

Potential future distribution and abundance patterns of Common Buzzards *Buteo buteo*

Jennifer A. Border, Dario Massimino & Simon Gillings



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A report to Natural England

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SUMMARY

1. To contribute towards the definition of Favourable Conservation Status for the Common Buzzard *Buteo buteo*, estimates of local carrying capacity are required throughout England. In this report we aim to assess the potential for future expansion of the Buzzard breeding range in England and forecast potential densities in 10-km squares using species distribution models.
2. According to *Bird Atlas 2007–11*, Buzzards breed in 94% of English 10-km squares. Many of the 54 squares where Buzzards were present but not breeding, and the 34 where they were not recorded, are coastal (and contain little land) or are suburban/urban areas with limited breeding habitat. Few unoccupied squares contain extensive tracts of suitable breeding habitat so we assess the potential for future range expansion to be limited.
3. To inform the selection of environmental variables required for distribution modelling, a literature review was conducted. This identified 25 factors likely to positively or negatively influence Buzzard presence or abundance; from these we sourced 25 spatially explicit variables. Seven were highly inter-correlated and were not used in models. For some potentially important factors we were unable to source spatial data to incorporate into models.
4. Buzzard abundance data were obtained from the BTO/JNCC/RSPB Breeding Bird Survey, giving numbers of birds counted in a stratified random sample of over 5,000 1-km squares. Count data were corrected for detectability using distance sampling to yield densities (birds per surveyed 1-km square). Two metrics were calculated for modelling: a) maximum observed density per square, and b) mean observed density per square, both calculated over the most recent five years.
5. Generalised additive models were used to relate the two metrics of Buzzard density to the chosen environmental variables. Ten-fold cross validation was used to assess model performance and the effects of individual environmental variables were checked for biological realism. Density predictions were made for all 1-km squares in England, then summed to give estimates per 10-km square.
6. Models trained on maximum observed densities (the “maximum density model”) and mean observed density (the “mean density model”) performed similarly well; performance was reasonable, and good by abundance modelling standards. Comparisons of predictions and observations showed that models were reasonably well calibrated but they were unable to accurately predict the highest observed densities. Nevertheless, predicted densities were higher compared to published density estimates.
7. The long-term trend in density in each 100-km square was assessed for evidence of stability. Densities were high and stable in the west compared to low but rapidly increasing in the east with little evidence of densities plateauing. In the west, annual densities in the stable parts of the trend fell short of densities predicted from the maximum density model but matched those from the mean density model. In areas of rapid increase in the east, observed densities have already exceeded predictions from the mean density model and appear likely to exceed those from the maximum density model in future.
8. In conclusion, we can be highly confident about the extent of the Buzzards breeding range and its limited scope to expand further. The species distribution models are as robust as we can expect with the data available and they perform comparably to other models of abundance. However, many of the predicted densities are high compared to those in the literature, although it should be noted many of these are quite old and limiting factors may have reduced since then.
9. Further, the ongoing population increase in eastern England and anticipated exceedance of our density predictions indicates that correlative relationships built on variables such as land cover are unable to capture all the fine-scale local environmental influences acting on Buzzards, thereby limiting the application of these models for local management purposes. Mechanistic models using demographic rates are likely to yield more robust predictions.

1. INTRODUCTION

The Common Buzzard, *Buteo buteo* (Buzzard hereafter) is a large raptor which resides in England year round. England's Buzzard population declined in the late 1950s due to plummeting Rabbit *Orytolagus cuniculus* populations from the myxomatosis virus (Taylor et al., 1988), persecution in the 18th, 19th and early 20th centuries (Elliott & Avery, 1991), and organochloride pesticides in the 1950s and 1960s (Parkin & Knox, 2010). However, in the last 40 years the Buzzard population has undergone a rapid increase and associated range expansion, more than doubling its previous range size (Balmer et al., 2013). Reasons for this expansion are not yet well understood, though the reduction in illegal killing (Prytherch, 2013), the ban on organochloride pesticides which came into force in the 1984, recovery of Rabbit populations and upland afforestation are all likely to have played a role (Taylor et al., 1988; Balmer et al., 2013).

In the 20 years between the breeding distribution atlases of 1988–91 (Gibbons et al., 1993) and 2008–11 (Balmer et al., 2013) Buzzard range has expanded eastwards leading to the colonization of eastern Britain, plus the Isle of Man and the Channel Islands, while territory density has increased in western areas. There have been a few small-scale local studies on Buzzard densities in the UK (e.g. Dare & Barry, 1990), and some older ones covering Britain or the UK as a whole (e.g. Moore, 1965; Taylor et al., 1988, Clements, 2002). However, there is still little understanding of how much further Buzzards could spread and how much more populations could increase until they reach the limit of their local environment. There is also little understanding of the influence of environmental variables on Buzzard densities; again, there have been a several small-scale studies looking at correlations between certain environmental variables and breeding success (Austin & Houston, 1997, Sim et al., 2001; Krüger, 2004; Rooney & Montgomery, 2013) or local breeding densities (Graham et al., 1995, Sim et al., 2001), but no large scale studies to identify the key influences on Buzzards across the country.

Conservation and management decisions relating to Buzzards need to take account of these changes, but it is unclear whether populations have stabilised or how much further Buzzards could spread and increase. In particular, information on the potential future extent of Buzzard distribution and expected densities are needed for an assessment of Favourable Conservation Status (FCS) being undertaken by Natural England.

FCS requires “securing the inherent genetic diversity of a species” and “maintaining a viable representation across their natural range and distribution”. The species must be either stable or increasing and have good prospects of continuing to do so in the future (for more details see: http://jncc.defra.gov.uk/pdf/FCS18_InterAgencyStatement.pdf). Ideally such information would be based on a detailed population model considering demographic rates including survival, productivity, dispersal and density dependence and how these relate to habitat suitability. An alternative approach is to use species distribution models (SDM; Franklin, 2010). SDMs seek to identify the relationships between the presence or abundance of a species and various biologically limiting environmental factors. Knowledge of these relationships can be used to make predictions of species presence or abundance in new settings or under new environmental conditions. In this study we assess whether an SDM approach can help inform the production of the FCS statement. Specifically we aim to:

1. Assess the current 10-km resolution distribution of Buzzards in England, identify unoccupied areas and assess their potential to support breeding Buzzards.
2. Produce 10-km resolution estimates of the saturation density of breeding Buzzards throughout England.

2. METHODS

2.1 Data used in the analyses

The following datasets on Buzzard distribution and abundance were used in these analyses.

2.1.1 Bird Atlas distribution data

The current range extent of Buzzards was determined from *Bird Atlas 2007–11* (Balmer et al., 2013). The atlas presents the latest comprehensive information on the distribution of breeding Buzzards at a 10-km resolution. Full field methods are in Balmer et al. (2013) but in brief each 10-km square was surveyed to assess the likelihood of breeding by each bird species, using standard evidence of breeding criteria. Following the four years of surveys, each 10-km square was assigned one of five categories: i) absent, ii) present but no breeding evidence, iii) possible breeding, iv) probable breeding or v) confirmed breeding. Note that for breeding evidence to be associated with a square, birds must be seen/heard using the square, displaying a number of behaviours that could constitute breeding, and the behaviour must be observed in suitable breeding habitat. For this species, 10-km squares where the species was present but no breeding evidence was assigned are most likely to arise either because of a lack of suitable breeding habitat (e.g. dense urban fabric) or because birds were not using the square (e.g. migrating over the square).

2.1.2 Breeding Bird Survey data

Abundance data for modelling spatial patterns of abundance and for assessing long-term trends came from the BTO/JNCC/RSPB Breeding Bird Survey (BBS; Harris et al., 2017). The survey has been conducted since 1994 and uses a stratified random sampling design. BBS squares are allocated randomly to volunteers. Surveys are conducted during 6am–10am and volunteers are requested not to survey in strong winds and heavy rain. In each square two 1-km transect lines are walked at a slow constant pace and all birds seen or heard are recorded. The transect lines are ideally 500 m apart and 250 m from the edge of the 1-km square, though some deviation may be necessary due to access rights, obstacles and terrain. Each transect line is split into five 200 m sections for recording purposes. Each square receives two visits per year, one in April to mid-May and a second in mid-May to the end of June. The following habitat descriptions are assigned to each 200 m transect section: woodland, scrubland, semi-natural grasslands/marsh, heathland and bogs, farmland, human sites, waterbodies, coastal and inland rock. Birds are recorded in three distance categories measured at right-angles to the transect

line: < 25 m, 25–100 m, 100+ m. Birds seen only in flight are recorded separately. Recording of birds in distance bands allows a formal evaluation of how the detectability of a species declines with distance from the transect line, enabling numbers of birds encountered to be corrected for under-detection to derive estimates of absolute density (Buckland et al., 2005). For most species the majority of individuals are recorded in one of the distance bands, with very few encountered only in flight. Exceptions are hirundines, Skylarks *Alauda arvensis* and raptors such as Buzzard. For the purposes of this report we refer to all birds encountered in distance bands as ‘perched birds’. Hence we are able to assess how detectability varies with distance for perched birds and make due corrections. Detectability corrections are not possible for flying birds and we have to assume that at any distance (within the 1-km square) flying birds would have been uniformly detectable.

2.2 Assessing current distribution and potential for range expansion

Bird Atlas data (Section 2.1.1) were used to identify all squares where at least possible breeding evidence was noted (= breeding range) and all squares where the species was absent or present only (= unsuitable and potential future range). The latter list of squares was retained for later use. To aid interpretation we determined the land area of each 10-km square.

2.3 Modelling spatial variation in Buzzard densities

Producing species distribution models to enable predictions of Buzzard density per 10-km square involved the following seven steps:

1. Convert observed counts on transects to densities (birds per km²);
2. Identify key environmental variables likely to determine Buzzard density and obtain spatially referenced data for every 1-km square in the study region;
3. Develop a statistical species distribution model relating the observed density of Buzzards in surveyed squares to the identified environmental variables;
4. Use cross-validation to determine the explanatory power of the best model;
5. Use the model to make predictions for every 1-km square in the study region;

6. Sum 1-km predictions per 10-km square to derive estimates of birds per 10-km square (birds per 100 km²);
7. Sense-check densities derived in 5) and 6) with published estimates of Buzzard density.

Steps 1–4 are explained in more detail in the following sections.

2.3.1 Converting counts to densities

To convert transect counts to densities of birds per 1-km square, raw count data of Buzzards in each transect section were adjusted via the program Distance (Buckland et al., 2005) to account for detectability using the model: $distance \sim habitat + visit$ where habitat was the main habitat assigned to the transect section and visit was a categorical factor indicating whether the count was derived from the early or late visit. For this purpose some habitat types (waterbodies, coastal and inland rock) that were very rarely occupied by Buzzards had to be combined into a single 'open habitat' category. Detectability estimates were calculated for each year, although as year is not a model covariate the same transect section will get the same detectability over years (unless habitat has changed).

These detectability estimates were used to calculate densities by multiplying the number of individuals in each 200 m section in the distance bands < 25 m and 25–100 m by the habitat-specific detectability coefficients. Sightings in the 100 m+ distance band were discarded due to the lack of an upper bound for this category preventing accurate density estimates. Including Buzzards sighted up to 100 m away means each 200 m transect section covers 400 m², so this density was expressed in individuals/4 ha. This was then multiplied by 2.5 to obtain individuals/10ha, under the assumption that density beyond 100 m is the same as density within 100 m. The total number of flying birds detected in each 200 m section was then added to this density estimate. Given the size and high visibility of flying Buzzards, we assumed flying birds were equally detectable throughout the 1-km square. Then the counts were summed over all transect sections to get an estimated density per 1-km square for each visit and each survey year. For each square and survey year the visit with the highest total Buzzard density was selected.

In the development of previous SDMs using BBS data we have summarised multiple years of data from each surveyed square to produce a single estimate per square, usually taking the maximum density across

years (e.g. Massimino et al. 2017a). This approach is adopted in an effort to reduce the influence of stochasticity in the observed counts, either due to failure to detect birds or chance year to year fluctuations in abundance. A further argument for this approach is it may more closely reflect the upper bound of density that squares may attain, which is the desired aim of this modelling exercise. However, for a species such as Buzzard, with a potentially large home range, this approach could artificially inflate local density estimates and the mean density across years may be a more realistic figure. For this work we calculated maximum observed density and mean observed density for each surveyed square over the 5-year period, 2012 to 2016. We then repeated all analyses described below using both metrics and we discuss which of these approaches is likely to be most appropriate for Buzzards in Section 3.2.2 and Section 4. It should be noted here that it is not possible to distinguish between breeding and non-breeding Buzzards in these data.

2.3.2 Identifying environmental variables

A literature search was undertaken to identify relevant environmental variables likely to determine Buzzard occurrence and abundance (Table 1). Table 2 lists the variables for which we were able to acquire contemporary spatially referenced data. There are some variables that ideally we would have liked to include but data are either completely lacking or available at an inappropriate spatial or temporal resolution. These include information on the abundance of small mammals such as voles, other rodents and moles, abundance of amphibians and a measure of the number of footpaths in an area as a proxy of human disturbance. There is also evidence that songbirds, thrushes and medium-sized birds are a good food source for Buzzards (Taylor et al., 1988, Jędrzejewski et al., 1994, Swann and Etheridge, 1995, Austin & Houston 1997, Selås, 2001, Rooney & Montgomery, 2013). However, diet seems to be highly dependent on what is available in the local area and these bird food sources tend to be used when other larger food sources are unavailable (Austin & Houston, 1997, Rooney & Montgomery, 2013). Also, including so many species of birds together as a variable is likely to reflect overall habitat quality rather than prey abundance. For these reasons we did not use songbird abundance as a covariate. The following sections detail how the selected environmental variables were sourced.

