

The population and range expansion of the Egyptian Goose (*Alopachen aegyptiacus*) across the UK 1993-2014



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Abstract

Non-native waterbird populations are increasing through much of Europe with some species showing conspicuously successful invasions. Much uncertainty surrounds the potential impacts of invasive waterbirds on native waterbird communities and wetlands. Understanding the processes and phases of population and range expansion of non-native waterbirds, and their environmental drivers, is an important research topic to inform management of these species. This study investigates the trajectories of population and range expansion of the Egyptian Goose (*Alopochen aegypticus*) across the UK between 1993 and 2014, and the environmental and spatial drivers of population density and site occupancy for three representative time periods, using the British Trust for Ornithology's Wetland Bird Survey (WeBS) data. Egyptian Goose showed an accelerating rate of occupancy of new grid cells (at 20-km resolution) over the time period of the study. There is no apparent reduction in the rate of spread of this species, insofar as through time there is an increase of both grid cell occupancy and of wetland area occupancy, although in the latter stages of expansion (post-2003) it appears that there is more of a filling out effect going on, at the same time as the increased rate of expansion. Environmental models supported the a priori hypothesis that waterbodies have a negative association with densities of Egyptian Goose, which was born out in the results. Environmental models also showed that rainfall was consistently negatively associated with density and presence/absence, whilst stately homes were shown to be consistently positively associated.

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Chapter 1

Introduction

This thesis aims to in the first instance, to provide a background summary of the knowledge of relevant invasive species to this project. The first chapter then aims to provide a visualisation in order to understand the temporal trajectory and spatial pattern of range expansion and population change of the Egyptian Goose across the United Kingdom between 1993 and 2014. Whilst the second chapter aims to determine which of multiple competing environmental variables best explain the spatial extent of range occupancy, and of population density, of the Egyptian Goose across the UK for three time periods representative of early (1998-2001), mid (2005-2008) and late (2010-2013) range expansion

Definition of invasive species

Invasive species are widely heralded as the second greatest agent of species endangerment and extinction after habitat destruction, particularly on islands (Wilcove *et al.*, 1998). There are many different terms that are used to define non-indigenous species (NIS) across the scientific literature, including 'introduced', 'invasive' and 'exotic'. The Convention on Biological Diversity (CBD) uses the term 'alien' without defining it. Some of the greatest confusion arises from the use of the term 'invasive'. There is evidence for at least 5 separate definitions for invasive species that appear throughout the literature. These include: 1) as a synonym for non-indigenous species (e.g. Radford and Cousens, 2000); 2) NIS that have colonised new natural areas (e.g. Burke and Grime, 1996); 3) discrimination between NIS established in cultivated habitats as opposed to those established in natural habitats (e.g. Reichard and Hamilton, 1997). Of the two definitions presented in the Reichard and Hamilton paper, the second is the one that is truly considered invasive, whilst it is important to note that this definition was created for plant species, so may not be wholly applicable to other taxa; 4) NIS that are widespread (e.g. van Clef and Stiles, 2001); or 5) NIS that confer adverse effects onto the invaded habitat (e.g. Mack *et al.*, 2000).

The definition of an invasive species that we are going to use for the purposes of this study is: "Invasive alien species are plants, animals, pathogens and other organisms that are non-native to an ecosystem,

and which may cause economic or environmental harm or adversely affect human health. In particular, they impact adversely upon biodiversity, including decline or elimination of native species - through competition, predation, or transmission of pathogens - and the disruption of local ecosystems and ecosystem functions.” (Convention on Biological Diversity, n.d.)

Effects of invasive species

The widely reported negative effects of invasive species on native flora and fauna and ecosystems may be grouped under three types: species extinctions (Ricciardi, 2000; Clavero and Garcia-Berthou, 2005); loss of genetic diversity (Chapin III *et al.*, 2000; Tsutsui, 2000); and loss of ecosystem services (Pejchar and Mooney, 2009).

Gurevitch and Padilla (2004) came to the conclusion that whilst invasive species are causing major changes in ecosystems worldwide, there is a lack of evidence definitively proving that invasive species can be linked to extinctions of native species. They say that whilst the presence of invasive species and the decline of native species frequently overlap in both space and time, these co-occurrences are often errantly causally linked together, and that other common factors, such as habitat alteration and degradation might be responsible. They also pointed out that extinctions are often attributable to multiple causes. The authors focussed on the example of the zebra mussel (*Dreissena polymorpha*), and said that the link between the introduction of this species and the decline of North American unionid mussels is unclear. Ricciardi (2004) responded to this paper saying that empirical modelling shows that the rate of decline of N. American unionid species has increased since the introduction of zebra mussels, and that the focus of modelling should be at the population level, as species can undergo range contractions and population losses without going globally extinct. Other authors conclude that invasive species are causing extinctions both at a local and global scale. On a combined local and global scale, Wiles *et al.* (2003) showed that the introduction of the Brown Tree Snake to Guam caused the extinction or severe population reduction of the majority of the 25 endemic bird species. On a global scale Clavero and Garcia-Berthou analysed the IUCN Red List database for extinctions on a species-by-species scale and showed that of the 170 extinct species for which a cause could be definitively identified, 91 (54%) included the effects of invasive species, and for 34 of these species (20%) invasive species were the sole cause of extinction.

What makes an invasion successful?

When discussing the effects of invasive species on native species it is also important to consider what it is that makes some invasions more successful than others. There are a lot of biological invasions that occur that are not successful for a variety of reasons (Lodge, 1993; Williamson and Fitter, 1996). In this context 'success' is referring to a biological invasion that establishes a viable breeding population in a new area of range.

It has been hypothesised that it will be very difficult to attempt to define, using a trait-based approach, what it is that makes a species a successful invader. This is hypothesised to be due to the large variation in the traits of species both within and between taxa, for example the traits that define whether an avian species is going to be successful are likely to be different to those that will define whether a mammalian species invasion is going to be successful. However, there have been a number of studies attempting to define these traits, either by looking at a specific taxon and extrapolating from it, or by looking at the life history traits of a large number of successful invaders. It has often been hypothesised that a higher reproductive rate will lead to a higher likelihood of an invasion becoming successful, however, this has received little empirical support (Sol *et al.*, 2012).

It was later shown that the more successful invaders are more often characterised as giving priority to future, rather than current, reproduction. Increasing the breeding expectations of future generations reduces the cost of reproductive failure, and can lead to increased opportunities to explore the environment and respond to novel ecological pressures in the current time period (Sol *et al.*, 2012; Morris *et al.*, 2012)

What it is that makes an invading species successful will vary from taxa to taxa, and the majority of studies have focussed on attempting to quantify successful botanic invasions (e.g. Pysek, Prach and Smilauer, 1993; Rejmanek and Richardson, 1996; Sutherland, 2004). However, Kolar and Lodge (2001) came up with traits defining success for a broader range of taxa. They showed that for birds the probability of success increases with the number of individuals introduced and the incidence of introduction events. They also showed that plant species that have a history of invasiveness and

reproduce vegetatively have a higher chance of being successful. They also showed that there is no correlation between time since the primary invasion event and the ultimate success of an invasion (Kolar and Lodge, 2001).

An important question to ask when regarding invasive species would be whether climate change is having an impact upon the incidence rate of successful invasions. As more polar climates warm up, it has been hypothesised that these ecosystems could become more suitable to biological invasions (Rahel and Olden, 2007; Thuiller, *et al.*, 2007). It has also been predicted that other results of global change, such as increased atmospheric carbon dioxide, nitrogen deposition and eutrophication of ecosystems could be having impacts upon the prevalence of successful invasions. Research from a variety of authors has shown this to be true, for example Dukes and Mooney (1999) showed that increases in atmospheric CO² and nitrogen deposition suit species that share certain traits, and that these traits are often displayed by successful invaders. Stachowicz *et al.* (2002) showed that for certain marine species, ocean warming was facilitating invading species by allowing them to arrive earlier in the season, whilst the timing of native species' recruitment remained unaffected.

Hellmann *et al.* (2008) attempted to qualitatively predict the effects of climate change on invasive species by looking at the 'invasion pathway' and identifying 5 non-exclusive consequences of climate change. They showed that climate change will alter: 1) the transport and introduction mechanisms; 2) the establishment of new invasive species; 3) the impact of current invasive species; 4) the distribution of existing invasive species; and 5) the effectiveness of control strategies (Hellman *et al.* 2007).

In summary, studies appear to show that climate change is having an impact upon invasive species in a variety of ways. However, the effects will in all likelihood increase the prevalence of successful invasions, and will alter, in a variety of ways the effects of current invasions. As well as climate change, there are a number of other potential environmental variables that have the potential to impact upon the success of an invasion. A selection of those that may affect the success of the Egyptian Goose are discussed in the methodology.

It has been observed that non-native species tend to be associated with human-modified ecosystems in their invaded range, such as urban and agricultural areas (Gellardo, 2014). Chace and Walsh (2006) showed that increased urbanisation tends to increase avian biomass for a number of taxonomic groups, including cavity nesters, such as the Egyptian Goose. Bonter, Zuckerberg and Dickinson (2009) showed that there was a link between urbanisation and the success of an invasive bird (the Eurasian collared-dove).

A link has been hypothesised by Rehfisch, Allen and Austin (2010) between successful invasions by non-native species and ecosystems with high nutrient inputs. Due to this hypothesised link, it would be interesting to analyse whether there is a link between successful invasions and eutrophication.

Hiley, Bradbury and Thomas (2014) showed that protected areas (PAs) are susceptible to colonisation by invading species after their populations had established themselves, and that one of the species showing this link was the Egyptian Goose. Therefore, when investigating why invasions have been successful, it would be interesting to identify whether there is a link between any given successful invasion, and either the area or the proximity of protected areas in the invaded ecosystem.

If analysis of the range expansion of an invasive species is undertaken using a gridded approach, then one variable that would logically impact upon the presence of the invasive species would be occupancy of adjacent grid cells. This could be used to account for the link between density and/or presence/absence being higher in grid cells that are adjacent to those that are already occupied.

Management solutions

When looking at biological invasions in a practical context, it is important to consider the implications of managing environments to mitigate against their negative effects.

There are three successive practices recommended for managing invasive species: prevention, eradication and control (Hulme, 2006). Of these, prevention is the preferred, cheapest and easiest to achieve option. Once an invasive species has become established, the costs for eradicating it increase rapidly with population and range expansion, whilst controlling it is still an expensive, and often impractical, method. However, the prevention of biological invasions is hindered by the difficulty in separating invasive and non-invasive species in any control method used. Given that any given control method will be aimed at only impacting the non-native species, and will aim to avoid the native species, it is important to note the difficulties associated with separating native and non-native species (Hulme, 2006). Within the short history of attempting to control or eradicate populations of invasive species, there have been successes and failures, as well as considerable controversy (Myers *et al.*,

2000). The majority of successful eradications have either occurred on islands, or were part of a rapid response when invasive species were found in limited areas of population establishment (Myers *et al.*, 2000). The three management solutions suggested by Hulme are not mutually exclusive, and it is possible to imagine a situation where all three processes are used in combination to attempt to remove a current invasive species.

