83 (8), 2248–2255.
- MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L., Hines, J.E., 2017. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence, 2nd edn. Elsevier.
- MacKenzie, D.I., Reardon, J.T., 2013. Occupancy methods for conservation management. In: Biodiversity monitoring and conservation: bridging the gap between global commitment and local action. John Wiley & Sons Ltd, pp. 248–264.
- MacSwiney, G.M.C., Clarke, F.M., Racey, P.A., 2008. What you see is not what you get: the role of ultrasonic detectors in increasing inventory completeness in neotropical bat assemblages. *J. Appl. Ecol.* 45, 1364–1371.
- Maes, D., Isaac, N.J.B., Harrower, C.A., Collen, B., van Strien, A.J., Roy, D.B., 2015. The use of opportunistic data for IUCN red list assessments. *Biol. J. Linn. Soc.* 115, 690–706.
- Marchant, J.H., Wilson, A.M., Chamberlain, D.E., Gregory, R.D., Baillie, S.R., 1997. Opportunistic bird species - enhancements for the monitoring of populations. In: British Trust for Ornithology, Thetford, England.
- 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. In: A report by the Mammal Society under contract to Natural England, Natural Resources Wales and Scottish Natural Heritage. Natural England, Peterborough. ISBN 978-1-78354-494-3.
- McGuire, C., Whitfield, D., Perkins, H., Owen, C., 2014. National water vole database and mapping project guide to the use of project outputs to end of 2012. In: The Wildlife Trusts.
- McNew, L.B., Handel, C.M., 2015. Evaluating species richness: biased ecological inference results from spatial heterogeneity in detection probabilities. *Ecol. Appl.* 25 (6), 1669–1680.
- Moss, S.R., Turner, S.L., Trout, R.C., White, P.J., Hudson, P.J., Desai, A., et al., 2002. Molecular epidemiology of rabbit haemorrhagic disease virus. *J. Gen. Virol.* 83, 2461–2467.
- Outhwaite, C.L., Chandler, R.E., Powney, G.D., Collen, B., Gregory, R.D., Isaac, N.J.B., 2018. Prior specification in bayesian occupancy modelling improves analysis of species occurrence data. *Ecol. Indic.* 93, 333–343.
- Outhwaite, C.L., Powney, G.D., August, T.A., Chandler, R.E., Rorke, S., Prescott, O.L., et al., 2019. Annual estimates of occupancy for bryophytes, lichens and invertebrates in the UK, 1970–2015. *Sci. Data* 6, 259.
- Outhwaite, C.L., Gregory, R.D., Chandler, R.E., Collen, B., Isaac, N.J.B., 2020. Complex long-term biodiversity change among invertebrates, bryophytes and lichens. *Nat. Ecol. Evol.* 4, 384–392.
- Plummer, M., 2017. JAGS version 4.3.0 user manual. ed. <http://mcmc-jags.sourceforge.net/>.
- Pocock, M.J.O., Roy, H.E., Preston, C.D., Roy, D.B., 2015. The biological records centre: a pioneer of citizen science. *Biol. J. Linn. Soc.* 115, 475–493.
- Powney, G.D., Isaac, N.J., 2015. Beyond maps: a review of the applications of biological records. *Biol. J. Linn. Soc.* 115, 532–542.
- Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A., et al., 2019. Widespread losses of pollinating insects in Britain. *Nat. Commun.* 10, 1018.
- Prendergast, J.R., Wood, S.N., Lawton, J.H., Eversham, B.C., 1993. Correcting for variation in recording effort in analyses of diversity hotspots. *Biodivers. Lett.* 1 (2), 39–53.
- Preston, C.D., Harrower, C.A., Hill, M.O., 2011. Distribution patterns in British and Irish liverworts and hornworts. *J. Bryol.* 33 (1), 3–17.
- R Core Team, 2018. R: a language and environment for statistical computing, version 3.2.2. ed. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rossman, S., Yackulic, C.B., Saunders, S.P., Reid, J., Davis, R., Zipkin, E.F., 2016. Dynamic N-occupancy models: estimating demographic rates and local abundance from detection-nondetection data. *Ecology* 97 (12), 3300–3307.
- Royle, J.A., Kéry, M., 2007. A bayesian state-space formulation of dynamic occupancy models. *Ecology* 88 (7), 1813–1823.
- Royle, J.A., Nichols, J.D., 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84 (3), 777–790.
- Santos, R.A.L., Mota-Ferreira, M., Aguiar, L.M.S., Ascensao, F., 2018. Predicting wildlife road-crossing probability from roadkill data using occupancy-detection models. *Sci. Total Environ.* 642, 629–637.
- Schmeller, D.S., Henry, P.Y., Julliard, R., Gruber, B., Clobert, J., Dziock, F., et al., 2009. Advantages of volunteer-based biodiversity monitoring in Europe. *Conserv. Biol.* 23 (2), 307–316.
- Soga, M., Gaston, K.J., 2017. Shifting baseline syndrome: causes, consequences and implications. *Front. Ecol. Evol.* 16, 222–230.
- van Strien, A.J., van Swaay, C.A.M., Termaat, T., 2013. Opportunistic citizen science data of animal species produce reliable estimates of distribution trends if analysed with occupancy models. *J. Appl. Ecol.* 50, 1450–1458.
- Toms, M.P., Greenwood, J.J.D., 1999. Developing a mammal monitoring programme for the UK, BTO Research Report N. 223. A report by the British Trust for Ornithology under contract to the Joint Nature Conservation Committee, Thetford.
- van Strien, A.J., Bekker, D.L., La Haye, M.J.J., van der Meij, T., 2015. Trends in small mammals derived from owl pellet data using occupancy modelling. *Mamm. Biol.* 80, 340–346.
- Su, Y.S., Yajima, M., 2015. Package 'R2jags'. ed. <https://cran.r-project.org/web/package/s/R2jags/index.html>.

- Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D., Kelling, S., 2009. eBird: a citizen-based bird observation network in the biological sciences. *Biol. Conserv.* 142, 2282–2292.
- Szabo, J., Vesk, P.A., Baxter, P.W., Possingham, H.P., 2010. Regional avian species declines estimated from volunteer-collected long-term data using list length analysis. *Ecol. Appl.* 20 (8), 2157–2169.
- Telenius, A., 2011. Biodiversity information goes public: GBIF at your service. *Nord. J. Bot.* 29, 378–381.
- Ward, A.I., 2005. Expanding ranges of wild and feral deer in Great Britain. *Mamm. Rev.* 35 (2), 165–173.
- Westcott, D.G., Choudhury, B., 2015. Rabbit haemorrhagic disease virus-2-like variant in Great Britain. *Vet. Rec.* 176, 74.
- Wilson, G., Harris, S., McLaren, G., 1997. Changes in the British badger population 1988–1997. In: Peoples Trust for Endangered Species, London.
- Wright, L.J., Newson, S.E., Noble, D.G., 2014. The value of a random sampling design for annual monitoring of national populations of larger british terrestrial mammals. *Eur. J. Wildl. Res.* 60, 213–221.
- Wright, W.J., Irvine, K.M., Rodhouse, T.J., 2016. A goodness-of-fit test for occupancy models with correlated within-season revisits. *Ecol. Evol.* 6, 5404–5415.
- Zipkin, E.F., Rossman, S., Yackulic, C.B., Wiens, J.D., Thorson, J.T., Davis, R.J., et al., 2017. Integrating count and detection–nondetection data to model population dynamics. *Ecology* 98 (6), 1640–1650.