Table 1. Factors identified from literature review that positively or negatively affect Buzzard distribution and abundance

Environmental factor	Direction of expected effect/explanation	Reference
Rabbit abundance	Positive effect, important food source	Rooney & Montgomery, 2013; Swann & Etheridge, 1995; Austin & Houston, 1997; Graham et al., 1995
Corvid abundance	Positive effect, important food source	Rooney & Montgomery, 2013; Sim et al., 2001
Abundance of medium sized birds (thrushes, woodpeckers)	Positive effect, important food source	Rooney & Montgomery, 2013; Jędrzejewski et al., 1994
Rat/rodent abundance	Positive effect, important food source	Rooney & Montgomery 2013; Goszczynski, 2001
Amphibians/toads abundance	Positive effect, important food source	Swann & Etheridge, 1995; Selås, 2001
Vole and mole abundance	Positive effect, important food source	Swann & Etheridge, 1995; Selås, 2001; Wuczynski, 2003; Graham et al., 1995
Woodpigeon and Pheasant abundance	Positive effect, important food source	Swann & Etheridge, 1995; Selås, 2001
Brown Hare abundance	Positive effect, important food source	Swann & Etheridge, 1995
Passerine abundance including Chaffinch	Positive effect, important food source	Swann & Etheridge, 1995; Selås, 2001; Taylor et al., 1988; Austin & Houston, 1997
Persecution	Negative, limits population growth	Elliot & Avery, 1991; Swann & Etheridge, 1995; Taylor et al., 1988; Goszczynski, et al. 2005
Rainfall	Negatively effects reproductive success	Krüger, 2002; 2004
Human disturbance	Negatively effects reproductive success	Krüger, 2004
Competition	Negatively effects reproductive success	Krüger, 2004
Cold temperatures	Reduces fitness	Krüger, 2002
Open areas	Positive relationship as used for foraging	Kruger, 2002
Number of buildings	Negative effect, unsuitable habitat	Krüger, 2002
Coniferous plantations	Positive relationship, good nesting and foraging habitat	Newton et al., 1982
Agricultural land	Positive relationship, good nesting and foraging habitat	Baltag et al., 2013
Natural perches-bushes and shrubs	Positive relationship, good nesting and foraging habitat	Baltag et al., 2013
Woodland fringes and scrubs	Good prey densities	Dare & Barry, 1990
Unimproved pasture	Positive relationship, good nesting and foraging habitat	Sim et al., 2001
Mature deciduous woodlands	Positive relationship, good nesting and foraging habitat	Sim et al., 2001; Gibbons et al., 1994
Corvids	Negative, predate on chicks, cause nest failure	Sim et al., 2001
Agricultural intensification	Possible negative effect, makes habitat more unsuitable	Sim et al., 2001
Grazed pasture	Positive relationship, good nesting and foraging habitat	Gibbons et al., 1994

Table 2. A summary of the environmental variables collated and their sources. The variables shown in *bold italics* were those retained for use in the models after excluding highly correlated ones.

Influence	Variable	Data source
Prey availability	<i>Rabbit relative abundance per 1-km</i>	Modelled BBS mammal counts ¹
	<i>Brown Hare relative abundance per 1-km</i>	Modelled BBS mammal counts ¹
	<i>Mean Pheasant count per 10-km</i>	<i>Bird Atlas 2007–11</i> ²
	<i>Mean corvid count per 10-km</i>	<i>Bird Atlas 2007–11</i> ²
Predation/competition	<i>Mean corvid count per 10-km</i>	<i>Bird Atlas 2007–11</i> ²
	<i>Goshawk presence/absence</i>	<i>Bird Atlas 2007–11</i> ²
	<i>Mean Buzzard count from Bird Atlas</i>	<i>Bird Atlas 2007–11</i> ²
Habitat	<i>% cover semi-natural grassland</i>	2015 Land Cover Map ³
	<i>% cover improved grassland</i>	2015 Land Cover Map ³
	<i>% cover arable</i>	2015 Land Cover Map ³
	<i>% cover built up areas and gardens</i>	2015 Land Cover Map ³
	<i>% cover of mature trees</i>	National Forest Inventory for 2011 ⁴
	<i>% tree cover</i>	Pan-European HRL Tree Cover Density 2012 ⁵
	<i>Log ratio of % cover of coniferous to deciduous woodland</i>	2015 Land Cover Map ³
Climate	Mean monthly temperature over whole year (°C)	UKCP09 ⁶
	<i>Mean monthly breeding temperature (°C)</i>	UKCP09 ⁶
	Mean monthly wintering temperature (°C)	UKCP09 ⁶
	Mean of total monthly precipitation over whole year (mm)	UKCP09 ⁶
	<i>Mean of total monthly breeding precipitation (mm)</i>	UKCP09 ⁶
	Mean of total monthly wintering precipitation (mm)	UKCP09 ⁶
	Total precipitation over whole year (mm)	UKCP09 ⁶
	Total breeding precipitation (mm)	UKCP09 ⁶
Topography	<i>Slope (degrees)</i>	GGIAR-SRTM 90m raster ⁷
	<i>Elevation (m above sea level)</i>	GGIAR-SRTM 90m raster ⁷

¹ (Massimino et al., in review)

² (Balmer et al., 2013)

³ (Rowland et al., 2017)

⁴ Forestry Commission (<https://www.forestry.gov.uk/inventory>)

⁵ Copernicus (land.copernicus.eu/pan-european/high-resolution-layers)

⁶ Met Office <https://www.metoffice.gov.uk/climate/uk/data/ukcp09/datasets#monthly>

⁷ (Jarvis et al., 2008, available at <http://srtm.csi.cgiar.org>)

Prey availability

Data on abundance of European Rabbit and Brown Hare *Lepus europaeus* were extracted from Massimino et al. (in review) which gives spatially interpolated estimates (at 1-km resolution) of relative abundance for mammals across Britain. It is important to note that these values are not densities or 'real abundances' but an index of abundance. Common Pheasant *Phasianus colchicus* abundance came from *Bird Atlas 2007–11* (Balmer et al., 2013) data. Using a sample of timed tetrad visits in each 10-km square we calculated the mean count per survey hour for Common Pheasant to give a measure of relative abundance per 10-km square. In the same way we calculated the mean count per survey hour for each of Carrion Crow *Corvus corone*, Hooded Crow *Corvus Cornix*, Jay *Garrulus glandarius*, Raven *Corvus corax* and Rook *Corvus frugilegus*, and then summed these values to give a measure of corvid relative abundance for each 10-km square.

Predation/competition

Corvids (crows) are both potential prey items and potential predators of Buzzard chicks, and the variable mean corvid count per 10-km square is explained in the prey availability section above. To reflect the abundance of Northern Goshawks *Accipiter gentilis* we used the presence or absence of breeding Goshawks in each 10-km square because densities of this species are so low the data were likely to be highly zero inflated and there is minimal variation in density between squares. In order to account for intraspecific competition, data on Buzzard abundance was included using mean count per survey hour at the 10-km square resolution. This variable is also likely to provide a further proxy for the suitability of 10-km squares for Buzzards and in some way compensates for the lack of detailed habitat quality data (e.g. of other mammalian prey). The atlas dataset is an entirely different dataset from the BBS data set used as the dependent variable (see section 2.1), and is collected using different methods, therefore including it as a variable will not compromise model independence.

Habitat

Land cover data came from the 1-km square percentage cover summary of the 2015 Land Cover Map (LCM) from the Centre for Ecology and Hydrology (Rowland et al., 2017). The percentage cover of Improved Grassland and Arable (encompassing Arable and Horticultural habitat) were taken directly from this dataset. For the other variables, land cover categories within the LCM data set were combined to create two broader categories: (i) Semi-Natural Grasslands, inclusive of neutral grassland, calcareous grassland, acid grassland,

fen, marsh and swamp; (ii) Built-up areas, inclusive of urban and suburban habitats which includes settlements, other man-made structures such as industrial estates and urban gardens and parks. The log ratio of coniferous to deciduous woodlands was also calculated using the following equation:

$$\log_{10}((\% \text{ cover coniferous woodland} + 0.01) / (\% \text{ cover deciduous woodland} + 0.01))$$

The 0.01 was added to all counts to avoid obtaining infinite values when the percentage cover equalled zero.

Data on percentage tree cover came from the Copernicus Pan-European HRL Tree Cover Density 2012 raster dataset (HRL; land.copernicus.eu/pan-european/high-resolution-layers). The dataset consists of a raster of 20 m resolution giving the percentage tree cover per pixel. The data were re-projected from the European ETRS89 grid to the British National Grid and percent cover estimates were derived for each 1-km square. This dataset includes single trees and hedgerows and was therefore preferred over the 2015 LCM which only includes blocks of trees.

To determine the percentage cover of mature woodland we used the Forestry Commission's National Forest Inventory for 2011 (<https://www.forestry.gov.uk/inventory>). Area of mature woodland was extracted for each 1-km square by intersection of the forestry shape file and a polygon layer of 1-km squares in ARCGIS.

Climate (temperature and precipitation)

Gridded climate data at the 5 km resolution were obtained from the Metoffice UKCP09 (available at: www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/download/index.html). The data are generated for a regular 5 km grid via regression and interpolation of data from the irregular weather station network, taking into account longitude, latitude, elevation, terrain shape, coastal influence, and urban land use (Perry & Hollis, 2004). For year round conditions mean monthly temperature and total monthly rainfall were averaged over all months of the year. To encompass conditions when the birds were breeding we used the mean monthly temperatures and the total monthly rainfall averaged over the months March, April, May and June. For winter conditions, the mean monthly temperatures and the total rainfall were averaged over the months of December, January and February before the breeding season of interest (i.e. December 2010 for the 2011 survey). For rainfall we also calculated the total rainfall for each period (yearly, breeding, wintering) by

summing the monthly total values. These annual values for each 5 km square were then averaged over the years 2012 to 2016 to match the BBS data used in models.

Topography (elevation and slope)

Elevation (in meters above sea level) was extracted from the GGIAR-SRTM 90 m raster (Jarvis et al., 2008) taking the mean elevation over each 1-km square. Slope was calculated from elevation in ARCGIS (ESRI 2011). The slope of each elevation raster cell is the maximum rate of change in elevation in one raster cell compared to its eight neighbours. The lower slope values indicate flatter areas, higher values indicate steeper areas. The mean slope was taken for each 1-km square.

2.3.3 Developing a Species Distribution Model for Buzzard densities

Prior to attempting future predictions we developed models to test how well the environmental variables could explain current observed spatial variation in Buzzard abundance. We chose to use Buzzard data from the whole of Britain rather than just England to increase the sample size and particularly to allow better parameterisation of predictions in upland sites of which there are relatively few in England. Generalised Additive Models (GAMs) were used to quantify the form of relationship between environmental factors and Buzzard abundance. GAMs were chosen as they allow non-linear relationships which are more biologically plausible than linear effects for many of these variables. Additionally GAMs reduce the likelihood of extreme predictions arising when predicting outside the range of the model input data. For example, a strong positive linear relationship with forest cover might lead to implausibly high predictions of Buzzard abundance (in the 100s) in squares with very high forest cover, compared to the rest of Britain.

With so many potential environmental predictors it is very likely that pairs of variables could be very highly correlated (collinearity). In such cases, entering both variables into models can prevent the identification of the causal relationship. To test for the degree of collinearity, univariate models relating each environmental variable (from Table 2) to Buzzard abundance were run and Variance Inflation Factors (VIFs; Zuur et al., 2009) were calculated. Pearson's Product Moment Correlation Coefficients were also calculated among all pairwise combinations of variables. Ideally, variables with VIFs > 3 and correlations to other variables > 0.7 were removed. Where two or more variables were strongly correlated, variables with a stronger relationship to Buzzard abundance from the

single models were preferred over variables with weaker relationships. In this way the climate variables mean breeding season temperature and mean breeding precipitation were selected to represent the climate and arable habitat and improved grassland habitat were combined into one category (farmed habitat). After combining, farmed habitat was no longer highly correlated to any of the other variables; however it still had a VIF > 3 due to moderate correlations with many different variables. Elevation also presented a problem, as it was highly correlated to the climate variables. Both of these variables are likely to be very important determinants of Buzzard abundance, therefore we decided to include them in the final model despite possible multi-collinearity issues. Multi-collinearity can lead to unstable parameter estimates that are very sensitive to changes in the model specification but it will not affect the overall fit or the predictions made, nor will it cause any bias in the parameter estimates (Studenmund, 2000; Kutner et al., 2004). The purpose of this model was mainly to make reliable predictions and not to determine how different environmental parameters influence Buzzards, therefore possible inaccuracies in parameter estimates will not interfere with the model's main purpose.

Next the chosen variables (shown in bold italic) were put into a model together. A negative binomial family was used to account for over-dispersion and a weight was included to account for regional variation in survey effort. Initially, smoothed terms, using thin plate splines, were applied to every variable but in order to avoid overfitting and to ensure biologically meaningful relationships, k was restricted to a maximum of 3, meaning only linear or quadratic relationships were allowed. Then smoothed terms were removed one at a time based on the effective degree of freedom (edf) values, where values close to 1 indicate a linear trend. The smoothed term with the lowest edf was removed and the Akaike Information Criterion (AIC) was used to compare the models with and without the smoothed term. If dropping a smoothed term resulted in a rise in $AIC > 2$ then the smoothed term was retained. No variables were removed from the model as all variables had been selected for inclusion based on scientific evidence and the objective was to create a good predictive model so a conservative model was preferred. Model residuals were examined visually to ensure a reasonable fit.

As mentioned earlier, these procedures were performed twice, once with the maximum observed density per square (“maximum density model”) and again using the mean observed density per square (“mean density model”).

2.3.4 Assessing the predictive ability of the model

The best model as outlined in the previous section is the one that uses the available variables optimally, but we need to assess how good it is at explaining Buzzard abundance with independent data (i.e. data not used to train the model). To assess this we conducted ten-fold cross validation using the cvAUC package (Sing et al., 2005). The best model formulation was fitted using 90% of the data (“training data”). This model was then used to predict Buzzard abundance based on the variable values from the remaining 10% of the data (“test data”). The predicted abundances were then compared to the observed abundances from the test data using Spearman’s Rank Correlation Coefficient. This process was repeated 10 times using a different 10% of the data for testing each time and the mean correlation coefficient (and 95% confidence intervals) across the 10 replicates was calculated. The predicted values for each of the 10 folds were also plotted against the observed BBS values to visually assess fit.