Invasive birds in UK/Europe

One example of hybridisation between an invasive and native species of bird in Spain, is between the Ruddy Duck and the native White-headed Duck (*Oxyura leucocephala*) (Hughes *et al.*, 1999), which occurs in Spain and the UK (Hughes, Henderson and Robertson, 2006). Outside of Europe there are similar examples of hybridisation between the Mallard (*Anas platyrhynchos*) and other *Anas* species in Australasia, North and Central America and Africa (Fox, 2009). In order to save the White-headed Duck from extinction a programme has been undertaken to eradicate Ruddy Duck from its invasive range. As of a 2010 study, 95% (>6,800) of all Ruddy Duck individuals have been culled in England, however, sustainable populations are still present on the European mainland, for example in the Netherlands (Henderson, 2010).

Hughes, Kirby and Rowcliffe (1999) demonstrated conflict between both the Canada Goose and the Ruddy Duck and native species. They discussed how the Canada Goose harasses Cormorants and damages amenity grassland, whilst the Ruddy Duck doesn't cause conflict in the UK, but individuals from the UK do migrate to the continent and harass the White-headed duck. However, it is suspected that there are more conflicts that occur between invasive geese and native waterbirds, however, some of this is anecdotal evidence.

Strubbe, Matthysen and Graham (2010) estimate that the population of the invasive Rose-ringed Parakeet (*Psittacula krameria*) in Flanders, Belgium is roughly 22,000 pairs. They discussed how this species interacts with and impacts upon the native Nuthatch (*Sitta europaea*). It was also suggested by Strubbe and Matthysen (2007) that there is a negative relationship between the Nuthatch and the Rose-ringed Parakeet, whereby the latter outcompetes the former when considering nest availability. A number of other studies have shown that the Rose-Ringed Parakeet competes with native cavity nesting species (Hernandez-Brito *et al.* 2014), although it does not appear to compete with native woodpecker species (Strubbe *et al.* 2009).

The Mandarin Duck (*Aix galericulata*) is an introduced species across a number of European countries, including the Netherlands, Belgium, the Britain, France, Switzerland and Austria (Banks *et al.* 2008). It was first recorded breeding in the Netherlands in 1964, near The Hague (van Kleunen and Lemaire, 2014). Since then it has expanded to having successful breeding populations across much of the country (van Kleunen and Lemaire, 2014). In Germany, it is estimated that there are between 430-600 breeding pairs resident (van Kleunen and Lemaire, 2014), whilst in Austria it is estimated that there are between 40-60 breeding pairs (Banks *et al.* 2008). As mentioned, the Mandarin Duck also has viable breeding populations in Britain. By 2011 the species' range had expanded up through Northern England and into Scotland from its original area of introduction in Southern England. However, the most recent counts available are those for 1988 when the population was roughly 3500 breeding pairs.

The Mandarin Duck is a cavity nester, and therefore competes with native species such as Great Tits (*Parus major*), Eurasian Jackdaws (*Corvus monedula*) and Common Kestrels (*Falco tinnunculus*) (Lever, 2013). There are occasional suggestions in the literature that the Mandarin Duck competes with certain native species for food, for example Lever (2013) report cases of this species chasing off Eurasian Jackdaws among other species. Whilst hybridisation appears possible, it is unlikely that it would be successful, due to the chromosomal differences between the species (Lever, 2013).

Since the 1980s, the Canada goose has started to establish permanent breeding populations in Greenland (Bennike, 1990). Fox *et al.* (2006) showed that in 1999 there were 35,600 breeding pairs of Canada goose in Greenland. This expansion into new territory has had impacts upon native Greenland White-fronted Geese, for example Fox *et al.* (2006) suggest that interspecific competition, such as for food, between these two species was a partial reason for the decline of the population of White-fronted Geese. They also suggest that aggressive actions by Canada Goose, such as restrictions on the access to favoured sites, may have played a part in the decline of the White-fronted population. Kristiansen and Jarrett (2002) showed that in all observed encounters between these two species, Canada Goose were seen to behaviourally dominant over White-fronted Geese. This supports suggestions that dominance and restricted access to feeding sites may have played a part in the decline of the White-fronted Goose population.

Egyptian Goose

The Egyptian Goose is native to sub-Saharan Africa and the Nile Delta, with the exception of heavily wooded areas and deserts (Brown, Urban and Newman, 1982; Goodman and Meininger, 1989) and has been introduced to a number of countries. It has self-sustaining breeding colonies in Northwest Europe and Great Britain, and has been known to breed occasionally in Florida, New Zealand and Australia (Braun, 2004). In Britain, it was introduced to East Anglia in the 17th century, mainly as an ornamental species to stately homes (Kear, 1990), and was breeding widely across the region by the following century (Sutherland and Allport, 1991). The preferred habitat of this species in both the UK and the Netherlands is open grassland, <1km away from freshwater bodies, and with a few trees present (Sutherland and Allport, 1991; Gyimesi and Lensink, 2012). In the Netherlands, this species feeds mainly on grass, and most commonly nests in trees, old nests of other species or in tree cavities (Lensink 1998).

The Netherlands also holds a major population of introduced Egyptian Goose, where they were introduced as ornamental species to city parks in the 20th century. They started breeding ferally in 1967 near The Hague, and had expanded across the majority of the country, and into neighbouring Germany by 1994 (28 years after initial breeding). However, they were absent from areas that were either heavily forested or lacked waterbodies (Gyimesi and Lensink, 2012). In 1972 there were 7 pairs of Egyptian Goose recorded breeding in the wild in the Netherlands, which increased exponentially to 4,994 pairs by 2000, and the estimated population in 2010 was 45,253 individuals (Lensink, 1998; Lensink, 2002; Gyimesi and Lensink, 2012). Comparisons between counts in 2000 and 2008 showed that the species population was increasing in all regions of the country. However, rate of increase was greater in those regions that had lower counts in 2000, thus suggesting a potential carrying capacity being approached (Gyimesi and Lensink, 2012). The majority of the preferred habitat is found either on farmland or grassland in the Netherlands, and Gyimesi and Lensink (2012) showed that there are higher population concentrations of this species found on grassland, compared with arable land. The highest population concentrations were found in the riparian zones in the lowest parts of the country (generally the Western and Northern provinces) (Gyimesi and Lensink, 2012). Prior to 1974 the population was increasing in all colonised regions however, post-1974 the population stabilised in the first area of settlement and was increasing in the newly colonised areas of the expansion wave and in the new expansion foci, thus suggesting a change in the rate of population change across the country (Lensink, 1998). In the last decade, population growth has slowed, possibly due to increased culling intensity (circa 20,000 individuals are culled a year), or because all suitable breeding sites are already occupied, or a combination of both of these factors (Gyimesi and Lensink, 2012).

This contrasts with the UK, where after being introduced via private estates across scattered locations in England and Scotland between 340 and 100 years ago, the population appears to have expanded its occupancy of UK sites only gradually until relatively recent times. As Sutherland and Allport (1991) discussed, there had been an apparent lack of range expansion or major population change over the last 200 years. They agreed with Sharrock (1976) that the Egyptian Goose population outside of East Anglia was not viable at that time, and stated that it was unlikely that the species would ever show the increases in population and range increases of the Canada Goose or Ruddy Duck. Sutherland and Allport (1991) showed that at the time, the Egyptian Goose was mainly located in North Norfolk on the major river valleys, whereas few individuals were sighted in South Norfolk, however, the reason for this difference was unknown. Much of East Anglia (both Norfolk and Suffolk) as well as many other parts of the UK, were observed by Sutherland and Allport (1991) to have suitable habitat, although the Egyptian Goose was only just expanding into Suffolk at the time.

Lensink (1998) showed that population growth of the Egyptian Goose in the Netherlands was lower after severe or very severe winters, when compared to normal or mild winters. This was also inferred in Sutherland and Allport (1991). Due to this high rate of mortality in severe winters, there were then fewer adult birds available to breed in the next breeding season, thus lowering the overall rate of population increase for that year. This is therefore likely to have an impact upon the rate at which the Egyptian Goose can expand its range. It has been suggested that the 0°C isocline could present a barrier to expansion, due to the severe effect of cold winters on populations (Lensink, 1998). Successful population and range expansion may be limited by one of three broad factors: environmental variables, life history, and the movement ecology of a species (Cumming, Gaidet and Ndlovu, 2012). It has been observed that in its native range, the Egyptian Goose may be limited by its fidelity to moulting sites, and that internal drivers of movement, particularly those relating to life history traits of breeding and moulting, appear to dominate over external drivers of movement (Cumming, Gaidet and Ndlovu, 2012).

Unlike native species, it has been suggested that invasive species are more likely to breed and nest in protected areas (PAs) the longer they are resident in a particular region (Hiley *et al.*, 2013). Hiley, Bradbury and Thomas (2014) showed that this was the case for 50% of the introduced wetland bird species that have expanded in Britain since 1960. One of those species that did increase its use of PAs was the Egyptian Goose, which went from ~40% to ~65% of its population within PAs between first colonisation and 14-16 years after.

The Egyptian Goose causes many environmental and social problems as an invasive species in its non-native range. There is evidence of them bio-fouling and causing eutrophication in the UK (Rehfishch,

Allan and Austin, 2010), of them attacking people who approach them whilst they are breeding, and of competition with native species, hybridisation and/or the spreading of disease to native species (Curtis, Hockey and Koeslag, 2007). However, this hybridisation is normally with other introduced species such as the Ruddy Shelduck, Barnacle Goose and Canada Goose (Lensink, 1996; Harrop, 1998). In the Netherlands, the Egyptian Goose often uses Goshawk and Buzzard nests and chases those species away, as well as sharing nesting sites with Shelducks and Mallards. This is due to it being a tree hole nester, and being territorial, therefore competing with, and chasing away, these species (Lensink, 1996). In South Africa, an outbreak of avian influenza at an ostrich farm was traced back to Egyptian Goose (Thompson *et al.*, 2008), thereby raising the prospect of introduced individuals in other countries also being potential vectors. Due to these impacts, and the severity of them, the Egyptian Goose would be classed as a species of Moderate impact according to Blackburn *et al.* (2014).

It is common for invasive species to undergo an exponential increase in their population post colonisation (Lensink, 1999). For some species, such as the Common Waxbill (*Estrilda astrild*), there is a phase of limited to no population growth before this exponential phase (Silva, Reino and Barralho, 2002). Another example of differing phases of population growth in an invasive species can be seen in the Eurasian Collared-Dove (*Streptopelia decaocto*), whereby it undergoes an immediate exponential growth to above the carrying capacity, the population then levels off for a time, before dropping back down to the carrying capacity (Schiedt and Hurlbert, 2014). Prentis *et al.* (2008) show how adaptive evolution in invasive plant species can a) alter their success in non-native ranges, and b) alter the trajectory of population change after initial colonisation in the new range. The Egyptian Goose can be used as a model species against which to test the validity of alternative potential range expansion trajectories and the evidence for different phases of range expansion post colonisation.