2.3 Assessing suitability of the unoccupied range

In section 2.2 we explained how existing atlas distribution data were used to identify 10-km squares that were currently unoccupied by breeding Buzzards. We used the SDM developed above to make predictions of the likely current abundance of Buzzards in the 1-km squares within these unoccupied squares to determine how suitable they were. For this analysis one minor change was made to the model formula: we removed the mean Buzzard count from Bird Atlas variable from the model because this variable might restrict the abundance of Buzzards predicted for these squares as they are squares where no Buzzards have yet been found breeding. Predictions made at 1-km resolution were summed for each 10-km square to assess square suitability. Two sets of predictions were made, based on the maximum density model and the mean density model. Model fit and the magnitude (and biological realism) of the densities predicted by these two models were investigated and one of them was selected as the most appropriate method to predict Buzzard densities.

2.4 Predicting saturation densities of Buzzards

Having developed a model and ascertained its ability to explain and predict currently observed Buzzard

densities, it was our intention to use the same environmental variables in a quantile regression model which would have given us the ability to predict the likely maximum density achievable under certain environmental conditions. However, currently available quantile regression methods are only designed to work with normally distributed data as opposed to count data (which typically follows a Poisson distribution, with a lower bound of zero). Transforming our densities to a normal distribution did not work as models then returned negative predicted densities which are biologically unrealistic.

Instead we adopted the following approach, using the model developed above to predict abundances and using locally generated population trends to ascertain the likelihood that predictions reflect realistic saturation densities. As Buzzards have spread across England at different times, and densities have had longer to stabilise in some areas, this analysis took a regional approach, using 100-km squares to delineate regions. First, the model created in section 2.3.3 was used to make predictions of Buzzard density in every 1-km square in England. These predictions were averaged in each 100-km square to give our nominal estimate of saturation density for that region. Next the full time series of BBS data in each 100-km square was used to generate a trend for that 100-km square. Squares which were only surveyed in one year were removed. The trends were produced using a simple Generalised Linear Model, similar to how national trends are produced. Buzzard density (from the detectability adjusted raw BBS count see section 2.3.1) was modelled as a function of year and 1-km square (both as factors) to account for repeat observations of the same square in multiple years. A weight was also included to account for regional variation in survey effort. These models were then used to predict the Buzzard density for each year and each surveyed 1-km square. The predicted abundances were then averaged for each year, over all surveyed 1-km squares in each 100-km square, and the trend plotted. The 95% confidence intervals for the trend were determined by averaging the standard errors for all 1-km predictions within each 100-km square for each year and then multiplying by 1.96 and either adding or subtracting from the mean predicted value for the square and year to get the upper and lower confidence interval respectively. We looked for an asymptote in the trend indicating a levelling off of the Buzzard density and compared this to the predicted densities from the SDM.

3. RESULTS

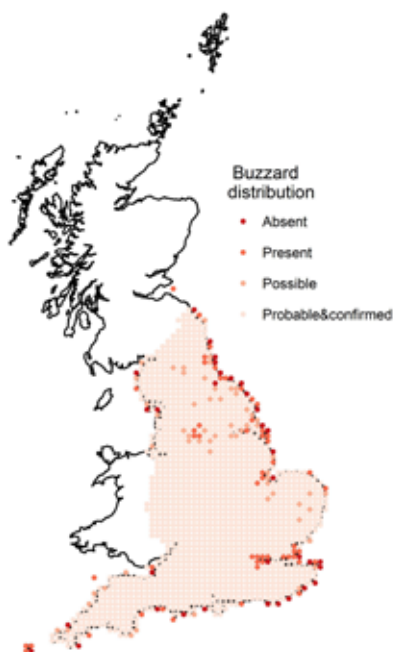
3.1 Current distribution and potential for range expansion

The current distribution of Buzzards in England according to *Bird Atlas 2007–11* is shown in Figure 1, coloured to emphasise gaps. Buzzards were recorded with breeding evidence (possible, probable or confirmed breeding) in 94% of 10-km squares in England (Table 3). The only squares where Buzzards were not recorded were mostly coastal or highly urbanised (e.g. centre of London). Squares with birds present but apparently not breeding included urban areas, coastal eastern England and small parts of the Pennines. In western England only a few coastal squares and the Isle of Scilly do not have breeding evidence.

Table 3. The number of 10-km squares where Buzzards were recorded as absent, present but not breeding, possibly breeding and probably or confirmed breeding from *Bird Atlas 2007–11*.

Buzzard status	Number of 10-km squares
Absent	34
Present	54
Possible breeding	59
Probable or confirmed breeding	1,347

Figure 1. A map showing the current status of occupancy by Buzzards of 10-km squares throughout England, based on *Bird Atlas 2007–11*.

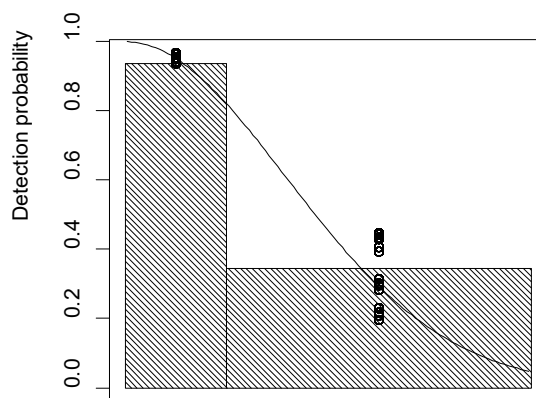


3.2 Species distribution model of Buzzard densities

3.2.1 Generating density estimates from counts

The total number of perched Buzzards detected in raw counts during 2012–16 was 5,248 and the total detected in flight was 10,808. Distance sampling, relating numbers in distance bands, produced an average detectability estimate of 0.49, indicating 49% of perched Buzzard individuals are detected within 100 m of the transect line (this number then needing to be extrapolated to the unsurveyed parts of the square, and flying birds added to produce final density). This is consistent with previous research where BBS data from 18 years were used (detection probability = 0.48, Johnston et al., 2014). There was moderate variation in detectability across habitats, with higher detectability in natural and semi-natural open habitats and human sites, intermediate detectability in farmland and lower detectability in woodland and scrubland. Variation between early and late visits was minimal.

Figure 2. The detectability function fitted to detected perched Buzzards. During the fitting of the curve detectability was permitted to vary with habitat and visit.



3.2.2 Assessing the explanatory and predictive ability of the model

The final model for current Buzzard abundance using the maximum density across years had an adjusted R-squared value of 0.19 and explained 23.4% of the model deviance. The final model for current Buzzard abundance using the mean density across years had an adjusted R-squared value of 0.17 and explained 24.4% of the model deviance.

For the maximum density model, from ten-fold cross validation the Spearman's rank correlation coefficient between observed and predicted counts was 0.503

(CI: 0.476–0.531), for the mean density model this was 0.526 (CI: 0.498 – 0.554). Both of these values may not seem high but for models of count data they actually represent a very good fit (c.f. Johnston et al., 2013; Newson et al., 2015; Border et al., 2017). To put these figures in context we also determined the correlation between maximum Buzzard counts in the same 1-km square for the period of 2012–16 and the period of 2007–11 and the mean 1-km square Buzzard counts for the same two time periods. The resulting figures of 0.453 and 0.498 respectively indicated that even within the same square over a relatively short period of time, observed Buzzard counts may show substantial fluctuation.

When comparing observed densities versus predicted densities at the 1-km square level, the predicted densities from the maximum density models are low compared to the observed maximum densities (Figure 3a & c). However, when predictions are averaged to give a 10-km level prediction, the match between predicted and observed densities improves substantially (Figure 3b & d). One of the key differences is that the observed BBS data contains some extreme densities (30–50 Buzzards per 1-km square), which skew the distribution (Figure 3, Figure 4), whereas the modelled densities follow an approximately normal distribution (see Figure 5 in the next section). The results of the mean density models and the maximum density models are relatively similar.

Figure 3. Relationships between observed densities and predicted densities at different scales. a) and b) use the predictions from the maximum density model as the response; c) and d) use the predictions from the mean density model as the response. Separate graphs are shown for the individual 1-km squares (a, c) and for values averaged over all 1-km squares in each 10-km (b, d). The red line shows the 1:1 relationship expected from a perfectly calibrated model.

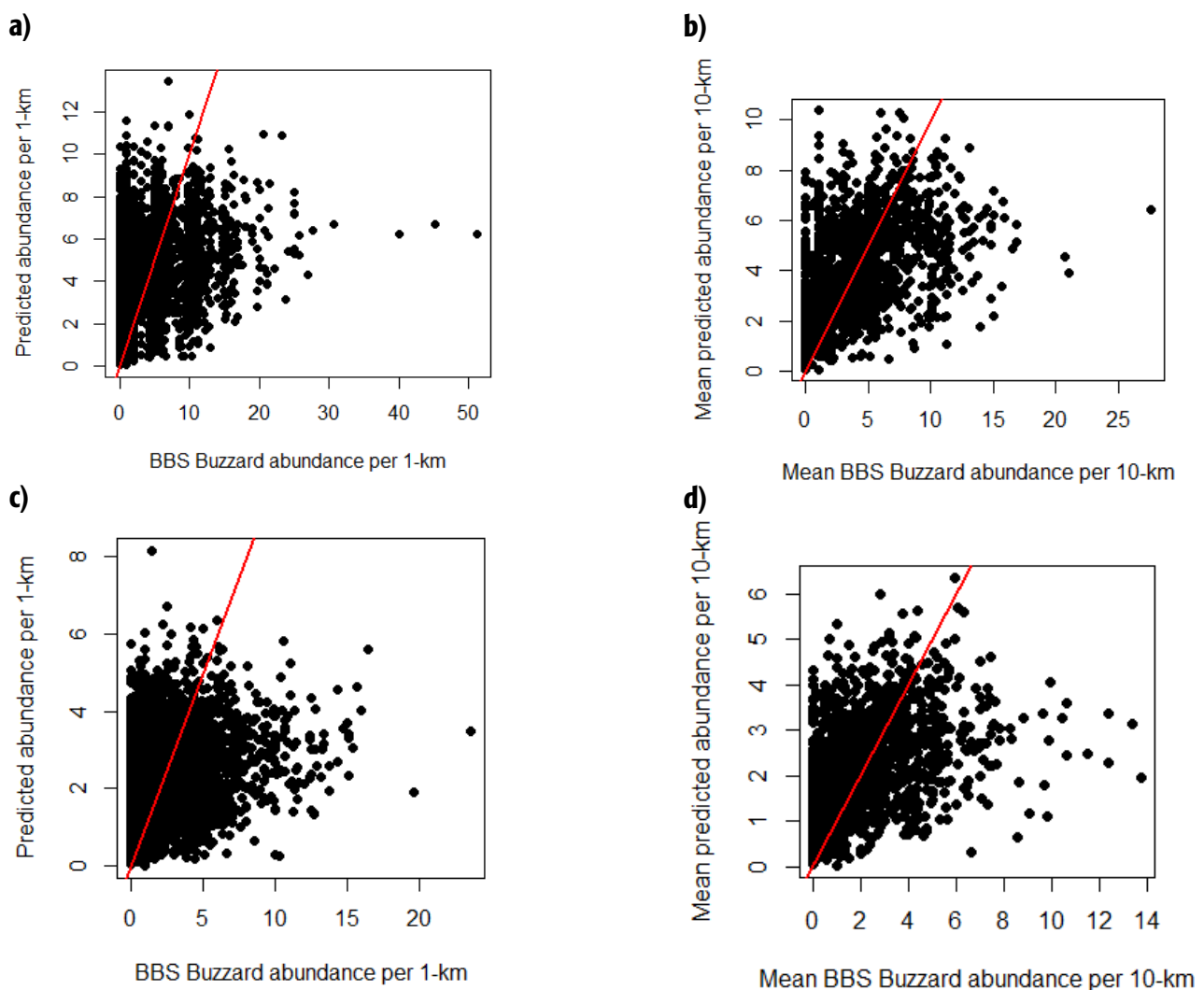
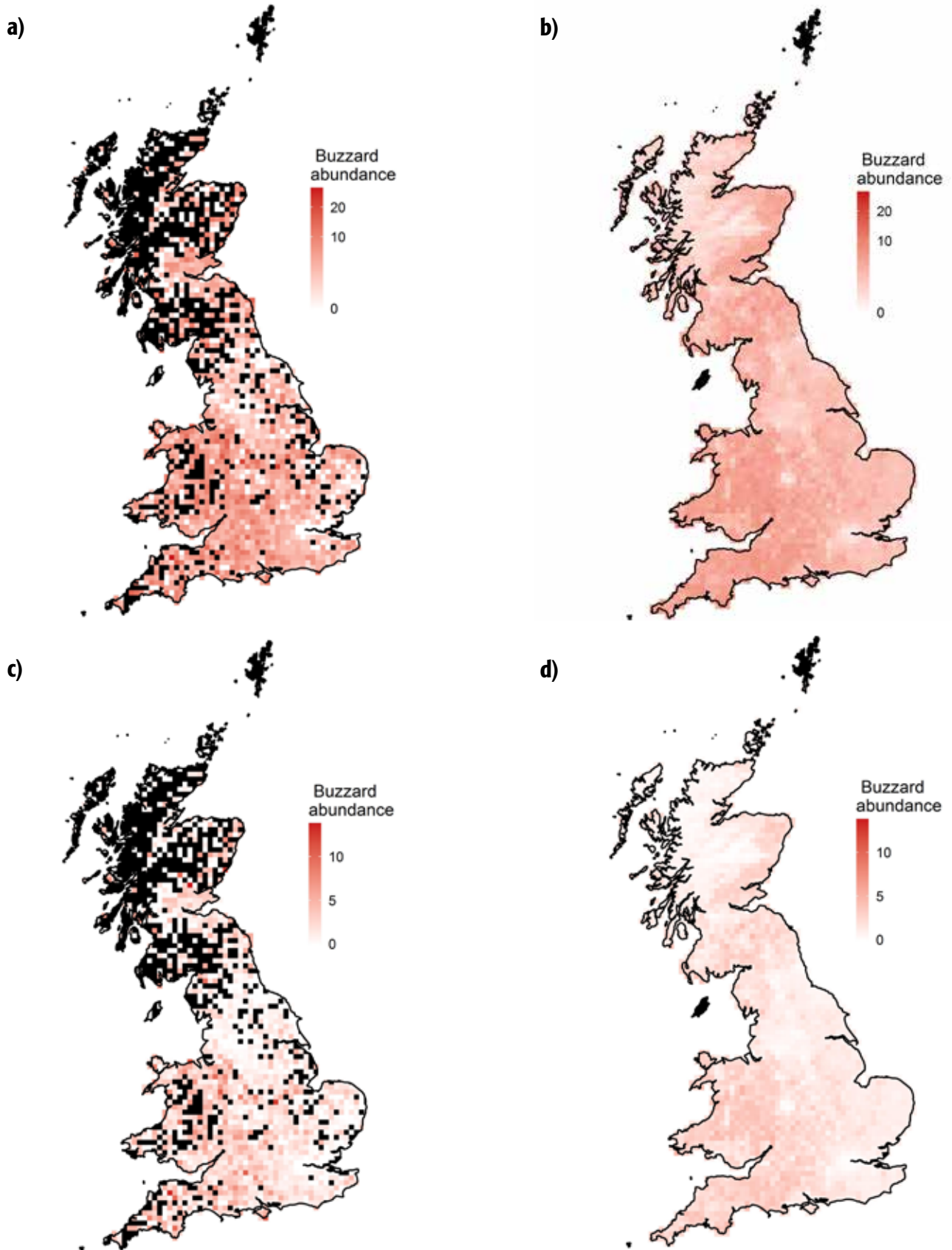


Figure 4. Maps showing a) observed maximum Buzzard density during 2012–16, b) predicted Buzzard density from the maximum density model, c) observed mean Buzzard density during 2012–16 and d) predicted Buzzard density from the mean density model. In a) and c) the observed BBS data were averaged over all 1-km BBS survey squares in each 10-km, in b) and d) the 1-km square predictions were averaged over all 1-km squares in each 10-km square. Black areas had no surveyed BBS squares during the study period or were excluded from modelling due to missing environmental data.

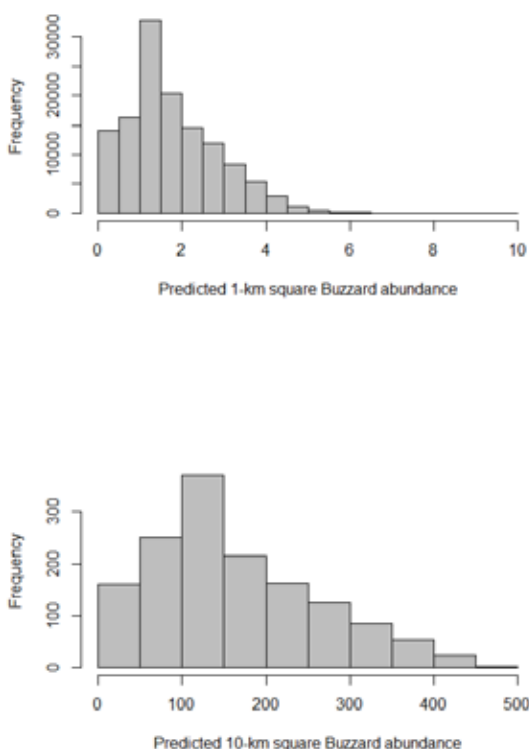


Examination of the density estimates from the maximum density model and mean density model indicated that the mean density model was more biologically realistic. Subsequent analyses use the mean density model results, with results of the maximum density model in Appendix A. Reasons for this decision are given in the Discussion.

3.2.3 Predicted abundance and importance of environmental variables

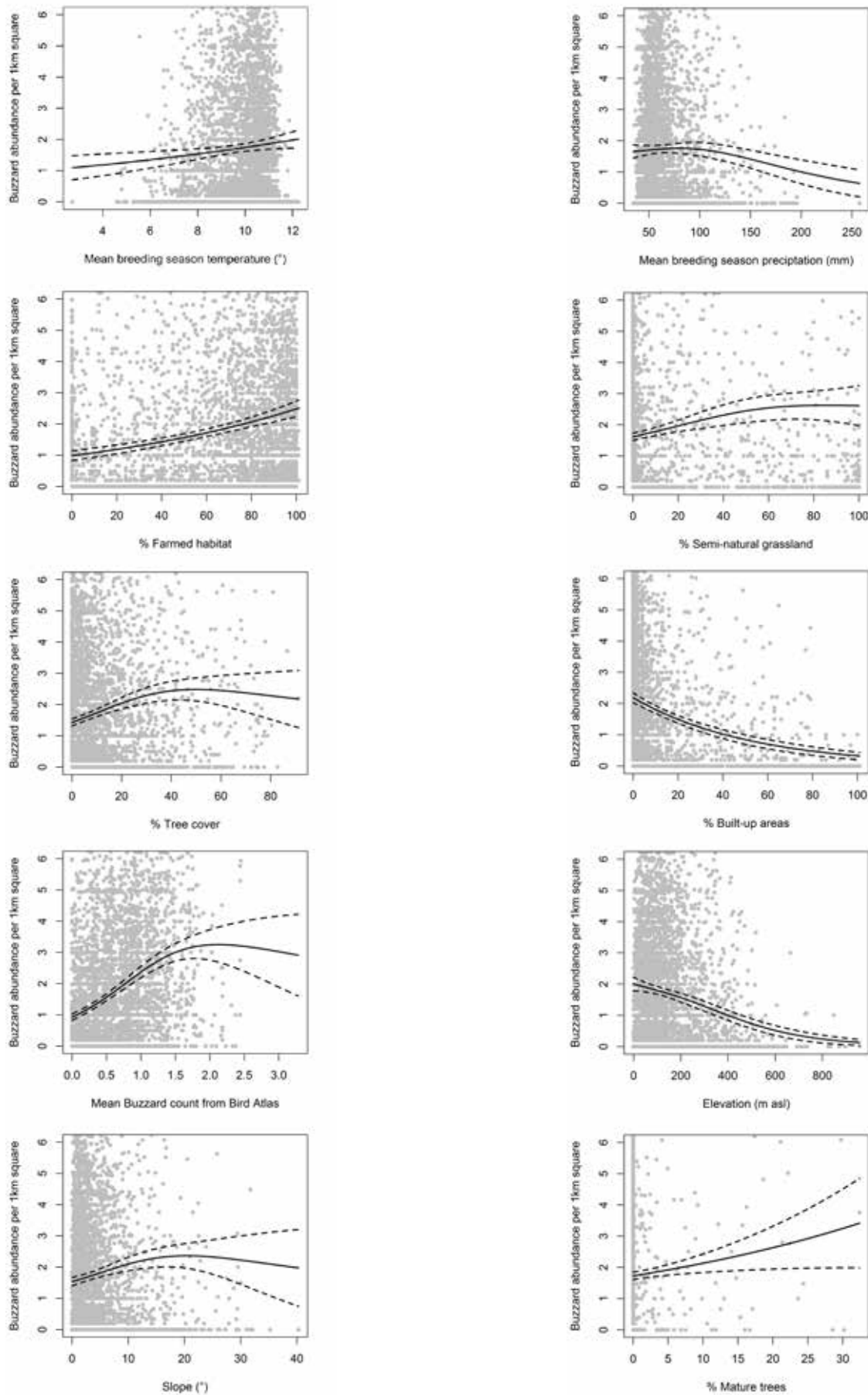
Predictions for Buzzard abundance in England (based on the mean density model) at the 1-km square level were in the range 0–10; when summed over all 1-km squares within a 10-km square predictions were in the range 0–482 (Figure 5). The predicted Buzzard abundances follow an approximately normal distribution, especially when summed over a 10-km square. Predicted Buzzard abundances for each 10-km square from the maximum density and mean density models are presented in Appendix B. In both cases these are from predictions for 1-km squares summed across all 1-km squares per 10-km.

Figure 5. Histograms of a) the predicted abundance of Buzzards in England per 1-km and b) the predicted abundance of Buzzards in England per 10-km (summed 1-km predictions), both from the mean density model.



Plots of the effect of all significant ($P < 0.05$) variables in the model are displayed in Figure 6. Buzzards were more abundant in areas with higher average breeding season temperatures and a higher percentage cover of farmland. High mean breeding season precipitation (above a monthly average of approximately 100 mm) was negatively associated with Buzzard abundance. Tree cover was positively associated with Buzzard abundance up to a point, when 40% of a 1-km square was covered in trees, further increases in tree cover did not correspond with further increases in Buzzards. Increases in the percentage of semi-natural grassland (up to 40%), and in the percentage of mature trees, were linked to small increases in Buzzard abundance. Built-up areas were negatively correlated with Buzzard abundance. There was a quadratic or possibly asymptotic effect of local mean Buzzard count from the Bird Atlas. Buzzards were most abundant at lower elevations and in areas with moderate slopes (as opposed to very flat or very mountainous areas). However, as mentioned earlier, there is a possibility that the parameter estimates for average breeding season temperature, elevation and farmed habitat may be affected by multi-collinearity and therefore these interpretations should be treated with caution. The presence and absence of Goshawks had a marginally significant positive effect on Buzzard abundance. Corvid abundance, Rabbit abundance, Brown Hare abundance and Pheasant abundance, all variables relating to food sources, were not significant ($P > 0.05$) in the model.

Figure 6. The effect of significant variables ($P < 0.05$) in final GAM model of Buzzard abundance. Buzzard abundance is modelled at the 1-km square level using the mean density model. The solid black line is the predicted effect of a variable when all other variables are set to their mean levels, the dotted black lines depict the 95% confidence interval, the grey dots are the raw data.



3.3 Suitability of currently unoccupied range for Buzzards

For the 86 10-km squares where Buzzards are either absent or present with no breeding evidence, Table 4 gives predicted total Buzzard abundances (summed 1-km abundances per 10-km). As mentioned earlier, these predictions were made from our above model but the variable, mean Buzzard count from Bird Atlas, was removed. Thirty-five of the squares do not have predictions for Buzzard abundance because data were missing for one or more of the environmental variables needed to make the prediction, usually due to very little

of the square being on land. Based on these predictions, the squares in the east of Britain which are not right on the coast seem the most suitable for Buzzards (e.g. SE,TA, TF grid references). The squares with lower predicted Buzzard abundances often had very little land or were highly urbanized (e.g. TQ38, TQ37, TQ28, TQ48, all in central London). There were also a few squares with apparently high land cover and low predicted Buzzard abundance which were predominantly estuaries or sandbanks (e.g. TQ88, TA31, TA09).

Table 4. A list of all 10-km squares where Buzzards were absent or present without breeding evidence, with the % of the square on land (as determined by LCM 2015, Rowland et al., 2015), and the total abundance of Buzzards predicted to occur in that square from the mean density model (PA). Squares without a prediction represent gaps in the coverage of the environmental variables included in the model, usually due to very little of the square being on land.

10-km	Status	Land	PA	10-km	Status	Land	PA	10-km	Status	Land	PA
NT69	present	0.62	-	SV91	present	13.03	-	TL90	present	89.05	97
NU05	absent	4.74	-	SW65	absent	0.3	-	TQ18	present	100.00	26
NU14	present	15.53	-	SW81	absent	0.28	-	TQ26	present	100.00	40
NX90	present	7.83	9	SX03	present	0.44	-	TQ27	present	100.00	27
NX93	absent	1.42	-	SY07	present	2.47	-	TQ28	present	100.00	20
NZ25	present	100.00	87	SY38	absent	0.07	-	TQ37	present	100.00	19
NZ26	present	100.00	26	SY48	present	2.94	-	TQ38	present	100.00	17
NZ38	present	14.54	0	SY66	present	1.68	-	TQ47	absent	100.00	30
NZ39	absent	1.43	-	SY87	absent	3.25	-	TQ48	present	100.00	22
NZ41	absent	100.00	71	SZ28	absent	0.15	-	TQ78	present	98.16	61
NZ44	present	44.86	30	SZ99	present	9.2	1	TQ80	absent	3.19	-
NZ45	absent	15.54	5	TA02	present	83.31	49	TQ88	present	77.68	21
NZ46	absent	5.69	-	TA09	absent	22.27	15	TQ98	present	72.37	37
NZ52	present	81.18	26	TA14	present	100.00	146	TQ99	present	95.61	184
NZ53	absent	12.57	1	TA18	present	6.00	3	TR01	present	29.96	14
NZ62	present	31.69	20	TA26	absent	5.11	1	TR07	present	11.36	1
NZ72	absent	2.43	-	TA27	present	15.02	11	TR08	absent	24.40	-
NZ90	present	63.29	52	TA31	present	49.79	12	TR09	present	69.85	45
NZ91	absent	3.44	-	TA32	present	67.05	64	TR12	absent	0.93	-
SD16	absent	15.65	0	TA33	absent	5.57	4	TR27	absent	0.31	-
SD36	absent	41.02	-	TA40	present	9.08	-	TR33	absent	0.51	-
SE01	present	100.00	131	TA41	present	13.28	1	TR37	present	10.70	0
SE02	present	100.00	124	TA42	absent	0.12	-	TR46	absent	0.36	-
SE11	present	100.00	100	TF22	present	100.00	134	TR47	absent	0.06	-
SE13	present	100.00	45	TF33	present	100.00	101	TV49	absent	5.46	0
SS14	present	4.34	-	TF34	present	100.00	106	TV69	absent	4.90	0
ST25	absent	32.09	-	TF53	absent	6.49	-				
ST26	present	1.38	-	TF56	present	75.50	66				
SV80	present	3.08	-	TF58	absent	13.77	6				
SV81	present	7.96	-	TG24	present	11.57	5				
SV90	absent	0.47	-	TG51	present	17.45	8				

3.4 Predicting Buzzard saturation densities

The published population trend for Buzzards in England shows a 194% increase during 1995–2015 (Massimino et al. 2017b) but there is substantial variation in regional trends. Figure 7 displays the trends in Buzzard abundance during 1994–2017 for each 100-km square and shows a pattern of long-term stability in the west and ongoing increases in the east. Note that 100-km squares which only contained a very small amount of land or had large numbers of zero counts, preventing trend model convergence, were combined with adjacent squares (TV+TR+TQ; SV+SW; TG+TM; SC+NX). For three 100-km squares, TA, SE and TM, the earlier year counts were zeros across all 1-km squares and this meant the trend model would not converge. Therefore for these squares we truncated the BBS data to remove the years before Buzzards colonized this region (for SE: 1994–2002 were removed, for TA: 1994–2010, for TM: 1994–2002) and fitted the trend for the remainder of the time series.