A number of papers (e.g. Hellmann *et al.*, 2008 and Colautti and Barrett, 2013) have discussed the effects of climate change on invasive species populations and ranges, mainly coming to the conclusion that climate change will allow invasive species to spread further. However, fewer papers have discussed the effects of other potential environmental drivers that could facilitate the spread of invasive species. The majority of the papers that have discussed this have focussed on either single drivers, or on a limited number of drivers. For this reason, the use of a model species to identify the extent to which other environmental drivers are associated with invasive species range expansion is of considerable interest.

The choice of the Egyptian Goose as a model species for understanding the phases of invasive species range expansion, and their drivers, is appropriate because of its known history of occupancy in the UK and its recent, and significant, expansion, coupled with good availability of environmental data for the UK across the expansion phase.

Aims

The aims of this project were as follows:

- 1) To visualise and describe the temporal trajectory and spatial pattern of range expansion and population change of the Egyptian Goose across the United Kingdom between 1993 and 2014. To attempt to identify phase changes in the overall rate of range expansion by exploring accumulation of total numbers of occupied grid cells and total occupied wetland area through time.
- 2) To determine which of multiple competing environmental hypotheses best explain the spatial extent of range occupancy (presence/absence), and of population density, of the Egyptian Goose across the UK for three time periods representative of early (1998-2001), mid (2005-2008) and late (2010-2013) range expansion. The time periods we used for the density analyses were: 1998-2001, 2005-2008 and 2010-2013, and for the presence/absence analyses: 1997-2001, 2004-2008 and 2009-2013.

Reporting of the research conducted to fulfil the aims outlined in 1) above, constitutes the remaining part of Chapter 1 (Methods, Results and Discussion), while the research addressing the aims outlined in 2) above, are reported in Chapter 2.

Methods

Count data

We used count data from the Wetland Bird Survey (WeBS) scheme between winter 1993/4 and 2014/5. WeBS is a joint scheme of the British Trust for Ornithology (BTO), the Royal Society for the Protection of Birds (RSPB), Natural England, the Wildfowl and Wetlands Trust (WWT), whereby volunteers conduct synchronised monthly counts at over 2000 wetland sites across the UK.

Data re-sampling to grid

WeBS data do not lend themselves readily to spatial visualisations for the purpose of understanding species' distributional range expansions because the average wetland surveyed is relatively too small in scale relative to the geographic extent of the entire (UK-wide) dataset. Hence, the wetland count data were re-sampled to a 20-km x 20-km Ordnance Survey of Great Britain (OSGB) grid for each of three seasons for every year of count data included: these were autumn (July-October); spring (April-June); and winter (November-March), resulting in total counts per 'season-year' for each grid cell. To calculate the winter season, the months of January, February and March of one year were combined with the month of November and December from the previous year. Simultaneous calculation of the total area of wetland within each 20-km x 20-km grid cell, allowed us to compute the correct redistribution of the count data as a proportion of the total area of each wetland within each grid cell. This takes account of wetlands straddling more than one grid cell. Counts were then summed to obtain a single count value per season-year period per grid cell. Density was then calculated by dividing the aggregated count value by the total area of wetland surveyed within a grid cell. Maps were then created in ArcGIS using a sliding colour scale for both counts and density for each season-year (see Appendix 1).

Analyses of range expansion

Following Silva et al. (2002) and others, we explored the temporal trajectory of range expansion by plotting: the total number of grid cells occupied for each season-year against year; and the square-root of the total number of grid cells occupied for each season-year against year. The square-root is here used to derive an approximation of the average speed of range expansion in terms of linear distance rather than area, following Silva et al. (2002), although we perform a square-root transformation on number of grid cells occupied rather than total grid cell area occupied. Additionally, we plotted: the total area of wetland (surveyed by WeBS) that was occupied by Egyptian Goose, for

each season-year; and the square-root of the total wetland area that was occupied, per season-year. Finally, we plotted the average total wetland area occupied per grid cell occupied per season-year, by dividing total wetland area occupied by total number of grid cells occupied in each season-year. This allowed us to infer what the relationship between occupied wetland area and the rate of range expansion was.

Breakpoint regression analysis was undertaken on bivariate relationships included in figure 1, using the R package ‘segmented’. In order to discover the breakpoint position for each figure, an iterative process was undertaken, whereby linear models of each year were compared in order to find the lowest residual mean squared error (MSE), and thus find the breakpoint. Once this breakpoint value had been discovered, it was included in the segmented model. These models were then plotted as breakpoint lines on the figures, and P values were extracted.

Results and discussion

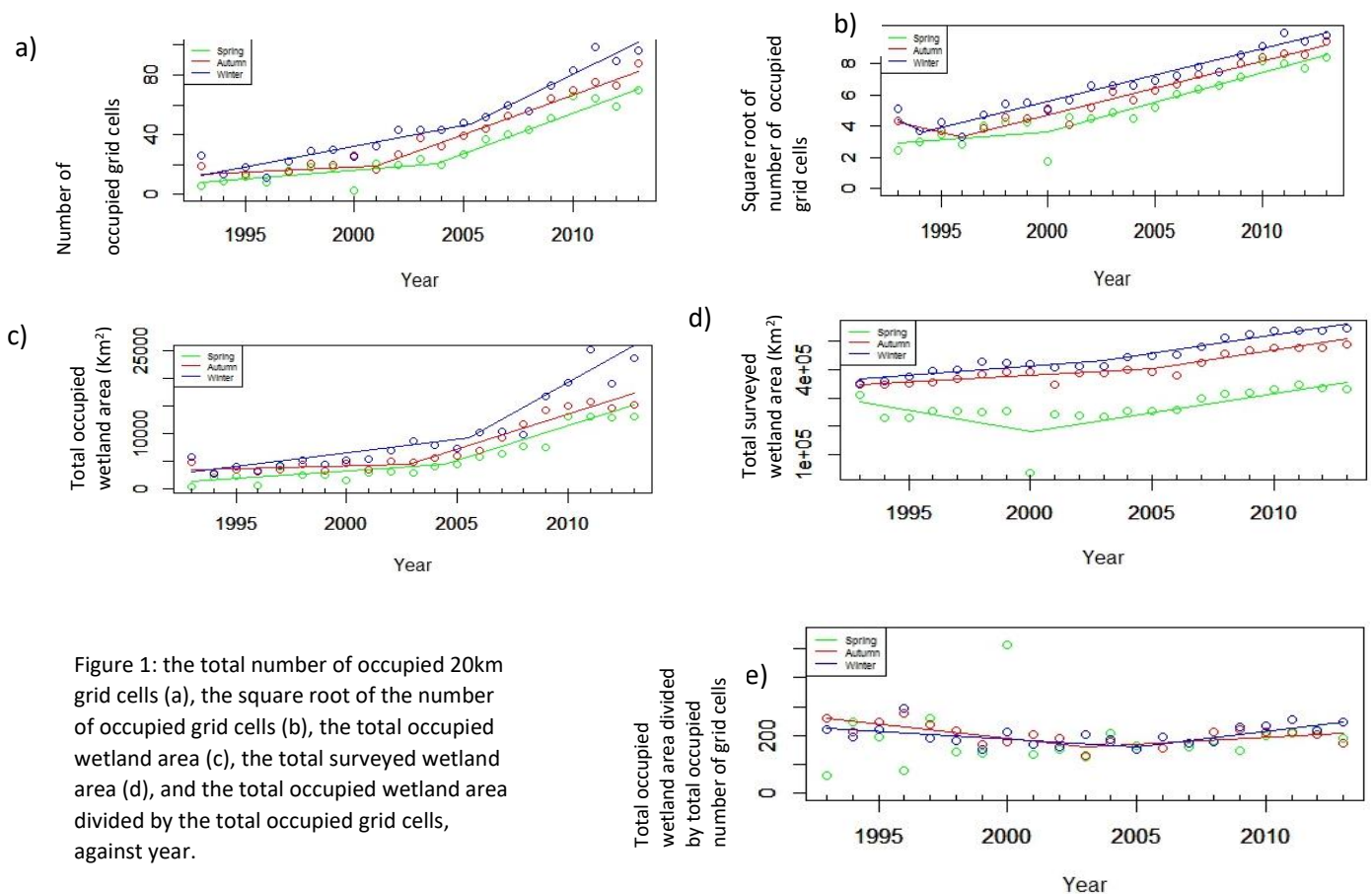


Figure 1: the total number of occupied 20km grid cells (a), the square root of the number of occupied grid cells (b), the total occupied wetland area (c), the total surveyed wetland area (d), and the total occupied wetland area divided by the total occupied grid cells, against year.

Table 1: The associated P values and the slopes of the first (B_1) and second (B_2) segments of the breakpoint analysis for figure 1, bold numbers signify those P values and associated slopes that were found to be significant at $P < 0.05$

Dataset	Model outputs								
	P value			B_1			B_2		
	Spring	Autumn	Winter	Spring	Autumn	Winter	Spring	Autumn	Winter
Occupied grid cells	0.012	0.122	<.001	1.39	0.8333	2.688	5.423	5.262	7.05
Square root of occupied grid cells	0.397	0.237	0.066	0.08899	-0.3086	-1.373	0.3805	0.3416	0.3354
Occupied area	0.056	0.576	0.022	198.8	68.45	376.6	1254	1255	2228
Surveyed area	0.067	0.002	<.001	-13800	4101	6173	13500	12770	13020
Occupied area/occupied grid cells	NA	0.001	0.042	-	-10.07	-4.943	-	4.883	10.47

Figure 1a shows the total number of 20km grid cells occupied across the entire time period, comparing the three seasons. The breakpoint analysis for this figure, along with the associated P values, as shown in Table 1, show that in the spring and winter seasons there is a significant break in the line. The year that this change occurs is different for the two seasons, in Spring the change occurs in 2004, whilst it occurs a year later in 2005 in the Winter season. This shows that after this date the rate of accumulation in the total number of occupied grid cells increases, therefore indicating an increase in the rate of range expansion.

Figure 1b shows the square-root of total grid cell occupancy through time. This figure smooths the slope, meaning that there are no longer two distinct slopes, as can be seen from the P values in Table 1.

Figure 1c shows the total occupied wetland area per season-year. Whilst it appears visually that there are two distinct slopes for each of the three seasons, this is not the case, as can be seen from the P values in Table 1. In this case, winter is the only season that has a significant break, with this occurring in 2006. This shows that as time progresses there is a significant increase in the amount of wetland area that is being occupied by the Egyptian Goose. That this is only apparent in winter is a potentially a result of the differences between numbers of Egyptian Goose resident within the country between seasons, and that the most surveys are undertaken by the WeBS team in winter.

Figure 1d shows the amount of wetland surveyed by the WeBS team per season-year. As can be seen from the P values in Table 1, there is a significant break in the amount of area being surveyed in both

winter and autumn, however, there is not in spring. The low value in Spring 2000 is a result of the foot and mouth outbreak within England. This low value may be obscuring a similar change in slope, as seen for the other two seasons.