The red band on the trend graphs is the 95 % confidence interval for the predicted mean Buzzard abundance per 1-km square across the region in question from our SDM. The predictions are averaged for all 1-km squares per 100-km, so theoretically encompass squares predicted to be unoccupied as well as those predicted to be occupied. In contrast, the trend line is based only on BBS squares that reported Buzzards at least once during the time series. Consequently we might not expect the trend line and predictions to coincide. We assessed the effect of this by creating a version of Figure 7 where the density predictions were averaged across only the BBS squares used to derive the trend but results were visually identical (Appendix C).

There is a distinctive regional divide with trends from squares in western Britain tending to reach an asymptote and stay relatively stable or remain stable throughout the entire time period, whereas squares in eastern Britain show a sharp increase in recent years and have yet to reach an asymptote. The predicted Buzzard abundance varies regionally, with the highest abundances predicted in the south-west and the lowest in the east. Generally, the modelled predictions from the maximum density model were higher than the observed trends (Appendix A) whereas those from the mean density model coincided with the observed trend better (Figure 7). In some eastern areas the trajectory of the trend suggests densities could increase beyond our predicted saturation densities based on either model.

From this study, using the mean density model, we predicted mean densities of 161 Buzzards per 10-km square (across the whole of England), and maximum densities of 482 Buzzards per 10-km square. The mean densities predicted by this model are within the range of the recorded densities in the literature, though at the high end (Table 5).

Figure 7. Map showing how population trends (blue line and shading) and modelled saturation densities (red line and shading) vary by 100-km square across England. Trends, which are all plotted to the same x-axis scale (1994–2017) and y-axis scale (0–7 birds km²) are based on a simple model of annual Buzzard densities in BBS squares with 95% confidence limits shown by blue shading. Saturation densities are from the species distribution model using the mean density across years per square and are averaged over all 1-km squares within the 100-km square.

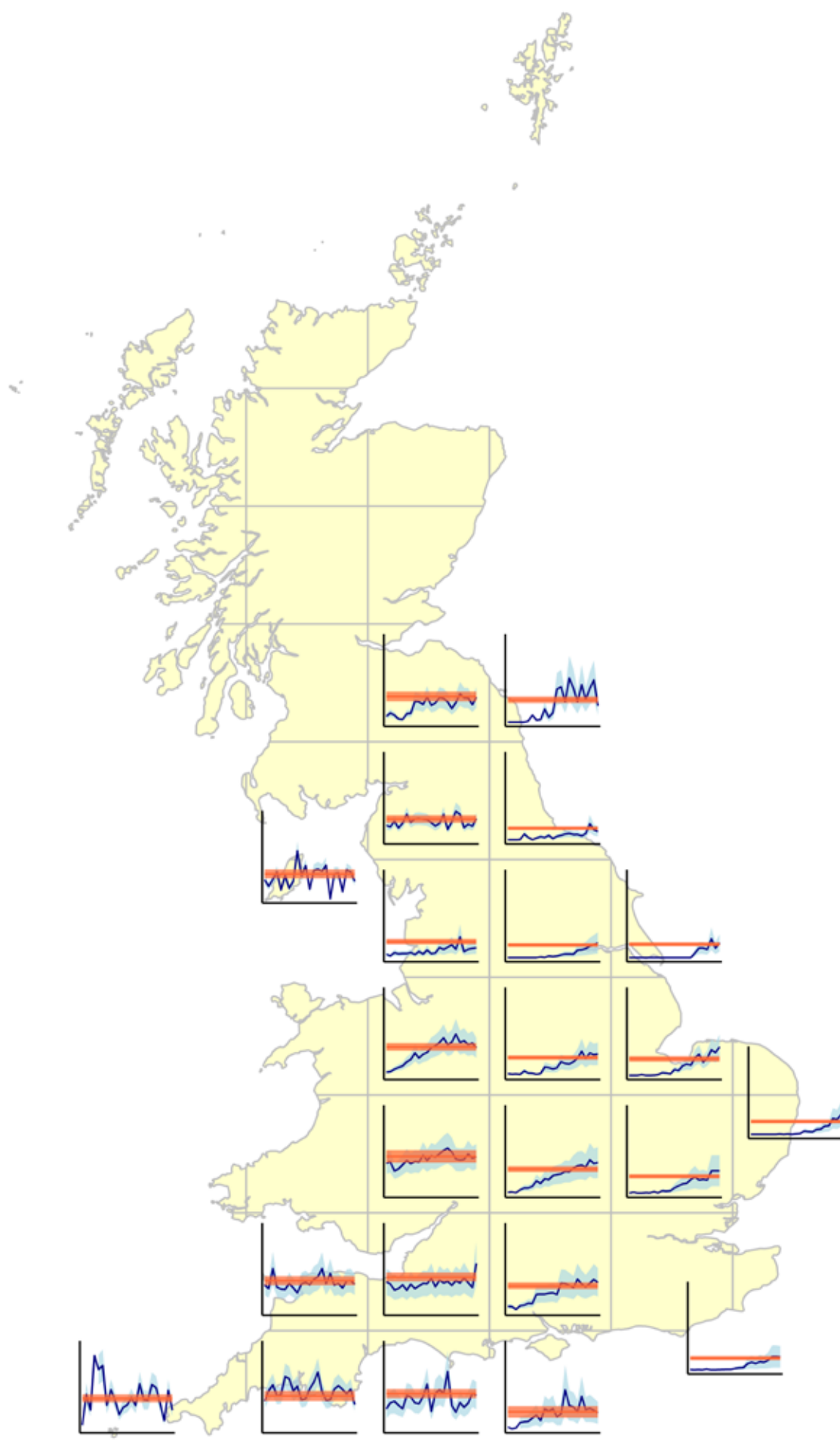


Table 5. Buzzard densities from published population studies. Rows with an asterisk are taken from a review by Clements (2002). Densities were converted into individuals per 10-km square, applying a factor of 2 to densities reported in pairs.

Region	Study period	Density per 10-km square	Study
West Midlands(SO37/SO77)	1994–96	44 and 162	Sim et al., 2001
Whole of Britain	2001	0–120	Clements, 2002
North Somerset (75 km ²)	2001	222	*Prytherch, 1997/verbally
Bath & North Somerset (60 km ²)	2001	156	*J. Holmes (verbally) (Clements, 2002)
Dorset (120km ²)	1996	197–200	*Kenward et al., 2000
Postbridge, Devon (33 km ²)	1990–93	96–102	*Dare, 1998
Devon (2,620 km ²)	1983	50–66	*Sitters, 1988
Cambrian Mountains (475 km ²) farmland	1975–79	82	*Newton et al., 1982
Cambrian Mountains (475 km ²) upland	1975–79	48	*Newton et al., 1982
Snowdonia (926 km ²)	1977–84	11.9–66.7	Dare & Barry, 1990
Migneint-Hiraethog (440 km ²)	1977–84	28.1–59.7	Dare & Barry, 1990
Snowdonia (926 km ²)	1977–84	20–22	*Dare, 1995
Snowdonia (926 km ²)	2000	28–30	*Dare, 1995
Denbigh, Clwyd (440 km ²)	1977–84	28	*Dare, 1995
Upper Strathspey (94 km ²)	1971	28–30	*Halley, 1993
Upper Strathspey (94 km ²)	1988–89	46–48	*Halley, 1993
Whole of Britain	1983	4.5–36	Taylor et al., 1988
Whole of Britain	1954	For mean densities: an average of 11, maximum of 47.9, for maximum densities: average of 116	Moore, 1957
North Eastern Romania	2010–11	33.4–53.9	Baltag et al., 2013
Bulgaria	2006	34	Nikolvo et al., 2006
Poland	1993–2000	70–212	Wuczynski, 2003

4. DISCUSSION

Buzzards are currently breeding or likely to be breeding across the vast majority of 10-km squares in the UK. Unoccupied squares are mainly restricted to coastal areas or city centres where the habitat is unsuitable. However, our model did predict potential high Buzzard abundances for some squares in the east. This suggests that Buzzards are still expanding their range eastward. Our trend plots confirm this conclusion; trends in the east show no sign of plateauing yet. However, eastern population densities are currently still lower than western densities which stabilised prior to the onset of the BBS time series.

We extracted two metrics to summarise BBS data across years – the mean density per square and the

maximum density per square. Models using these metrics performed equally well in a statistical sense but we judged the maximum density model to overestimate densities in currently stable areas and to exceed published estimates to a biologically unrealistic degree (Appendix A Figure 1). As evident from the yearly trends here and our comparison of Buzzard counts between two 5-year periods, Buzzard densities may show substantial fluctuation from year to year. It is likely the maximum density model predictions are generally higher than the local trend because the SDM was trained on the maximum density in each square over a 5-year period whereas the trend production essentially generates an average density per square. For bird species with home ranges less than 1-km square, selecting the maximum count would compensate for failures in detection. However, Buzzards have a large

range size (on average 180–190 ha, Sim et al., 2001). There may be several 1-km squares on the edge of a Buzzard's range and it is impossible to predict which one the Buzzard may be occupying when the survey is undertaken. Selecting the maximum density of Buzzards over a 5 year period predisposes the selection towards extreme outlier counts (Figures 3 & 4) which may be the result of Buzzards passing through a square, or due to territorial disputes at territory boundaries, and are unlikely to reflect true breeding densities.

Our modelled results matched actual Buzzard abundances recorded from BBS (during 2012–16) reasonably well, especially when averaged over each 10-km square. There was a tendency for high outlier densities from the BBS survey data (Figure 3). These densities could be inflated by Buzzards passing through a square, or due to territorial disputes at territory boundaries so may not reflect true breeding densities. Further information on territory sizes would help in understanding any likely errors here. Compared to the literature our density estimates were at the high end of recorded ranges. However, the densities estimates from the literature for Britain are all at least 17 years old. Although many come from western areas which may have been stable over this period, those applying to the whole of Britain are likely to be out dated. But they can at the least give us confidence that the modelled predictions are not too low. A potential issue with our SDM is the predicted counts for eastern England. Buzzards are still colonising and expanding in this area so while our model accurately represents current densities it is likely to underestimate future densities. One option to deal with this is to train models using data from stable areas but for this to work they would need to mirror conditions in the east in all ways except for the pattern of colonisation history. In reality, it is unlikely that many areas of comparable low-lying arable land exist in western Britain for training a model to make predictions in eastern England.

In terms of relevant habitat characteristics to consider when attempting to match squares in the west and east, our model here suggests important variables are tree cover, farmed area, urban area, climate and topography. The variables included in the model to represent prey sources were not significant. Findings from other studies (Austin & Houston, 1997; Rooney & Montgomery, 2013) indicate that Buzzards are opportunist and will prey on whatever is available, from Rabbits, invertebrates and amphibians to other birds and carrion. Therefore, it is perhaps not so surprising that we failed to find a strong relationship between Buzzard abundance and

individual food sources, as favoured food sources may vary substantially depending on what is locally available. Some of the variables likely to influence Buzzard abundance according to our literature review could not be included in models owing to a lack of suitable spatially referenced data. The most notable omission is human disturbance (Krüger, 2004). Therefore the amount of human disturbance in an area should also be considered in relation to our density estimates. The other variables we could not acquire data for were for prey items and as discussed above, this varies too widely from region to region to be a good predictor of Buzzard densities on a national scale so is unlikely to have affected conclusions.

The trends and density predictions produced here relate to numbers of birds in the breeding season. Counts in the breeding season may comprise a combination of breeding and non-breeding individuals but the data do not allow us to differentiate. Densities post breeding could be substantially higher once birds of the year have fledged. Densities may also vary spatially as birds disperse from breeding territories and potentially shift to habitats providing food in winter. Therefore the densities discussed here may bear little relationship to densities observed outside the breeding season.

4.1 Recommendations

We can be confident that the breeding range of the Buzzard has almost fully extended to all suitable 10-km squares, with only a few unoccupied squares capable of sustaining significant new populations. The species distribution models developed here are as good as we can currently hope to produce, being based on a large sample of high quality bird data and most of the key environmental variables. In a statistical sense, the models have reasonable predictive performance but predictions are high compared to published densities. We recommend using the predictions based on the mean density model to avoid over-estimating Buzzard abundance. However, the match between predictions and population trends varies regionally and it is likely predicted densities for eastern regions, where the Buzzard population is still increasing, are underestimates. Further modelling, using information from areas of stability, could help to inform use of densities in areas where populations are still increasing. Ultimately, the most robust estimates of density will likely come from mechanistic models that incorporate vital demographic rates, including productivity, survival, dispersal and density dependence.