Figure 1e shows the total occupied wetland area divided by the total number of occupied grid cells, per season-year. There is no breakpoint line for spring, due to the high spread of data within that season. The high value for 2000 is the inverse of what was seen in the previous figures, with regards to the foot and mouth outbreak. However, for both autumn and winter, there is a significant change in the slope of the line, which occurs in 2003 for both seasons. This shows that after an initial period of the rate of grid cell occupancy not being matched by a similar rate of wetland area occupancy, in the latter stages of the expansion, this trend is reversed.

This suggests that in the first instances the rate of expansion through grid cells is higher than the rate at which Egyptian Geese are occupying wetlands. There are a number of potential hypotheses for why this may be, including that meta-populations of the Egyptian Goose are not occupying the full potential area of waterbodies within any given grid cell, and instead are moving on rapidly and forming new meta-populations, thus only colonising certain waterbodies in a grid cell. Post-2003, there is a significant change in the slope, with the rate at which wetland area is being occupied now outstripping that of the rate of grid cell occupancy. This suggests that post this period, there is a slowdown in the rate at which grid cells are being colonised, and that instead, new meta-populations of Egyptian Geese are now filling out previously occupied grid cells. As previously shown, there is no slowdown in the overall rate of grid cell occupancy, thus suggesting that there are populations of Egyptian Geese both colonising new areas, as shown by grid cells, and filling out previously occupied areas.

As seen can be seen from the time series of maps shown in Figures S1-S6, the Egyptian Goose increases in both count and density across both a spatial and temporal range. When comparing between seasons, and not just across years, it appears that there may be differences between the counts and densities of the Egyptian Goose between seasons. The counts, and subsequently, the densities appear to be highest in winter, and then decrease through Autumn and Spring. However, this could be a result of the number of surveys that are undertaken by the WeBS team being highest in winter. It is unclear whether there is a true difference in the numbers of birds across seasons.

Figures S1-S3 show the sequential expansion of this species through count data. It can be seen that there has been a clear expansion of the Egyptian Goose's range, starting from it being limited to Norfolk, and expanding through the Thames Valley and West towards Bristol and Wales, and a corresponding expansion across the East Midlands. Figures S4-S6 show the change in density of this species across the country, in a pattern that mirrors figures S1-S3.

It is possible that this species is being driven to move between wetlands by corridors of dispersal, such as rivers and canals. If this is the case, then a possible explanation for the early pattern observed in Figure 1e), would be that the Egyptian Goose is first colonising those waterbodies that have the highest connectivity, and that these could be the largest wetlands in a given area. It could have been informative to therefore conduct a connectivity analysis, whereby the relative connectivity of any given waterbody and/or grid cell is considered across a temporal scale, thereby allowing analysis of the level of connectivity that is favoured for both colonisation and dispersal.

In conclusion, based on Figure 1, and the associated slopes and P values, it is possible to say that there is no apparent reduction in the rate of spread of this species, insofar as through time there is an increase of both grid cell occupancy and of wetland area occupancy, although in the latter stages of expansion (post-2003) it appears that there is more of a filling out effect going on, at the same time as the increased rate of expansion. It is also suggested through the maps presented in Figures S1-S6 that there is a change in the overall distribution of this species, and that there is an apparent difference in densities between seasons, although this would need further analysis to be established with greater certainty.

Chapter 2

Introduction

Hiley, Bradbury and Thomas (2014) showed that the Egyptian Goose used protected areas as colonisation points, from which to spread outwards. They showed that this species tends not to use protected areas early on in their range expansion across UK, but uses them increasingly once the population has become more established. It has also been shown by both Sutherland and Allport (1991) and Lensink (1998) that this species uses country and/or city parks as favoured habitat through which to disperse expand its range. It is also well-known that this species has population enclaves in stately homes across the country, since this is how they were first introduced into the UK, and it is assumed therefore that these stately homes were the starting point for the historical range expansion of the species (Sutherland and Allport (1991).

In the native range of the Egyptian Goose in South Africa, studies have showed that the species has been linked to urbanised land (van Rensburg, Peacock and Robinson, 2009) in addition to arable and grassland land types (Magnall and Crowe, 2002). In its non-native range in the Netherlands and the UK the Egyptian Goose has been linked to arable land (Sutherland and Allport, 1991) and grassland (Lensink, 1992).

The analysis for this chapter sets out to test the relative importance of alternative environmental hypotheses for the population density and presence/absence of Egyptian Goose for three selected stages of the range and population expansion of the species (i.e. 1997-2001, 2003-2007 and 2009-2013).

Using environmental data to predict occupancy and abundance has been done in a suite of studies, and is generally considered to be an effective way of modelling for either occupancy or abundance. It has been used to model how the abundance of 80 tree species will change as a result of climate change (Iverson and Prasad, 1998) and to measure how ecological niches overlap with occurrence and environmental data (Broennimann *et al.* 2012)

Methods

Count data

WeBS count data for the Egyptian Goose, across the time-series 1993-2014 was gridded at two grid cell resolutions prior to carrying out analyses (see below), namely 5-km x 5-km and 20-km x 20-km. Count data was only included for the winter season for these analyses. Only winter counts were included because this was the season at which the geographical range was greatest, and at which the highest number of surveys were undertaken, this allowed the use of the most complete datasets possible. To calculate the gridded count value, the total counts were summed together across all waterbodies in each respective grid cell. This gridded count data was then used to derive data for each season-year as presence/absence and density (calculated as total counts divided by total area of wetland surveyed in the given grid cell).

Environmental variable data

The differing hypotheses to be tested using the environmental data were selected based on candidate environmental drivers implicated or supported in previous research into the range and population expansion of Egyptian Goose. Environmental drivers tested were as follows:

Area of stately homes. It is well documented that the Egyptian Goose was first introduced to the UK as ornamental waterbirds on lakes, ponds and waterways in stately homes (Sutherland and Allport 1991), and range expansion is thought to have been via population growth and dispersal from these sites. The area of stately homes in each grid cell was calculated, referring to data on estates and gardens registered with Historic England and Scotland (<https://goo.gl/tjcx2>; <https://goo.gl/95Yqy3>).

Length of rivers and canals, and area of waterbodies. As waterbirds, it is likely that the Egyptian Goose will disperse outwards into new range via waterways, therefore data on the area of available river channels, lakes and reservoirs were used. The dataset on rivers and canals was downloaded from (<https://goo.gl/cEnzoq>) whilst the lakes and reservoirs were taken from the WeBS sectors dataset, which was supplied by the BTO. The waterbody data was edited so that for presence/absence, we calculated the total wetland area surveyed per grid cell, as opposed to total waterbody within a grid cell for the density analyses.

Average minimum temperature for the coldest month. As Lensink (1996) showed, minimum monthly temperature has a negative impact upon the rate of population increase, therefore suggesting that

that would be a suitable environmental variable. For this the UK Met Office's UKCP09 gridded datasets were used (<https://goo.gl/Q0qa5d>)

Average monthly rainfall. In addition to temperature variables, mean annual rainfall is a key climate gradient with the potential to influence range expansion of invasive species. For this the UK Met Office's UKCP09 gridded datasets were used (<https://goo.gl/Q0qa5d>)

Area of urban conurbations. It has been observed that non-native species tend to be associated with human-modified ecosystems in their invaded range, such as urban and agricultural areas (Gellardo, 2014). Chace and Walsh (2006) showed that increased urbanisation tends to increase avian biomass for a number of taxonomic groups, including cavity nesters, such as the Egyptian Goose. Bonter, Zuckerberg and Dickinson (2009) showed that there was a link between urbanisation and the success of an invasive bird (the Eurasian collared-dove), therefore urbanisation was included as an environmental variable. The European Environment Agency (EEA) CORINE landcover dataset was used (<http://bit.do/CORINE>) which defines urbanisation as any area where there is either continuous or discontinuous urban fabric.

Area of available grassland. As studies have shown grassland to be a preferred habitat of the Egyptian Goose (e.g. Lensink, 1998), including this habitat type as an environmental variable was logical. CORINE landcover data from the EEU was again used. All definitions for CORINE landcover types come from the EEU website: <http://bit.do/CORINE>

Area of combined urbanisation and grassland. After preliminary testing, it was decided to also include a variable that combined both grassland and urbanisation in the models. This variable was never included in a model with either of its constituent landcover types as predictors, instead, simultaneous models were run using both the combined, and the individual, variables, and the model with the highest adjusted R² variable was chosen as the final model.

Area of arable land. As studies, such as Sutherland and Allport (1991) and Magnall and Crowe (2002) have shown that the Egyptian Goose shows a habitat preference towards arable land, it was decided to include the area of available arable land as a predictor variable. Non-irrigated arable land, irrigated arable land, pastures and all heterogeneous agricultural areas were included to create this habitat specification. Data was downloaded from the CORINE section of the EEU website, which is where definitions for habitat specifications were also taken from (<http://bit.do/CORINE>)

Area of eutrophied lakes and length of eutrophied rivers. The dataset of eutrophied rivers was only available for 2015, whilst the eutrophied lakes were available for 2014, these were downloaded from (<https://goo.gl/ETD0QA> and <https://goo.gl/xCKP9X>). These were included for two reasons, 1) in

general, invasions by non-native species are hypothesised to be linked to ecosystems with high nutrient inputs, and 2) it has been suggested that similar species to the Egyptian Goose, e.g. Canada Geese, can cause eutrophication when aggregating (Rehfishch, Allan and Austin, 2010). Therefore, these eutrophication variables were included as predictors, although it is not possible to be certain of the direction of, should an association be found.

Area of protected areas. Hiley, Bradbury and Thomas (2014) showed that protected areas (PAs) are susceptible to colonisation by invading species after their populations had established themselves, and that one of these species with this link was the Egyptian Goose. Therefore, the total area of protected areas within each grid cell was quantified. The designations of protected area that we used were national nature reserved (NNRs), Ramsar sites, National Parks, sites of special scientific interest (SSSI), special areas of conservation (SACs) and special protected areas (SPAs). Data on SPAs, SACs and Ramsar sites were downloaded from (<https://goo.gl/M5V045>), whilst SSI and NNR data were downloaded from (<https://goo.gl/lvSQkY> and <https://goo.gl/nCrkmS>).

Country parks. As Hiley, Bradbury and Thomas only used PAs with a designation that met the International Union for the Conservation of Nature level IV protection, this was also the designation that we used. However, the area of country parks, as designated under the Countryside Management Act (1968), was also available. Because these sites do not carry the same levels of protection as other PAs, it was decided to keep them as a separate variable. They are generally found on the edge of urban and built up areas. Data was downloaded from: (<https://goo.gl/XEDZoV> and <https://goo.gl/Tb1Zvx>).

Longitude (X coordinate) and Latitude (Y coordinate) measured in decimalised degrees, as calculated by ArcGIS, were included to test whether space alone is a better predictor of range and population expansion than environmental factors. These are important to include as alternative predictors of range expansion of non-native species because 1) environmental gradients may appear to be strong predictors where they are simply correlated with spatial gradients along which species disperse. 2) These spatial variables may account for variation that is not explained by environmental variables tested, hence hinting at signals of dispersal unrelated to environment per se, or suggestive of environmental gradients that have not been accounted for.

Total land area of each grid cell. This was calculated using the Ordnance Survey of Great Britain (OSGB) 1km grid, and was included to control for some grid cells partially overlapping the ocean, hence partial land-area.

Occupancy of adjacent grid cells. The number of grid cells out of all grid cells adjacent to each focal grid cell, for which WeBS surveys had been carried out, and in which Egyptian Goose was present, as

a predictor of occupancy or not, and of density, of Egyptian Goose, was counted. This is intended to account for the expectation that the probability of a grid cell having Egyptian Goose presence will be proportional to the number of neighbouring grid cells that already show occupancy, or that the density of Egyptian Goose in a grid cell will be positively associated with the occupancy of neighbouring grid cells. Occupancy of adjacent grid cells was calculated using the Spatial Analyst toolbox of ArcGIS 10.4.

The temporal availability of relevant environmental datasets for the UK are presented in Table 1. Hence, we selected the three years for which CORINE landcover data is available, namely 2000, 2007 and 2012, as the time periods we focus on for our analyses (see details below) of the range and population expansion of Egyptian Goose.

Table 1. Summary of availability of the environmental data that was used in the analyses across the 21 year time period of the dataset. Crosses (x) indicate years for which data is available, semicolons (;) indicate years where the data was inferred for use in analysis and hyphens (-) indicate years for where data was not available, and was not inferred.

Environmental variables	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
Land area	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Number of surveys	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Waterbodies	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	x	;
Rivers and canals	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	x
Eutrophied rivers and lakes	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	;	;	;	;	;	x
Landcover designations	;	;	;	;	;	;	;	x	;	;	;	;	;	;	x	;	;	;	;	x	;	;
Average minimum winter temperature	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Average monthly rainfall	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Protected areas	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	x
Stately homes	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	x
Country parks	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	;	x
Time since occupation	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Occupancy	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
X and Y coordinates	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x

Environmental variables listed above were re-sampled to equivalent grid cell resolutions as the Egyptian Goose count data, namely 5-km x 5-km and 20-km x 20-km.

Analyses

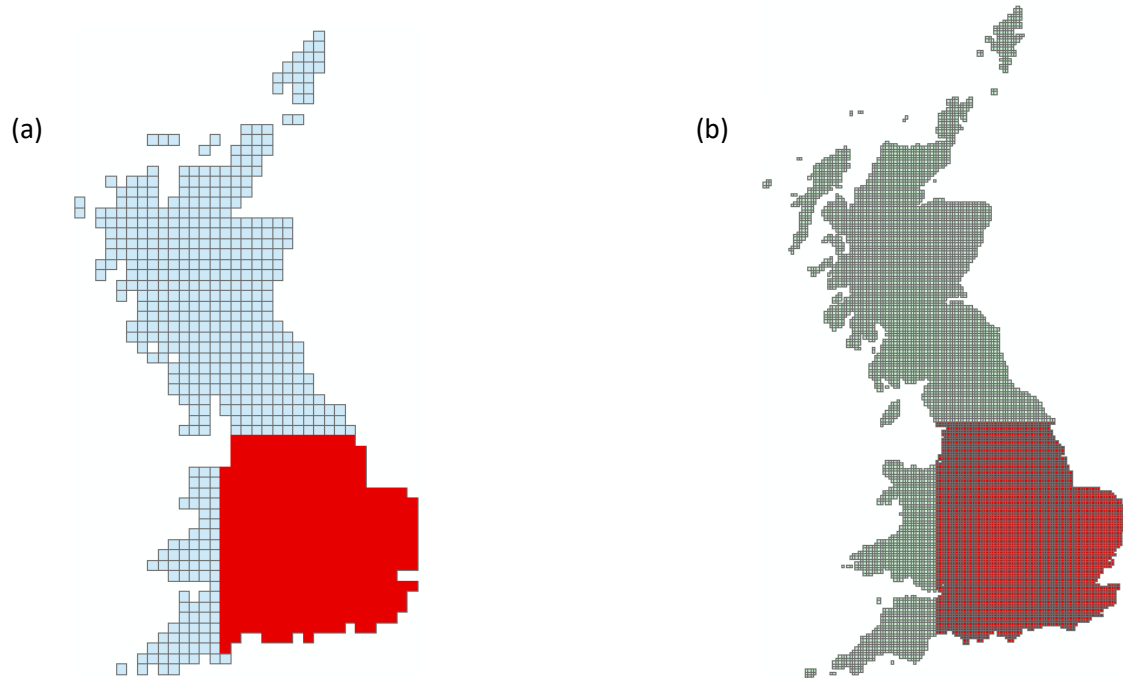
The importance of environmental variables for range and population expansion of Egyptian Goose were tested using presence/absence and population density as response variables. A model simplification technique was used to develop final models for these datasets. A backwards stepwise deletion was used from a maximal model containing all potential variables (Bradbury *et al.* 2000). Variables were entered into the model in the same order for each time period, resolution and analysis. Logistic regressions were used to model the presence/absence data, whereas generalised linear models (GLMs) with Poisson errors were used in the case of density data. As O'Hara and Kotze (2010) suggested, the data was not transformed prior to analysis.

Both sets of analyses were run at 5-km x 5-km resolution and 20-km x 20-km resolution in order to assess the influence of spatial resolution of the data on the testing of environmental hypotheses.

For the density analyses we only used grid cells (at both spatial scales) where there had been a sighting of the Egyptian Goose in at least three years across the 21 year time period, hence for which occurrence was not considered so temporary as to be accidental. Computation of final response variable data was then structured with reference to the three time periods for which there was CORINE landcover data (2000, 2007, 2012). For each of these three stages of range expansion, we chose to compute response variables over a four-year time period, running from two years prior to the CORINE data, to one year after it, hence 1998-2001, 2005-2008, and 2010-2013. At both resolutions for this part of the analysis, for all three time-periods, all grid cells showing zero density values were then removed, since we are interested in understanding the drivers of population density across grid cells in which Egyptian Goose occurred for each time-period.

For the presence/absence analyses we used a selection criterion whereby we split the count data into five-year time periods, surrounding the years for which there was availability of CORINE data, hence 1997-2001, 2004-2008 and 2009-2013. Whilst we would have ideally used two years either side of the CORINE data, this was not possible due to the most recent counts being from 2013. Using ArcGIS, we selected a continuous block of grid cells that contained the entire geographical extent-of-

occurrence of the Egyptian Goose up to 2012, including both occupied and unoccupied grid cells within this, at both 20-km x 20-km and 5-km x 5-km resolutions (Figure 1a and b, respectively). From these grid cells we then selected only those for which WeBS surveys have been carried out at least twice within each of the three time periods (Figure 2).



Figures 1. The UK grid cells approximating the geographical extent-of-occurrence within which The Egyptian goose was observed up to 2012, hence selected for analysis of presence/absence, highlighted in red: (a) at 20x20km resolution; and (b) at 5x5 km resolution.

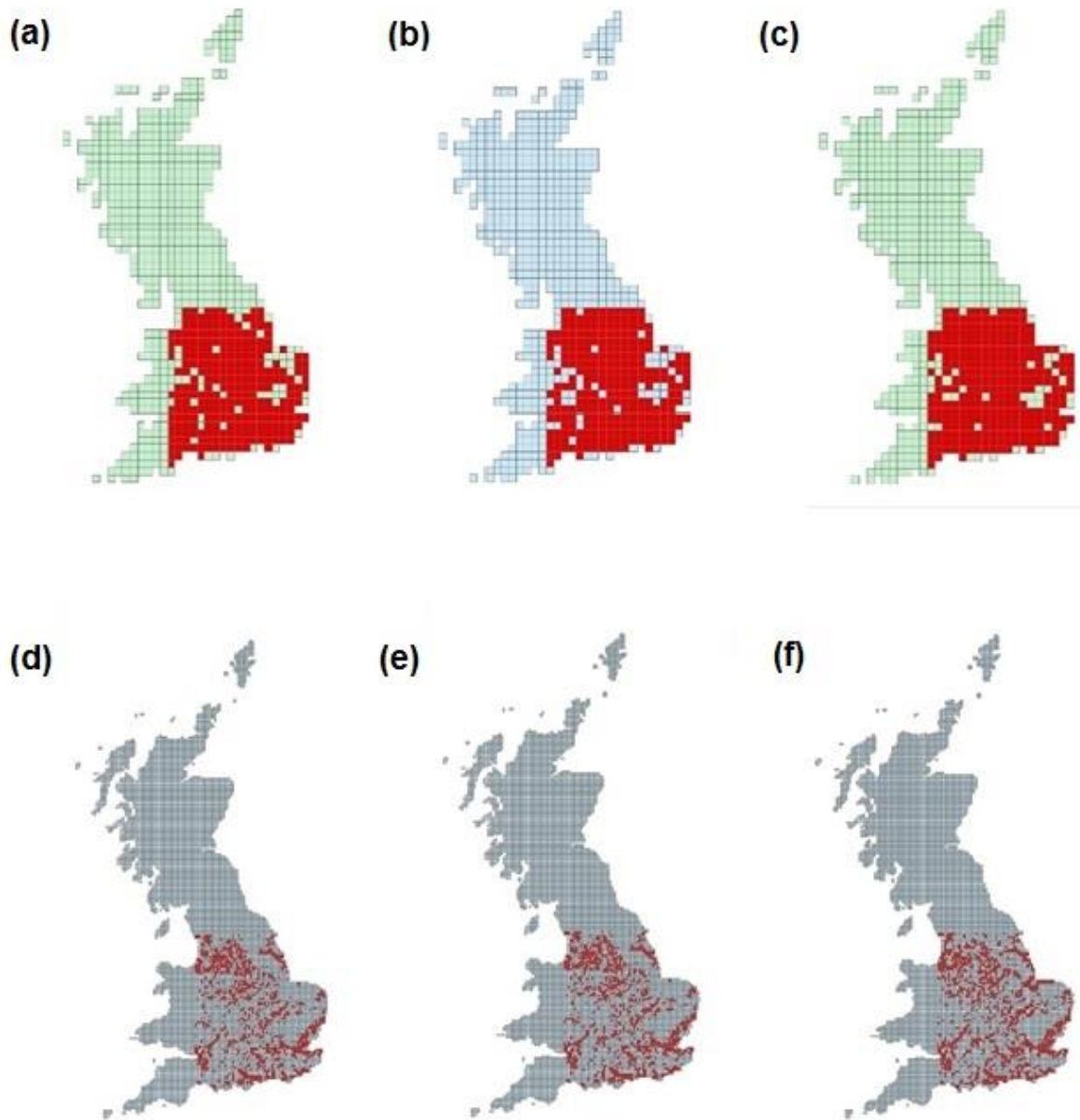


Figure 2. The UK grid cells (highlighted in red) in which WeBS surveys have been carried out at least twice within each of the three time periods: 1998-2001 (a) and (d); 2005-2008 (b) and (e); and 2010-2013 (c) and (f). (a) to (c) is at 20 x 20-km resolution; (b) to (f) is at 5 x 5-km resolution.