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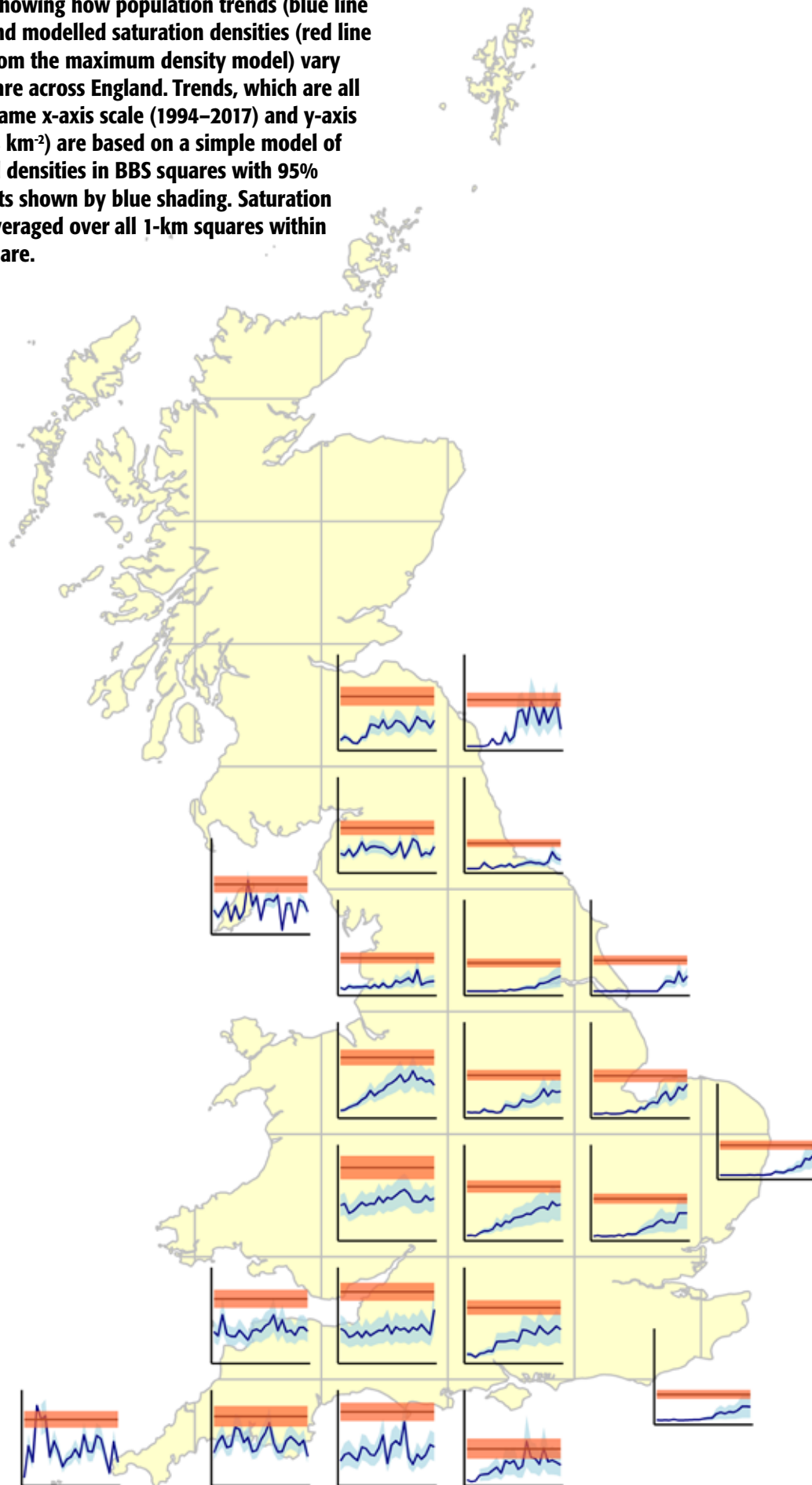
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APPENDIX A

Table 1. A list of all 10-km squares where Buzzards were absent or present without breeding evidence, with the % of the square on land (as determined by LCM 2015, Rowland et al., 2017), and the total abundance of Buzzards predicted to occur in that square based on the maximum density model (PA). Squares without a prediction represent gaps in the coverage of the environmental variables included in the model, usually due to very little of the square being on land.

10-km	Status	Land	PA	10-km	Status	Land	PA	10-km	Status	Land	PA
NT69	present	0.62	-	SV91	present	13.03	-	TL90	present	89.05	207
NU05	absent	4.74	-	SW65	absent	0.30	-	TQ18	present	100.00	70
NU14	present	15.53	-	SW81	absent	0.28	-	TQ26	present	100.00	97
NX90	present	7.83	17	SX03	present	0.44	-	TQ27	present	100.00	70
NX93	absent	1.42	-	SY07	present	2.47	-	TQ28	present	100.00	53
NZ25	present	100.00	189	SY38	absent	0.07	-	TQ37	present	100.00	51
NZ26	present	100.00	67	SY48	present	2.94	-	TQ38	present	100.00	46
NZ38	present	14.54	1	SY66	present	1.68	-	TQ47	absent	100.00	79
NZ39	absent	1.43	-	SY87	absent	3.25	-	TQ48	present	100.00	62
NZ41	absent	100.00	164	SZ28	absent	0.15	-	TQ78	present	98.16	130
NZ44	present	44.86	68	SZ99	present	9.20	3	TQ80	absent	3.19	-
NZ45	absent	15.54	10	TA02	present	83.31	118	TQ88	present	77.68	54
NZ46	absent	5.69	-	TA09	absent	22.27	35	TQ98	present	72.37	83
NZ52	present	81.18	65	TA14	present	100.00	321	TQ99	present	95.61	353
NZ53	absent	12.57	3	TA18	present	6.00	7	TR01	present	29.96	31
NZ62	present	31.69	47	TA26	absent	5.11	2	TR07	present	11.36	1
NZ72	absent	2.43	-	TA27	present	15.02	25	TR08	absent	24.40	-
NZ90	present	63.29	108	TA31	present	49.79	30	TR09	present	69.85	87
NZ91	absent	3.44	-	TA32	present	67.05	150	TR12	absent	0.93	-
SD16	absent	15.65	0	TA33	absent	5.57	8	TR27	absent	0.31	-
SD36	absent	41.02	-	TA40	present	9.08	-	TR33	absent	0.51	-
SE01	present	100.00	258	TA41	present	13.28	2	TR37	present	10.70	1
SE02	present	100.00	246	TA42	absent	0.12	-	TR46	absent	0.36	-
SE11	present	100.00	213	TF22	present	100.00	301	TR47	absent	0.06	-
SE13	present	100.00	107	TF33	present	100.00	234	TV49	absent	5.46	1
SS14	present	4.34	-	TF34	present	100.00	255	TV69	absent	4.90	1
ST25	absent	32.09	-	TF53	absent	6.49	-				
ST26	present	1.38	-	TF56	present	75.50	161				
SV80	present	3.08	-	TF58	absent	13.77	15				
SV81	present	7.96	-	TG24	present	11.57	13				
SV90	absent	0.47	-	TG51	present	17.45	19				

Figure 1. Map showing how population trends (blue line and shading) and modelled saturation densities (red line and shading, from the maximum density model) vary by 100-km square across England. Trends, which are all plotted to the same x-axis scale (1994–2017) and y-axis scale (0–7 birds km⁻²) are based on a simple model of annual Buzzard densities in BBS squares with 95% confidence limits shown by blue shading. Saturation densities are averaged over all 1-km squares within the 100-km square.



APPENDIX B

Table 1. Spreadsheet with predicted number of Buzzards per 10-km square in England from the maximum density model (A) and the mean density model (B).

10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B
NT60	179	86	NY24	400	203	NY77	273	135	NZ24	175	78	SD33	200	93
NT70	369	191	NY25	312	149	NY78	318	164	NZ25	129	56	SD34	101	45
NT71	563	305	NY26	209	103	NY79	258	132	NZ26	45	18	SD37	78	36
NT73	348	172	NY30	273	171	NY80	93	43	NZ27	179	81	SD38	397	209
NT80	487	268	NY31	180	121	NY81	166	81	NZ28	183	82	SD39	200	108
NT81	329	166	NY32	356	201	NY82	69	31	NZ29	227	108	SD40	256	122
NT82	631	337	NY33	315	166	NY83	107	47	NZ30	255	121	SD41	491	238
NT83	598	328	NY34	351	174	NY84	90	40	NZ31	226	105	SD42	284	127
NT84	442	227	NY35	290	134	NY85	168	79	NZ32	218	103	SD43	349	162
NT90	374	192	NY36	232	110	NY86	444	226	NZ33	193	90	SD44	437	210
NT91	317	166	NY37	532	292	NY87	304	153	NZ34	185	86	SD45	178	82
NT92	365	190	NY40	315	193	NY88	327	177	NZ35	97	41	SD46	118	53
NT93	533	274	NY41	238	145	NY89	536	286	NZ36	65	27	SD47	115	55
NT94	507	263	NY42	447	242	NY90	81	38	NZ37	50	21	SD48	295	144
NT95	292	145	NY43	365	186	NY91	123	58	NZ38	1	1	SD49	360	180
NU00	249	121	NY44	353	178	NY92	211	102	NZ40	231	110	SD50	188	83
NU01	464	239	NY45	451	220	NY93	150	72	NZ41	124	53	SD51	287	129
NU02	360	182	NY46	587	311	NY94	178	83	NZ42	171	77	SD52	162	67
NU03	517	262	NY47	498	258	NY95	195	93	NZ43	160	73	SD53	243	110
NU04	170	84	NY48	438	241	NY96	253	124	NZ44	48	20	SD54	269	125
NU10	333	162	NY50	410	237	NY97	381	193	NZ45	7	3	SD55	224	110
NU11	424	220	NY51	443	250	NY98	411	218	NZ50	172	81	SD56	431	213
NU12	394	198	NY52	382	191	NY99	413	220	NZ51	144	63	SD57	663	370
NU13	184	87	NY53	433	227	NZ00	353	179	NZ52	52	20	SD58	422	211
NU20	167	79	NY54	279	137	NZ01	212	102	NZ53	3	1	SD59	344	173
NU21	176	87	NY55	464	244	NZ02	193	93	NZ60	107	51	SD60	168	71
NU22	108	51	NY56	487	255	NZ03	181	87	NZ61	141	64	SD61	169	79
NU23	9	4	NY57	480	258	NZ04	138	66	NZ62	34	14	SD62	164	74
NX90	9	4	NY58	228	113	NZ05	220	104	NZ70	164	81	SD63	231	107
NX91	84	38	NY59	411	220	NZ06	321	155	NZ71	138	64	SD64	240	116
NX92	25	11	NY60	363	199	NZ07	288	146	NZ80	198	92	SD65	184	96
NY00	307	157	NY61	376	194	NZ08	229	112	NZ81	59	26	SD66	334	168
NY01	299	156	NY62	530	287	NZ09	362	185	NZ90	85	40	SD67	328	164
NY02	569	306	NY63	250	128	NZ10	433	224	SD08	17	8	SD68	397	213
NY03	212	102	NY64	156	76	NZ11	297	146	SD09	60	29	SD69	404	227
NY04	48	23	NY65	234	118	NZ12	213	103	SD16	0	0	SD70	102	41
NY10	251	160	NY66	372	189	NZ13	198	94	SD17	7	3	SD71	150	71
NY11	170	110	NY67	289	143	NZ14	189	91	SD18	431	246	SD72	156	71
NY12	357	200	NY68	155	75	NZ15	144	64	SD19	411	235	SD73	207	96
NY13	342	172	NY69	217	110	NZ16	169	77	SD20	10	4	SD74	232	111
NY14	393	193	NY70	330	169	NZ17	402	196	SD26	23	11	SD75	236	116
NY15	120	56	NY71	323	163	NZ18	276	134	SD27	282	133	SD76	259	129
NY16	169	85	NY72	155	79	NZ19	323	158	SD28	560	308	SD77	248	132
NY20	106	83	NY73	48	20	NZ20	223	104	SD29	524	362	SD78	195	104
NY21	150	104	NY74	161	74	NZ21	218	103	SD30	326	151	SD79	222	117
NY22	231	129	NY75	197	91	NZ22	166	77	SD31	277	132	SD80	84	34
NY23	347	184	NY76	303	150	NZ23	183	84	SD32	60	27	SD81	123	57

10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B
SD82	174	83	SE29	232	110	SE76	320	154	SJ45	513	261	SJ92	323	153
SD83	151	71	SE30	138	58	SE77	248	118	SJ46	415	199	SJ93	325	161
SD84	223	107	SE31	200	89	SE78	228	109	SJ47	456	241	SJ94	158	73
SD85	360	181	SE32	131	55	SE79	144	69	SJ48	161	71	SJ95	314	152
SD86	212	107	SE33	104	46	SE80	477	225	SJ49	317	152	SJ96	335	169
SD87	197	101	SE34	269	139	SE81	219	98	SJ50	644	363	SJ97	248	123
SD88	228	120	SE35	253	119	SE82	202	91	SJ51	516	267	SJ98	215	100
SD89	151	74	SE36	460	224	SE83	293	134	SJ52	575	308	SJ99	104	44
SD90	99	43	SE37	304	145	SE84	281	126	SJ53	522	273	SK00	199	92
SD91	120	56	SE38	230	109	SE85	399	194	SJ54	640	364	SK01	262	123
SD92	139	67	SE39	228	110	SE86	320	151	SJ55	634	347	SK02	426	212
SD93	115	54	SE40	183	81	SE87	322	154	SJ56	543	274	SK03	505	259
SD94	206	97	SE41	203	90	SE88	206	96	SJ57	569	296	SK04	282	137
SD95	252	122	SE42	151	64	SE89	143	68	SJ58	158	69	SK05	338	170
SD96	265	137	SE43	296	141	SE90	257	118	SJ59	242	108	SK06	231	112
SD97	210	108	SE44	259	120	SE91	311	152	SJ60	425	222	SK07	248	122
SD98	205	101	SE45	302	147	SE92	138	61	SJ61	519	291	SK08	218	104
SD99	176	85	SE46	272	129	SE93	327	155	SJ62	593	316	SK09	126	59
SE00	88	42	SE47	261	125	SE94	305	142	SJ63	595	323	SK10	382	190
SE01	136	63	SE48	208	98	SE95	264	120	SJ64	622	334	SK11	300	143
SE02	133	61	SE49	202	95	SE96	343	167	SJ65	511	260	SK12	420	209
SE03	135	60	SE50	202	90	SE97	256	120	SJ66	573	297	SK13	642	353
SE04	158	73	SE51	308	143	SE98	282	109	SJ67	467	223	SK14	449	225
SE05	221	108	SE52	236	105	SE99	162	77	SJ68	385	184	SK15	304	154
SE06	144	69	SE53	255	117	SJ18	41	20	SJ69	408	193	SK16	273	136
SE07	98	46	SE54	261	123	SJ20	510	268	SJ70	460	237	SK17	263	132
SE08	233	116	SE55	204	94	SJ21	629	340	SJ71	550	331	SK18	229	114
SE09	204	100	SE56	266	126	SJ22	628	350	SJ72	622	338	SK19	138	65
SE10	173	82	SE57	224	104	SJ23	471	250	SJ73	505	270	SK20	303	144
SE11	119	51	SE58	178	85	SJ27	92	43	SJ74	424	211	SK21	467	237
SE12	128	53	SE59	137	67	SJ28	116	50	SJ75	519	263	SK22	255	116
SE13	67	27	SE60	265	118	SJ29	9	3	SJ76	398	189	SK23	511	253
SE14	153	70	SE61	271	122	SJ30	533	284	SJ77	560	278	SK24	400	195
SE15	178	87	SE62	314	144	SJ31	600	323	SJ78	485	238	SK25	253	121
SE16	148	71	SE63	233	106	SJ32	632	342	SJ79	204	93	SK26	306	141
SE17	155	75	SE64	300	137	SJ33	517	266	SJ80	444	226	SK27	338	168
SE18	202	95	SE65	181	79	SJ34	387	187	SJ81	524	284	SK28	197	93
SE19	287	142	SE66	258	120	SJ35	530	271	SJ82	580	302	SK29	139	65
SE20	202	95	SE67	285	139	SJ36	361	169	SJ83	564	302	SK30	507	263
SE21	185	85	SE68	246	117	SJ37	469	232	SJ84	113	50	SK31	441	223
SE22	94	38	SE69	143	69	SJ38	65	28	SJ85	221	100	SK32	363	171
SE23	90	38	SE70	269	124	SJ39	34	13	SJ86	513	263	SK33	115	49
SE24	233	110	SE71	223	104	SJ40	601	343	SJ87	512	253	SK34	399	190
SE25	235	113	SE72	216	98	SJ41	466	241	SJ88	134	57	SK35	385	182
SE26	252	121	SE73	246	119	SJ42	486	252	SJ89	41	17	SK36	265	126
SE27	275	134	SE74	247	118	SJ43	466	239	SJ90	289	141	SK37	146	64
SE28	215	101	SE75	261	123	SJ44	640	341	SJ91	392	196	SK38	64	27

APPENDIX B (CONT)

Table 1. (continued). Spreadsheet with predicted number of Buzzards per 10-km square in England from the maximum density model (A) and the mean density model (B).

10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B
SK39	133	58	SK86	343	157	SO56	601	322	SP03	523	267	SP50	217	97
SK40	384	187	SK87	305	140	SO57	580	311	SP04	385	181	SP51	550	281
SK41	265	124	SK88	284	130	SO58	595	332	SP05	498	247	SP52	450	232
SK42	418	198	SK89	283	132	SO59	527	292	SP06	376	183	SP53	502	263
SK43	216	98	SK90	383	184	SO60	300	142	SP07	191	89	SP54	510	263
SK44	193	85	SK91	389	189	SO61	302	153	SP08	32	13	SP55	373	183
SK45	176	77	SK92	446	220	SO62	739	401	SP09	97	43	SP56	414	207
SK46	217	98	SK93	459	228	SO63	784	417	SP10	602	336	SP57	262	121
SK47	195	86	SK94	446	216	SO64	730	385	SP11	556	299	SP58	584	325
SK48	158	68	SK95	380	177	SO65	640	364	SP12	462	241	SP59	267	125
SK49	137	59	SK96	293	131	SO66	611	327	SP13	580	300	SP60	518	257
SK50	168	74	SK97	203	101	SO67	618	346	SP14	684	390	SP61	449	218
SK51	287	131	SK98	269	122	SO68	568	315	SP15	413	204	SP62	406	223
SK52	339	157	SK99	304	139	SO69	510	272	SP16	513	258	SP63	416	210
SK53	254	117	SO17	592	377	SO70	575	307	SP17	367	182	SP64	271	130
SK54	92	40	SO18	530	364	SO71	760	394	SP18	64	27	SP65	433	213
SK55	242	111	SO22	355	195	SO72	855	482	SP19	166	79	SP66	559	285
SK56	200	91	SO23	442	232	SO73	692	403	SP20	434	217	SP67	415	210
SK57	493	262	SO24	674	397	SO74	512	260	SP21	506	252	SP68	294	142
SK58	288	137	SO25	594	340	SO75	686	365	SP22	387	190	SP69	332	159
SK59	253	115	SO26	556	393	SO76	648	365	SP23	553	281	SP70	332	160
SK60	198	93	SO27	417	340	SO77	520	268	SP24	490	243	SP71	414	203
SK61	378	179	SO28	671	417	SO78	558	298	SP25	659	372	SP72	349	172
SK62	296	141	SO29	666	414	SO79	603	337	SP26	402	195	SP73	476	239
SK63	259	119	SO32	609	335	SO80	390	189	SP27	415	206	SP74	457	226
SK64	287	130	SO33	703	394	SO81	360	176	SP28	529	269	SP75	345	164
SK65	354	171	SO34	517	273	SO82	602	300	SP29	432	213	SP76	218	100
SK66	476	233	SO35	636	365	SO83	489	240	SP30	564	293	SP77	482	239
SK67	437	208	SO36	666	396	SO84	740	404	SP31	273	128	SP78	274	133
SK68	469	226	SO37	705	408	SO85	429	204	SP32	417	213	SP79	373	181
SK69	319	145	SO38	667	409	SO86	603	316	SP33	441	223	SP80	231	108
SK70	374	188	SO39	676	383	SO87	276	129	SP34	541	278	SP81	287	136
SK71	261	125	SO41	675	360	SO88	354	176	SP35	464	233	SP82	453	221
SK72	324	156	SO42	670	399	SO89	384	192	SP36	433	215	SP83	148	66
SK73	328	154	SO43	617	332	SO90	465	249	SP37	267	127	SP84	389	190
SK74	423	202	SO44	578	308	SO91	496	261	SP38	244	112	SP85	555	292
SK75	363	168	SO45	638	378	SO92	376	185	SP39	395	196	SP86	357	171
SK76	370	173	SO46	736	414	SO93	605	310	SP40	421	206	SP87	303	142
SK77	341	159	SO47	685	402	SO94	580	294	SP41	344	166	SP88	236	110
SK78	351	165	SO48	683	384	SO95	442	218	SP42	586	308	SP89	327	156
SK79	354	165	SO49	456	249	SO96	508	249	SP43	541	276	SP90	284	133
SK80	254	121	SO50	411	214	SO97	317	153	SP44	355	177	SP91	401	197
SK81	420	205	SO51	429	215	SO98	82	36	SP45	528	272	SP92	341	162
SK82	357	172	SO52	720	409	SO99	39	16	SP46	425	207	SP93	362	174
SK83	294	134	SO53	517	267	SP00	566	310	SP47	272	130	SP94	509	255
SK84	505	244	SO54	752	433	SP01	489	256	SP48	402	198	SP95	443	215
SK85	294	136	SO55	570	312	SP02	537	290	SP49	329	157	SP96	282	129

10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B
SP97	269	123	ST13	628	356	ST73	385	199	SU20	307	153	SU67	255	119
SP98	293	140	ST14	261	161	ST74	398	200	SU21	255	123	SU68	334	162
SP99	461	234	ST16	20	9	ST75	583	301	SU22	471	228	SU69	438	221
SS20	481	240	ST20	517	270	ST76	452	225	SU23	705	395	SU70	134	59
SS21	316	158	ST21	558	304	ST77	644	355	SU24	626	332	SU71	511	257
SS22	202	101	ST22	569	291	ST78	357	177	SU25	546	289	SU72	358	171
SS30	508	263	ST23	665	357	ST79	499	251	SU26	436	228	SU73	357	173
SS31	437	226	ST24	196	97	ST80	554	296	SU27	558	363	SU74	407	205
SS32	130	64	ST30	586	301	ST81	571	303	SU28	637	363	SU75	306	144
SS40	423	213	ST31	717	383	ST82	522	274	SU29	393	197	SU76	384	183
SS41	464	235	ST32	735	383	ST83	640	350	SU30	236	110	SU77	209	92
SS42	549	278	ST33	729	383	ST84	390	196	SU31	248	111	SU78	431	213
SS43	129	61	ST34	620	321	ST85	447	220	SU32	500	247	SU79	457	230
SS44	111	55	ST35	449	221	ST86	606	322	SU33	416	206	SU80	350	177
SS50	643	340	ST36	136	63	ST87	489	252	SU34	339	160	SU81	393	190
SS51	388	186	ST40	718	408	ST88	480	247	SU35	619	333	SU82	256	117
SS52	476	236	ST41	746	400	ST89	594	316	SU36	462	234	SU83	153	69
SS53	578	303	ST42	683	357	ST90	720	398	SU37	552	308	SU84	177	79
SS54	353	183	ST43	695	368	ST91	659	359	SU38	523	275	SU85	82	35
SS60	509	263	ST44	686	362	ST92	621	336	SU39	478	239	SU86	95	41
SS61	568	297	ST45	477	244	ST93	573	304	SU40	139	60	SU87	403	189
SS62	573	290	ST46	498	247	ST94	742	427	SU41	107	44	SU88	370	172
SS63	584	321	ST47	268	138	ST95	667	364	SU42	333	155	SU89	299	139
SS64	421	235	ST48	213	104	ST96	388	191	SU43	552	281	SU90	373	172
SS70	477	245	ST50	516	273	ST97	361	178	SU44	437	215	SU91	388	196
SS71	576	377	ST51	466	237	ST98	618	322	SU45	639	348	SU92	369	179
SS72	655	362	ST52	705	375	ST99	423	216	SU46	287	134	SU93	294	142
SS73	451	242	ST53	552	283	SU00	492	251	SU47	506	276	SU94	233	106
SS74	421	232	ST54	552	284	SU01	554	281	SU48	547	289	SU95	138	60
SS80	645	347	ST55	436	227	SU02	718	419	SU49	357	173	SU96	163	69
SS81	478	251	ST56	489	252	SU03	656	356	SU50	122	52	SU97	239	105
SS82	417	217	ST57	145	65	SU04	699	393	SU51	451	215	SU98	251	113
SS83	490	256	ST58	273	133	SU05	608	341	SU52	534	274	SU99	227	106
SS84	266	136	ST59	338	170	SU06	480	250	SU53	514	257	SW32	156	81
SS90	756	422	ST60	611	327	SU07	463	240	SU54	429	215	SW33	81	41
SS91	583	311	ST61	610	327	SU08	380	190	SU55	619	338	SW42	185	91
SS92	501	262	ST62	676	373	SU09	493	252	SU56	397	193	SW43	448	245
SS93	537	296	ST63	730	425	SU10	313	145	SU57	560	298	SW52	34	16
SS94	357	194	ST64	573	320	SU11	426	209	SU58	582	309	SW53	541	295
ST00	562	289	ST65	543	284	SU12	539	269	SU59	348	165	SW54	18	8
ST01	659	360	ST66	471	232	SU13	629	355	SU60	103	45	SW61	34	16
ST02	560	296	ST67	157	69	SU14	597	325	SU61	448	219	SW62	390	201
ST03	573	310	ST68	512	258	SU15	611	329	SU62	480	238	SW63	463	231
ST04	177	89	ST69	523	266	SU16	529	279	SU63	410	206	SW64	166	77
ST10	532	278	ST70	683	408	SU17	483	256	SU64	458	234	SW71	116	61
ST11	527	279	ST71	615	326	SU18	175	80	SU65	345	164	SW72	270	127
ST12	557	283	ST72	615	330	SU19	457	233	SU66	320	151	SW73	551	292

Table 1. (continued). Spreadsheet with predicted number of Buzzards per 10-km square in England from the maximum density model (A) and the mean density model (B).