For both presence/absence and density analyses, we performed a backwards removal (or step-down) procedure on full models in which all candidate environmental predictors were entered initially. At each step the most non-significant predictor was removed before performing the next step. Predictor removal was stopped when all remaining predictors were significant ($P < 0.05$). Single-predictor models were then performed for candidate variables as a guide to understanding relative explanatory power of predictors and to check consistency of slope of relationship with multi-predictor models. Bonferroni corrections were applied to all single-predictor results, in order to avoid inflated type I error rates (erroneous rejection of the null hypothesis) due to multiple tests.

All variables were tested for collinearity at both spatial scales prior to performing the multiple backwards-removal regressions. The combined UrbanGrassland variable was collinear with urbanisation. Pairs of predictors which showed Pearson correlations of >0.7 were not included together in the same initial model prior to performing backwards removal. Table 2 details the Pearson correlations between UrbanGrassland and Urbanisation for each of the datasets.

Table 2. Results of Pearson's correlation test between the UrbanGrassland variable and the Urbanisation variable

Time period					
Density 5km P1	Density 5km P2	Density 5km P3	Density 20km P1	Density 20km P2	Density 20km P3
Pearsons					
0.8	0.75	0.72	0.78	0.82	0.79
Time period					
P/A 5km P1	P/A 5km P2	P/A 5km P3	P/A 20km P1	P/A 20km P2	P/A 20km P3
Pearsons					
0.76	0.78	0.81	0.84	0.73	0.76

Results

The following tables show results for the outcomes of both multi- and single- predictor models. In all cases, the B value represents the slope of the model, occupancy variables refer to the occupancy of adjacent grid cells, temperature to the average minimum monthly temperature and rainfall to the average monthly rainfall. For the multi-predictor output tables, the R^2 value refers to the adjusted R^2 value for the entire model, and all variables that were originally included in the model are shown, however, P values are only given for those that showed significance in the final model. For the single-predictor output tables, all variables were analysed, but eutrophication data was only available for the third time period. Results that are highlighted in bold are those that are significant at $P < 0.05$, after Bonferroni post-hoc analysis was undertaken. The R^2 values for these outputs refer to the R^2 values for each individual predictor.

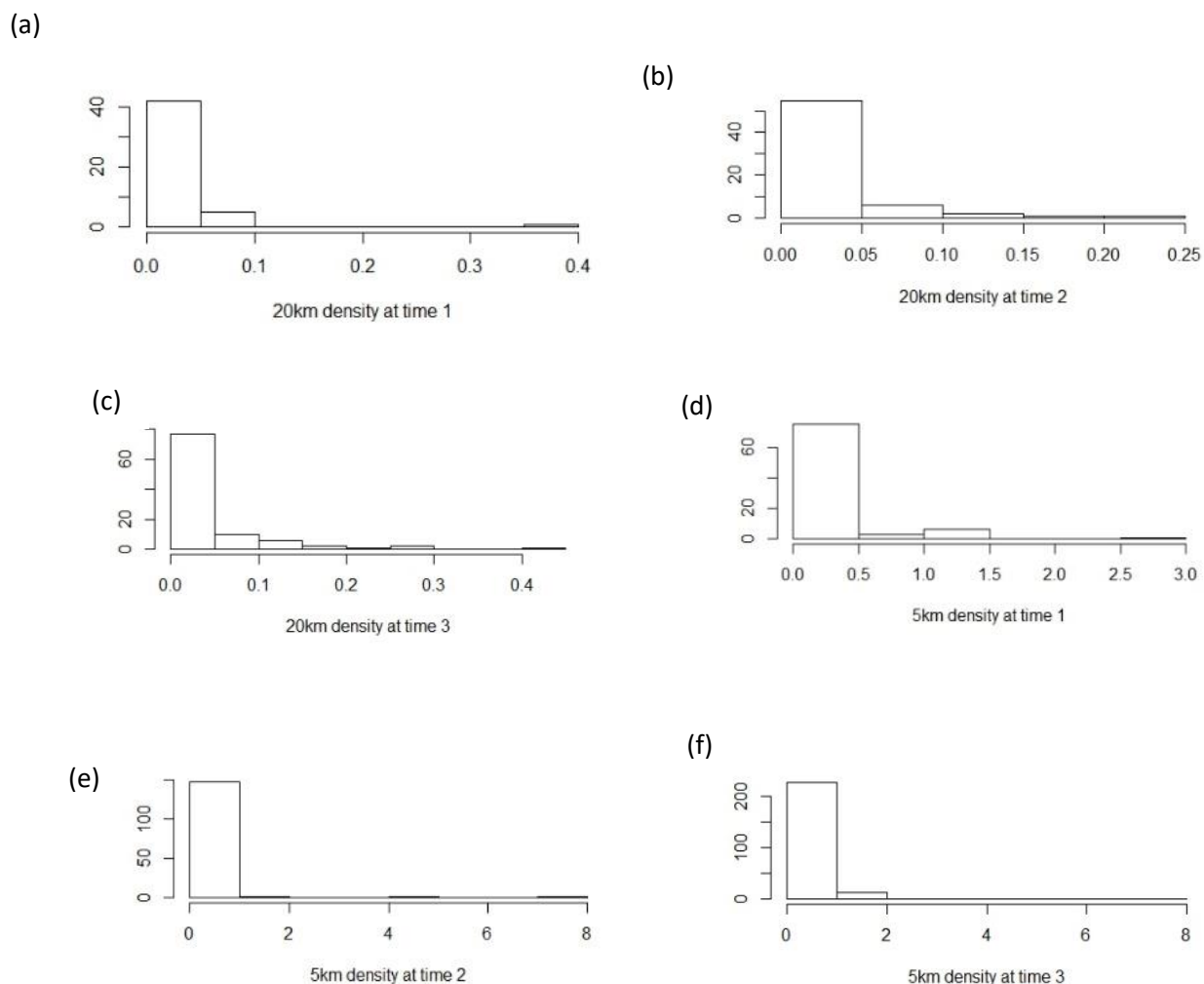


Figure 3. Histograms of density data at 20km and 5km resolution at three time periods. 3a)-c) show 20km density data at the three time periods. 3d)-f) show 5km data at the three time periods

Table 3. Results of Shapiro-Wilks test for normality with associated P values for density data at 20-km and 5-km resolution at three time periods

20km						5km					
1998-2001		2005-2008		2010-2013		1998-2001		2005-2008		2010-2013	
W	P	W	P	W	P	W	P	W	P	W	P
0.369	0	0.64	0	0.573	0	0.451	0	0.214	0	0.326	0

As can be seen from both figure 3 and from table 3, the data at both resolutions (5km and 20km) and at all three time periods were significantly different from normal. Therefore, GLMs with poisson errors were fitted. Data was not logged prior to analysis, as per (O’Hara and Kotze, 2010), who showed that GLMs with non-transformed data performed better than models fitted with transformed data.

Density

20-km x 20-km resolution

Table 4. Results of Poisson error multi-predictor models across the three time periods for density, at 20-km resolution.

Predictors	Time period (20km)								
	1998-2001			2005-2008			2010-2013		
	B	P	R ²	B	P	R ²	B	P	R ²
Land area	-	-		-	-		-	-	
Number of surveys	-	-		-1.067	<.001		-	-	
Waterbodies	-	-		-0.105	<.001		-0.074	<.001	
Rivers and Canals	-	-		-	-		-0.006	0.002	
Eutrophied rivers	-	-		-	-		-	-	
Eutrophied lakes	-	-		-	-		-	-	
Arable landcover	-	-		-	-		-	-	
Grassland landcover	-	-		-	-		-	-	
Urban landcover	-	-		-	-		-	-	
Urban grassland landcover	-1.497	<.001	0.477	-	-	0.405	-	-	0.435
Temperature	-	-		-	-		-	-	
Rainfall	-	-		-0.029	0.037		-	-	
Protected areas	-	-		0.006	<.001		-	-	
Stately homes	-	-		0.045	0.001		0.057	<.001	
Country Parks	-	-		-	-		-	-	
Time since occupation	-	-		-	-		-0.060	0.011	
Occupancy	-	-		0.024	0.029		-	-	
X coordinate	-	-		-	-		-	-	
Y coordinate	-	-		-	-		0.000	0.002	

Table 5. Results of Poisson error single-predictor models across the three time periods for density, at 20-km resolution. Superscript P values show the adjusted P value after applying Bonferroni corrections

Predictors	Time period (20km)								
	1998-2001			2005-2008			2010-2013		
	B	P	R ²	B	P	R ²	B	P	R ²
Land area	0.000	0.791	0.007	0.000	0.814	0.001	0.000	0.516	0.006
Number of surveys	-0.001	0.954	0.000	-0.016	0.202	0.000	0.037	0.954	0.010
Waterbodies	-0.001	0.149	0.173	-0.001	0.012 ^{0.204}	0.284	-0.001	0.007 ^{0.133}	0.243
Rivers and canals	0.000	0.467	0.027	0.000	0.177	0.039	0.000	0.138	0.034
Eutrophied rivers	-	-	-	-	-	-	0.000	0.660	0.003
Eutrophied lakes	-	-	-	-	-	-	0.000	0.958	0.000
Arable landcover	0.000	0.306	0.050	0.000	0.827	0.001	0.000	0.352	0.015
Grassland landcover	0.000	0.122	0.099	0.000	0.554	0.097	0.000	0.804	0.001
Urban landcover	-0.022	0.018 ^{0.306}	0.169	-0.010	0.195	0.037	0.027	0.047	0.062
Urban grassland landcover	-0.065	<.001 ^{<.001}	0.478	0.005	0.779	0.002	0.019	0.099	0.045
Temperature	-0.005	0.606	0.016	-0.007	0.429	0.013	0.003	0.652	0.003
Rainfall	0.000	0.702	0.009	-0.001	0.340	0.026	0.000	0.583	0.006
Protected areas	0.000	0.100	0.082	0.000	0.603	0.006	0.000	0.666	0.003
Stately homes	0.000	0.840	0.478	0.002	0.026 ^{0.442}	0.098	0.004	<.001 ^{<.001}	0.201
Country parks	0.001	0.664	0.010	0.000	0.830	0.001	-0.001	0.653	0.004
Time since occupation	-0.002	0.133	0.095	0.000	0.634	0.005	-0.002	0.050 ^{0.950}	0.001
Occupancy	0.001	0.905	0.001	0.003	0.206	0.038	0.005	0.963	0.049
X coordinate	0.000	0.857	0.002	0.000	0.150	0.044	0.000	0.347	0.016
Y coordinate	0.000	0.146	0.086	0.000	0.439	0.013	0.000	0.022 ^{0.418}	0.063

Table 4 shows the outputs from the multi-predictor models at the 20km resolution. In the first model, only urban grassland landcover remained significant. In the multi-predictor model for the second time period number of surveys, waterbodies, rainfall, protected areas, stately homes and occupancy are all significant. In the third time period there are five significant predictors remaining in the final model, these are: waterbodies, rivers and canals, stately homes time since occupation and Y coordinate.

In the single-predictor models at 20-km resolution, for the first time period, only urban grassland is significant and is negatively correlated with density (Table 4). There are no significant predictors in the second time period, and then in the third time period, only stately homes are significant, and this variable is positively correlated with density (Table 4).

5-km x 5-km resolution

Table 6. Results of Poisson error multi-predictor models across the three time periods for density, at 5-km resolution.

Predictors	Time period (5km)								
	1998-2001			2005-2008			2010-2013		
	B	P	R ²	B	P	R ²	B	P	R ²
Land area	-	-		19650.000	0.001		-	-	
Number of surveys	0.762	0.001		-	-		0.548	<.001	
Waterbodies	-0.834	0.013		-1.234	0.006		-1.339	<.001	
Rivers and canals	-	-		-	-		-	-	
Eutrophied rivers	-	-		-	-		-	-	
Eutrophied lakes	-	-		-	-		-	-	
Arable landcover	-	-		-	-		-0.101	0.001	
Grassland landcover	-	-		-	-		-	-	
Urban landcover	-	-		-	-		-1.107	0.010	
Urban grassland landcover	-	-	0.305	-	-	0.519	-	-	0.472
Temperature	-	-		-	-		-	-	
Rainfall	-	-		0.033	0.034		-	-	
Protected areas	-	-		-	-		-0.040	0.017	
Stately homes	-	-		-	-		-	-	
Country Parks	-	-		-	-		-	-	
Time since occupation	-	-		-	-		-	-	
Occupancy	-	-		-	-		-	-	
X coordinate	-	-		0.000	0.002		0.000	0.026	
Y coordinate	-	-		-	-		-	-	

Table 7. Results of Poisson error single-predictor models across the three time periods for density, at 5-km resolution. Superscript P values show the adjusted P value after applying Bonferroni corrections

Predictors	Time period (5km)								
	1998-2001			2005-2008			2010-2013		
	B	P	R ²	B	P	R ²	B	P	R ²
Land area	-2559.000	0.068	0.081	4539.000	<.001^{0.001}	0.139	1126.000	0.217	0.000
Number of surveys	0.154	<.001^{0.001}	0.330	0.062	0.042	0.039	0.064	0.005 ^{0.095}	0.058
Waterbodies	-0.043	0.011 ^{0.187}	0.364	-0.047	.001^{0.02}	0.261	-0.053	<.001^{0.001}	0.303
Rivers and canals	-0.009	0.153	0.048	-0.008	0.145	0.021	0.004	0.368	0.005
Eutrophied rivers	-	-		-	-		-0.020	0.018 ^{0.342}	0.042
Eutrophied lakes	-	-		-	-		-0.042	0.352	0.010
Arable landcover	-0.018	0.019 ^{0.323}	0.139	-0.009	0.107	0.025	-0.012	0.003 ^{0.057}	0.058
Grassland landcover	0.072	<.001^{0.001}	0.387	0.000	0.963	0.000	-0.014	0.005 ^{0.095}	0.058
Urban landcover	-0.166	0.272	0.029	0.129	0.170	0.017	0.100	0.179	0.011
Urban grassland landcover	0.480	0.029 ^{0.493}	0.116	0.170	0.271	0.012	0.082	0.271	0.007
Temperature	-0.303	0.001^{0.017}	-0.424	0.056	0.314	0.009	-0.011	0.794	0.000
Rainfall	0.005	0.111	0.045	0.001	0.780	0.001	0.002	0.283	0.006
Protected areas	0.007	0.017^{0.289}	0.105	-0.001	0.712	0.001	-0.004	0.040 ^{0.760}	0.037
Stately homes	-0.010	0.767	0.002	-0.002	0.896	0.000	0.020	0.197	0.008
Country parks	-0.004	0.920	0.000	-0.019	0.468	0.007	-0.028	0.289	0.013
Time since occupation	0.029	0.849	0.103	-0.006	0.465	0.005	-0.005	0.345	0.006
Occupancy	-0.028	0.334	0.022	-0.024	0.226	0.014	-0.007	0.018 ^{0.342}	0.042
X coordinate	0.000	0.871	0.001	0.000	0.005	0.084	0.000	0.328	0.006
Y coordinate	0.000	0.125	0.056	0.000	0.760	0.001	0.000	0.009 ^{0.171}	0.043

In the multi-predictor models at the 5km resolution, for the first time period, only number of surveys and waterbodies remained significant. In the second time period, land area, waterbodies, rainfall and the x coordinate were all shown to be significant (Table 6). The number of predictors that showed significance increases in the third model, where number of surveys, waterbodies, arable landcover, urban landcover, protected areas and the x coordinate are all significant.

In the single-predictor models at the 5km resolution, for the first time period number of surveys, grassland landcover and protected areas are all positively correlated with density, whilst temperature is negatively correlated (Table 7). In the second time period, land area is the only predictor that is significantly positively correlated, whilst waterbodies is the only predictor that is significantly negatively correlated. In the third time period the only significant predictor is waterbodies, which is negatively correlated.

Presence/Absence

20 x 20km resolution

For the multi-predictor logistic regression models at 20km resolution, the McFadden R^2 values increase from 0.235 in the first period, to 0.254 in the second, and finally to 0.473 in the third period (Table 7). In the first model, arable landcover, longitude country parks, rivers and canals and temperature are positively significant. In the second time period, only country parks, land area, latitude and protected areas are all significantly positively associated, whilst rainfall is significantly negatively associated. In the final time period, rivers and canals, latitude and occupancy are positively significant, whilst rainfall is negatively significant.

For the single-predictor logistic regression models at 20km resolution, occupancy, arable landcover, protected areas, longitude, latitude, rivers and canals and urban landcover are positively significant in the first time period (Table 8). Rainfall is the only predictor to be negatively correlated in the first period. The number of variables that were significantly positively associated remains the same in the 2nd period and includes protected areas, rainfall, rivers and canals, longitude, latitude and urban grassland landcover. Rainfall remains as the only negatively correlated significant predictor in the 2nd time period. In the final period occupancy, arable landcover, country parks, protected areas, rivers and canals, stately homes, temperature, urban landcover, urban grassland landcover, longitude and latitude are all positively significant. Rainfall and grassland landcover are the only two predictor variables that are significantly negatively associated in this period.

Table 8. Results of logistic regression multi-predictor models across the three time periods for presence/absence, at 20-km resolution. R² values shown are the McFadden R² value for the entire model.

Predictors	Time period (20km)									
	1998-2001			2005-2008			2010-2013			
	B	P	R ²	B	P	R ²	B	P	R ²	
Land area	-	-	0.424	0.007	0.024	0.347	-	-	0.608	
Number of surveys	-	-		-	-		-	-		
Waterbodies	-	-		-	-		-	-		
Rivers and canals	0.012	<.001		-	-		-	0.028		<.001
Eutrophied rivers	-	-		-	-		-	-		-
Eutrophied lakes	-	-		-	-		-	-		-
Arable landcover	0.003	0.005		-	-		-	-		-
Grassland landcover	-	-		-	-		-	-0.050		0.028
Urban landcover	-	-		-	-		-	-		-
Urban grassland landcover	-	-		-	-		-	-		-
Temperature	0.655	0.001		-	-		-	-		-
Rainfall	-	-		-0.018	0.002		-0.022	<.001		
Protected areas	0.009	0.002		0.022	<.001		-	-		
Stately homes	-	-		-	-		-	-		
Country parks	0.207	0.007		0.356	<.001		-	-		
Time since occupation	-	-		-	-		-	-		
Occupancy	-	-		-	-		-	0.330		<.001
X coordinate	0.000	<.001	-	-	-	0.000	0.000			
Y coordinate	-	-	0.000	<.001	-	0.000	0.006			

Table 9. Outputs of 20km logistic regression single-predictor models across the three time periods for presence/absence. Superscript P values show the adjusted P value after Bonferroni post-hoc analysis. R² values shown are the McFadden R² value for the individual predictors.

Predictors	Time period (20km)								
	1997-2001			2004-2008			2009-2013		
	B	P	R ²	B	P	R ²	B	P	R ²
Land area	0.004	0.114	0.006	0.006	0.027 ^{0.459}	0.012	0.005	0.003 ^{0.057}	0.018
Number of surveys	0.358	0.100	0.006	0.877	0.010 ^{0.170}	0.021	0.551	0.007 ^{0.133}	0.017
Waterbodies	1.590	0.887	0.448	3.178	0.830	0.519	4.083	0.505	0.628
Rivers and canals	0.015	<.001^{<.001}	0.147	0.019	<.001^{<.001}	0.229	0.037	<.001^{<.001}	0.347
Eutrophied rivers	-	-	-	-	-	-	0.444	0.003 ^{0.054}	0.023
Eutrophied lakes	-	-	-	-	-	-	23.814	0.095	0.318
Arable landcover	0.006	<.001^{<.001}	0.051	0.004	<.001^{0.001}	0.026	0.010	<.001^{<.001}	0.166
Grassland landcover	-0.001	0.593	0.001	0.001	0.206	0.003	-0.179	<.001 ^{<.001}	0.179
Urban landcover	0.677	.003^{0.048}	0.016	0.418	0.039 ^{0.663}	0.007	2.030	<.001^{<.001}	0.197
Urban grassland landcover	0.564	0.022 ^{0.374}	0.011	1.074	<.001^{0.006}	0.026	0.643	.001^{0.019}	0.019
Temperature	0.297	0.050 ^{0.850}	0.014	0.000	0.939	0.000	0.201	0.001^{0.018}	0.021
Rainfall	-0.026	<.001^{<.001}	0.076	-0.023	<.001^{<.001}	0.082	-0.038	<.001^{<.001}	0.210
Protected areas	0.014	<.001^{<.001}	0.185	0.032	<.001^{<.001}	0.121	0.271	<.001^{<.001}	0.220
Stately homes	1.258	<.001^{<.001}	0.023	1.346	<.001^{<.001}	0.044	0.089	<.001^{<.001}	0.045
Country parks	0.490	<.001^{<.001}	0.080	0.653	<.001^{<.001}	0.098	4.007	<.001^{<.001}	0.212
Time since occupation	0.073	0.672	0.024	0.064	0.083	0.049	0.060	0.046 ^{0.874}	0.126
Occupancy	0.732	<.001^{<.001}	0.100	0.610	<.001^{<.001}	0.144	0.599	<.001^{<.001}	0.306
X coordinate	0.000	<.001^{<.001}	0.123	0.000	<.001^{<.001}	0.121	0.023	<.001^{<.001}	0.100
Y coordinate	0.000	<.001^{<.001}	0.064	0.000	<.001^{<.001}	0.112	0.000	<.001^{<.001}	0.182

5km x 5km resolution

Table 10. Results of logistic regression multi-predictor models across the three time periods for presence/absence, at 5-km resolution.