10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B
SW74	421	206	SX67	541	310	SZ38	85	46	TF03	547	270	TF50	273	119
SW75	308	156	SX68	339	183	SZ39	152	69	TF04	327	150	TF51	248	107
SW83	133	66	SX69	369	187	SZ47	18	11	TF05	337	153	TF52	128	55
SW84	446	219	SX73	148	74	SZ48	274	162	TF06	332	150	TF55	45	19
SW85	513	256	SX74	655	330	SZ49	100	50	TF07	253	113	TF56	149	62
SW86	242	114	SX75	584	299	SZ57	64	44	TF08	291	132	TF57	138	58
SW87	91	41	SX76	606	315	SZ58	315	217	TF09	287	133	TF58	15	6
SW93	22	11	SX77	551	295	SZ59	70	37	TF10	243	109	TF60	339	155
SW94	715	387	SX78	484	253	SZ68	39	25	TF11	256	116	TF61	243	107
SW95	339	163	SX79	521	270	SZ69	7	3	TF12	370	174	TF62	233	103
SW96	502	259	SX83	11	5	SZ79	11	5	TF13	376	177	TF63	133	56
SW97	253	120	SX84	282	148	SZ89	124	56	TF14	367	166	TF64	15	6
SX04	94	48	SX85	547	308	SZ99	2	1	TF15	377	168	TF70	243	107
SX05	369	184	SX86	540	262	TA00	242	109	TF16	293	133	TF71	337	153
SX06	574	304	SX87	568	299	TA01	291	133	TF17	291	135	TF72	299	129
SX07	750	436	SX88	402	203	TA02	94	39	TF18	246	113	TF73	312	134
SX08	234	112	SX89	427	213	TA03	178	77	TF19	297	140	TF74	120	51
SX15	512	261	SX95	102	55	TA04	293	138	TF20	312	142	TF80	348	167
SX16	653	377	SX96	29	14	TA05	259	120	TF21	305	138	TF81	345	153
SX17	639	352	SX97	177	86	TA06	262	121	TF22	214	93	TF82	344	154
SX18	411	216	SX98	425	212	TA07	333	154	TF23	241	107	TF83	524	230
SX19	225	111	SX99	450	225	TA08	123	54	TF24	345	155	TF84	153	65
SX25	410	208	SY08	231	108	TA09	25	10	TF25	344	155	TF90	288	131
SX26	648	343	SY09	490	242	TA10	355	165	TF26	241	109	TF91	249	115
SX27	711	411	SY18	64	31	TA11	204	90	TF27	257	117	TF92	248	109
SX28	429	215	SY19	431	214	TA12	87	38	TF28	323	151	TF93	440	195
SX29	472	237	SY28	19	13	TA13	223	99	TF29	358	161	TF94	116	49
SX35	279	140	SY29	750	414	TA14	231	103	TF30	291	130	TG00	269	119
SX36	728	395	SY39	318	157	TA15	199	90	TF31	301	136	TG01	242	105
SX37	631	335	SY49	523	260	TA16	190	86	TF32	295	128	TG02	259	114
SX38	609	310	SY58	306	171	TA17	145	65	TF33	209	91	TG03	268	117
SX39	627	331	SY59	543	282	TA18	5	2	TF34	206	86	TG04	99	42
SX45	71	31	SY67	13	5	TA20	246	107	TF35	305	136	TG10	192	84
SX46	339	158	SY68	637	346	TA21	64	27	TF36	298	134	TG11	192	85
SX47	400	198	SY69	688	374	TA22	229	100	TF37	283	128	TG12	232	104
SX48	383	187	SY78	424	211	TA23	207	92	TF38	241	106	TG13	242	103
SX49	455	233	SY79	702	412	TA24	40	18	TF39	248	110	TG14	48	21
SX54	78	37	SY88	575	308	TA26	2	1	TF40	238	103	TG20	177	77
SX55	343	162	SY89	635	348	TA27	21	9	TF41	260	114	TG21	187	79
SX56	450	239	SY97	126	64	TA30	84	37	TF42	244	105	TG22	254	110
SX57	462	253	SY98	408	204	TA31	30	13	TF43	59	25	TG23	252	109
SX58	272	143	SY99	406	196	TA32	137	59	TF44	57	25	TG24	10	4
SX59	335	167	SZ07	26	12	TA33	8	3	TF45	240	105	TG30	247	109
SX63	9	4	SZ08	62	30	TA41	2	1	TF46	377	169	TG31	255	113
SX64	376	206	SZ09	142	62	TF00	520	253	TF47	419	199	TG32	259	112
SX65	644	330	SZ19	165	73	TF01	413	195	TF48	222	95	TG33	80	34
SX66	391	231	SZ29	165	74	TF02	291	137	TF49	113	49	TG40	234	112

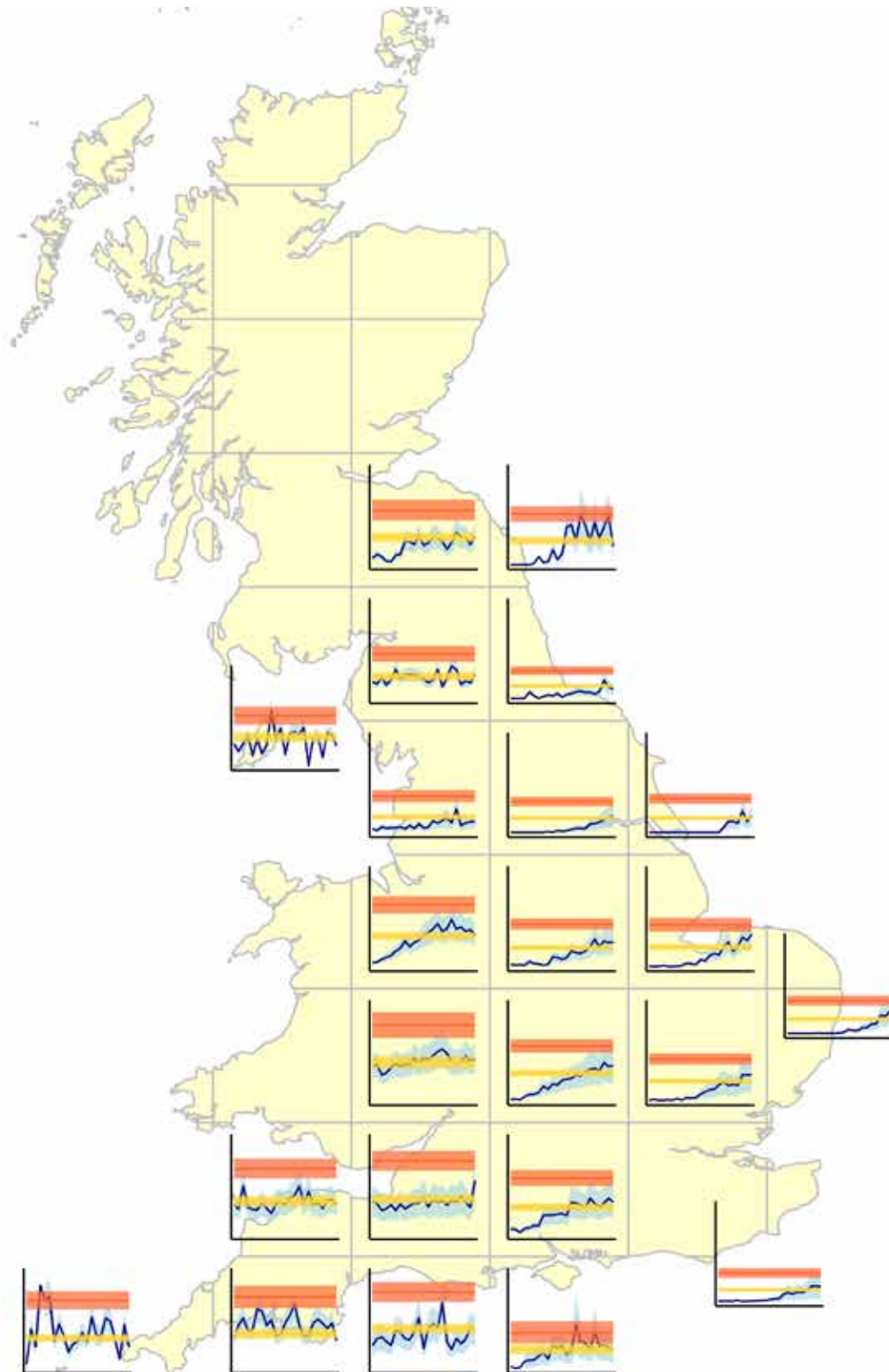
10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B	10-km	A	B
TG41	227	99	TL43	509	251	TL90	137	62	TM46	162	75	TQ40	400	199
TG42	110	50	TL44	385	180	TL91	238	111	TM47	208	94	TQ41	386	194
TG50	32	13	TL45	232	101	TL92	204	89	TM48	237	103	TQ42	234	111
TG51	17	7	TL46	215	95	TL93	283	134	TM49	243	111	TQ43	194	94
TL00	247	112	TL47	335	154	TL94	274	127	TM57	9	4	TQ44	304	153
TL01	321	153	TL48	298	140	TL95	264	123	TM58	72	32	TQ45	222	105
TL02	145	65	TL49	229	100	TL96	250	113	TM59	56	24	TQ46	122	54
TL03	291	134	TL50	269	127	TL97	303	140	TQ00	215	98	TQ47	56	21
TL04	248	113	TL51	315	150	TL98	228	101	TQ01	409	197	TQ48	46	17
TL05	194	86	TL52	214	100	TL99	224	100	TQ02	406	200	TQ49	158	69
TL06	393	189	TL53	412	199	TM00	73	33	TQ03	430	211	TQ50	247	122
TL07	398	192	TL54	482	236	TM01	67	31	TQ04	246	116	TQ51	224	113
TL08	553	280	TL55	308	143	TM02	210	94	TQ05	203	90	TQ52	205	98
TL09	483	237	TL56	306	140	TM03	287	135	TQ06	132	53	TQ53	193	91
TL10	211	94	TL57	303	136	TM04	299	138	TQ07	101	39	TQ54	214	104
TL11	303	143	TL58	269	119	TM05	225	102	TQ08	134	55	TQ55	183	87
TL12	434	212	TL59	260	115	TM06	268	122	TQ09	233	104	TQ56	201	93
TL13	296	135	TL60	339	161	TM07	251	113	TQ10	182	86	TQ57	104	41
TL14	403	186	TL61	281	129	TM08	228	105	TQ11	358	171	TQ58	129	54
TL15	282	125	TL62	303	144	TM09	242	106	TQ12	492	248	TQ59	215	97
TL16	351	166	TL63	278	131	TM11	110	47	TQ13	416	206	TQ60	148	70
TL17	511	247	TL64	269	128	TM12	275	123	TQ14	274	132	TQ61	217	109
TL18	461	222	TL65	305	146	TM13	171	78	TQ15	163	73	TQ62	194	95
TL19	313	145	TL66	295	139	TM14	147	65	TQ16	103	41	TQ63	197	95
TL20	269	124	TL67	314	141	TM15	260	120	TQ17	67	27	TQ64	205	96
TL21	264	120	TL68	291	133	TM16	244	110	TQ18	46	17	TQ65	200	94
TL22	309	148	TL69	265	119	TM17	248	111	TQ19	118	49	TQ66	201	93
TL23	329	153	TL70	186	82	TM18	235	104	TQ20	85	41	TQ67	110	45
TL24	363	169	TL71	283	129	TM19	217	94	TQ21	304	149	TQ68	202	91
TL25	357	168	TL72	217	97	TM21	18	8	TQ22	269	130	TQ69	171	75
TL26	336	156	TL73	260	122	TM22	72	32	TQ23	176	83	TQ70	19	9
TL27	293	132	TL74	253	120	TM23	96	43	TQ24	221	104	TQ71	167	80
TL28	401	186	TL75	429	208	TM24	167	76	TQ25	163	73	TQ72	245	121
TL29	243	108	TL76	416	195	TM25	287	133	TQ26	58	23	TQ73	186	88
TL30	203	89	TL77	428	198	TM26	252	113	TQ27	49	19	TQ74	232	113
TL31	301	138	TL78	235	104	TM27	247	110	TQ28	35	14	TQ75	133	56
TL32	306	147	TL79	329	149	TM28	235	107	TQ29	114	50	TQ76	110	46
TL33	399	195	TL80	200	89	TM29	252	111	TQ30	124	58	TQ77	166	76
TL34	317	147	TL81	231	104	TM33	23	10	TQ31	302	152	TQ78	83	37
TL35	320	149	TL82	251	114	TM34	193	88	TQ32	251	117	TQ79	193	83
TL36	294	135	TL83	280	129	TM35	258	119	TQ33	231	108	TQ81	171	85
TL37	264	118	TL84	238	109	TM36	237	108	TQ34	223	106	TQ82	214	107
TL38	262	118	TL85	318	149	TM37	259	114	TQ35	200	86	TQ83	192	95
TL39	281	127	TL86	231	109	TM38	228	101	TQ36	65	27	TQ84	223	110
TL40	226	100	TL87	257	117	TM39	310	137	TQ37	34	13	TQ85	213	101
TL41	251	115	TL88	204	91	TM44	15	6	TQ38	33	13	TQ86	164	75
TL42	362	180	TL89	371	182	TM45	111	52	TQ39	74	30	TQ87	74	34

Table 1. (continued). Spreadsheet with predicted number of Buzzards per 10-km square in England from the maximum density model (A) and the mean density model (B).

10-km	A	B
TQ88	39	15
TQ89	282	136
TQ91	39	18
TQ92	254	124
TQ93	299	148
TQ94	316	154
TQ95	473	243
TQ96	136	67
TQ97	13	9
TQ98	60	26
TQ99	196	94
TR01	28	13
TR02	205	94
TR03	248	118
TR04	259	124
TR05	238	114
TR06	98	46
TR07	2	2
TR09	52	25
TR13	117	57
TR14	192	94
TR15	177	82
TR16	127	58
TR23	30	14
TR24	258	128
TR25	300	142
TR26	241	112
TR34	117	53
TR35	152	70
TR36	113	50
TR37	1	0
TV49	0	0
TV59	67	33
TV69	1	0

APPENDIX C

Map showing how population trends (blue line and shading) and modelled saturation densities (red line and shading from maximum density model, yellow line and shading from mean density model) vary by 100-km square across England when predictions are averaged only across surveyed squares where Buzzards were reported at least once during the BBS time series and thus contributing to the trend line. Trends, which are all plotted to the same x-axis scale (1994–2017) and y-axis scale (0–7 birds km⁻²) are based on a simple model of annual Buzzard densities in BBS squares with 95% confidence limits shown by blue shading.





Images: Edmund Fellowes, Edmund Fellowes, Gary Haigh. Cover image: Edmund Fellowes.

Potential future distribution and abundance patterns of Common Buzzards *Buteo buteo*

To contribute towards the definition of Favourable Conservation Status for the Common Buzzard *Buteo buteo*, estimates of local carrying capacity are required throughout England. In this report we aim to assess the potential for future expansion of the Buzzard breeding range in England and forecast potential densities in 10-km squares using species distribution models.

We can be highly confident about the extent of the Buzzards breeding range and its limited scope to expand further. The species distribution models are as robust as we can expect with the data available and they perform comparably to other models of abundance. However, many of the predicted densities are high compared to those in the literature, although it should be noted many of these are quite old and limiting factors may have reduced since then.

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