Predictors	Time period (5km)								
	1997-2001			2004-2008			2009-2013		
	B	P	R ²	B	P	R ²	B	P	R ²
Land area	-	-	0.398	-	-	0.659	-	-	0.614
Number of surveys	-	-		-	-		0.298	<.001	
Waterbodies	-	-		-	-		-	-	
Rivers and canals	-	-		-	-		-	-	
Eutrophied rivers	-	-		-	-		0.527	0.005	
Eutrophied lakes	-	-		-	-		0.120	<.001	
Arable landcover	0.075	0.002		0.033	0.031		0.032	0.001	
Grassland landcover	-	-		0.088	<.001		-	-	
Urban landcover	-	-		-	-		-	-	
Urban grassland landcover	-	-		-	-		-	-	
Temperature	-	-		-	-		-	-	
Rainfall	-	-		-	-		-	-	
Protected areas	-	-		-	-		-	-	
Stately homes	-	-		-	-		0.115	0.037	
Country Parks	0.239	0.048		0.281	0.002		-	-	
Time since occupation	-	-		-	-		-	-	
Occupancy	0.757	<.001	0.911	<.001	0.599	<.001			
X coordinate	-	-	0.000	<.001	0.000	<.001			
Y coordinate	0.000	0.031	0.000	<.001	0.000	<.001			

Table 11. Results of logistic regression single-predictor models across the three time periods for presence/absence, at 5-km resolution. Superscript P values show the adjusted P value after Bonferroni post-hoc analysis

Predictors	Time period (5km)								
	1997-2001			2004-2008			2009-2013		
	B	P	R2	B	P	R2	B	P	R2
Land area	0.028	0.029 ^{0.493}	0.000	-0.007	0.727	0.000	-0.044	0.164	0.001
Number of surveys	0.233	0.032 ^{0.544}	0.002	0.178	0.033 ^{0.561}	0.002	0.289	<.001 ^{<.001}	0.007
Waterbodies	0.055	0.063	0.001	0.014	0.585	0.000	0.068	0.025 ^{0.475}	0.005
Rivers and canals	0.017	0.017 ^{0.289}	0.001	0.006	0.001 ^{0.017}	0.000	0.014	0.262	0.001
Eutrophied rivers	-	-	-	-	-	-	0.717	0.428	0.008
Eutrophied lakes	-	-	-	-	-	-	0.242	0.565	0.057
Arable landcover	0.119	0.275	0.025	0.079	0.118	0.020	0.080	0.038 ^{0.722}	0.042
Grassland landcover	-0.076	0.013 ^{0.221}	0.006	0.005	0.983	0.000	-1.816	<.001 ^{<.001}	0.051
Urban landcover	1.299	0.791	0.011	0.950	0.045 ^{0.765}	0.011	0.944	0.002 ^{0.038}	0.016
Urban grassland landcover	0.168	0.631	0.000	1.102	0.145	0.006	0.171	0.065	0.000
Temperature	0.223	0.019 ^{0.323}	0.003	0.166	0.159	0.022	0.260	0.304	0.015
Rainfall	-0.014	0.252	0.017	-0.011	0.596	0.019	-0.019	0.005	0.075
Protected areas	-0.003	0.680	0.000	-0.006	0.941	0.001	-0.002	0.141	0.000
Stately homes	0.077	0.436	0.000	0.187	0.006 ^{0.102}	0.005	0.151	0.061	0.004
Time since occupation	0.060	0.357	0.001	0.078	0.482	0.009	0.090	0.384	0.007
Country parks	0.343	0.350	0.004	0.415	0.431	0.009	0.271	0.283	0.004
Occupancy	0.821	0.716	0.201	1.216	0.266	0.130	0.996	0.180	0.195
X coordinate	0.000	0.087	0.057	0.000	0.019 ^{0.323}	0.074	0.000	<.001 ^{<.001}	0.153

Table 10 shows the outputs from the multi-predictor logistic regression models for the 5km resolution. In the first time period, latitude, occupancy, arable landcover and country parks are all positively significantly associated with presence/absence, whilst there are no variables that are significantly negatively associated with presence/absence. In the second time period, there are again no variables that are negatively associated with presence/absence, and occupancy, arable landcover, country parks, latitude, longitude and grassland landcover are all positively significant. In the third time period, number of surveys, stately homes, eutrophied rivers and lakes, arable landcover, longitude, latitude and occupancy are all positively significant, whilst there are no negatively significantly associated predictors. The McFadden R^2 value changes from 0.309 in the first period, to 0.659 (second period) to 0.614 in the third period.

For the single-predictor logistic regression models at 5-km resolution, none of the predictors showed significance in the first time period, following Bonferroni corrections (Table 11). In the second time period, only rivers and canals were significant, showing a positive slope. In the final period, number of surveys, urban landcover and longitude were significantly positively associated with presence/absence, whilst only grassland landcover was significantly negatively associated.

Discussion

Rivers and canals

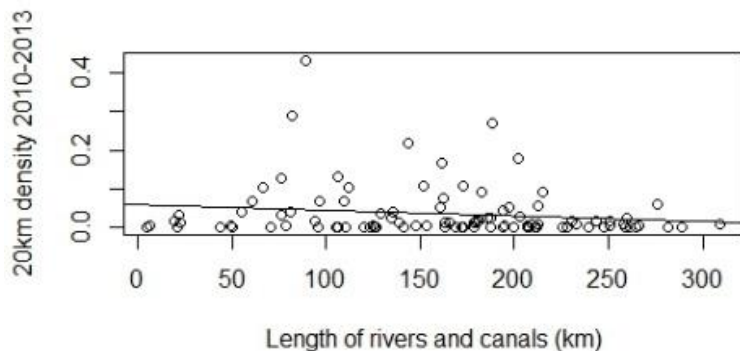


Figure 4. Plot of 20km density at the third time period (2010-2013) against the length of rivers and canals, fitted with a regression line

The a priori hypothesis for this project regarding the length of waterways was that they would be positively correlated with both density and with presence/absence, this was because studies have shown that both in their native range in South Africa, and in their non-native range in the Netherlands, they colonise rivers as well as other waterbodies (Lensink, 1999, Magnall and Crowe, 2002). Looking at the density GLMs, this variable was not significant in any of the multiple predictor models at the 5km resolution, and was only significant in the third time period at the 20km resolution. During this time period, it was negatively correlated with density, which appears to suggest that the Egyptian Goose prefers other types of waterbodies.

There is a significant positive relationship between lengths of rivers and canals and presence in the first and third time periods at the 20km resolution in the multi-predictor models, and throughout the single predictor models at the same resolution, as can be seen in Figure 4. This suggests that the greater the total length of rivers and canals is in a grid cell, the higher the likelihood of Egyptian Goose being present in that grid cell. The greater importance of this variable at the coarser sampling resolution is notable although the reasons for this are uncertain. It may be that rivers and canals provide a network of connectivity and proximity with suitable waterbodies in the surrounding landscape, but that the increased likelihood of Egyptian Goose presence in an associated grid cell is more apparent at coarser resolutions.

The importance of rivers and canals confirms what is known from other studies that have shown that the Egyptian Goose is resident on waterways in both its native and non-native ranges (Lensink, 1999; Magnall and Crowe, 2002). Nevertheless, it is of interest to contrast this finding with the weaker importance of waterbody area. A potential explanation for the positive correlation in the presence/absence analysis is that rivers and canals provide greater connectivity, and/or provide obvious linear features, promoting Egyptian Goose dispersal through landscapes.

A potential reason for the differences in direction of significance between the density and presence/absence analyses is that whilst a network of waterways is beneficial for colonisation of a given grid cell, the Egyptian Goose uses other waterbodies, such as lakes, to nest around. This could then lead to a negative correlation between density and length of waterways.

Stately homes

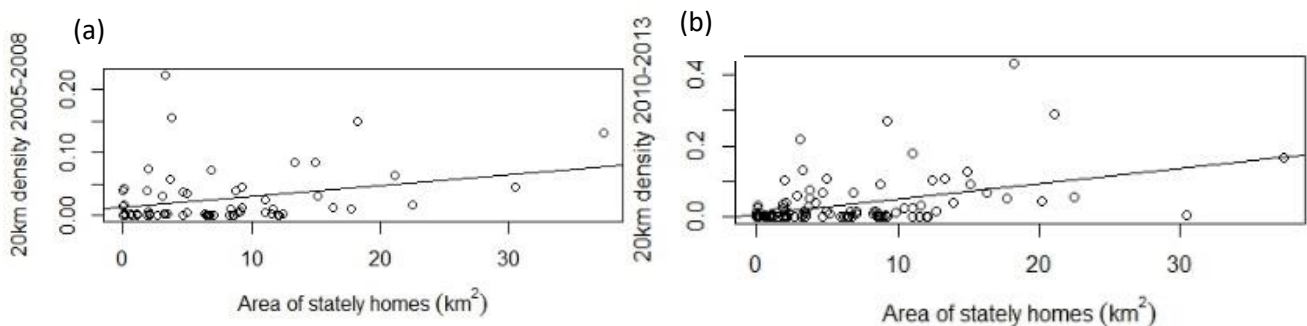


Figure 5: Plot of 20km density in the second time period (2005-2008) (a), and in the third time period (2010-2013) (b) against the area of stately homes within grid cells, both fitted with regression lines

Historically, interest in the Egyptian goose as an ornamental species is known to have been a reason for its introduction into England via privately owned country estates (Sutherland and Allport 1991). More recently, the species is known to have been resident at stately homes throughout Norfolk as well as in other parts of this species' range within England (Sutherland and Allport 1991). If any association between Egyptian goose and country estates is historical rather than for particular ecological, habitat-associated reason, then it would be expected that the earliest time periods might show stronger significance of stately homes as a predictor. However, this was contrary to our findings for density of Egyptian goose which were that area of stately homes was not significant at all at the 5-km resolution, and was significant in the second and third time periods at the 20-km resolution. The R^2 value increasing from 0.098 to 0.201 between second and third time periods, further indicates that this variable is becoming more important through time rather than less. A potential reason for the differences in significance between the sampling resolutions and the significance of the area of stately homes is that at 5-km this variable was much more zero-inflated. In other words, at 20-km resolution there is a larger area in which stately homes can potentially be found. The alternative ecological explanation to the historical hypothesis, that Egyptian Goose favours the habitats typical of stately homes, such as open grassland with accessible sources of water, is somewhat supported by the temporally increasing explanatory power of stately homes as a predictor of density. The much weaker support for stately homes as a predictor of presence/absence may be because there is an even smaller proportion of grid cells in which stately homes are found when the dataset additionally includes grid cells in which Egyptian goose is not found at all.

Waterbodies

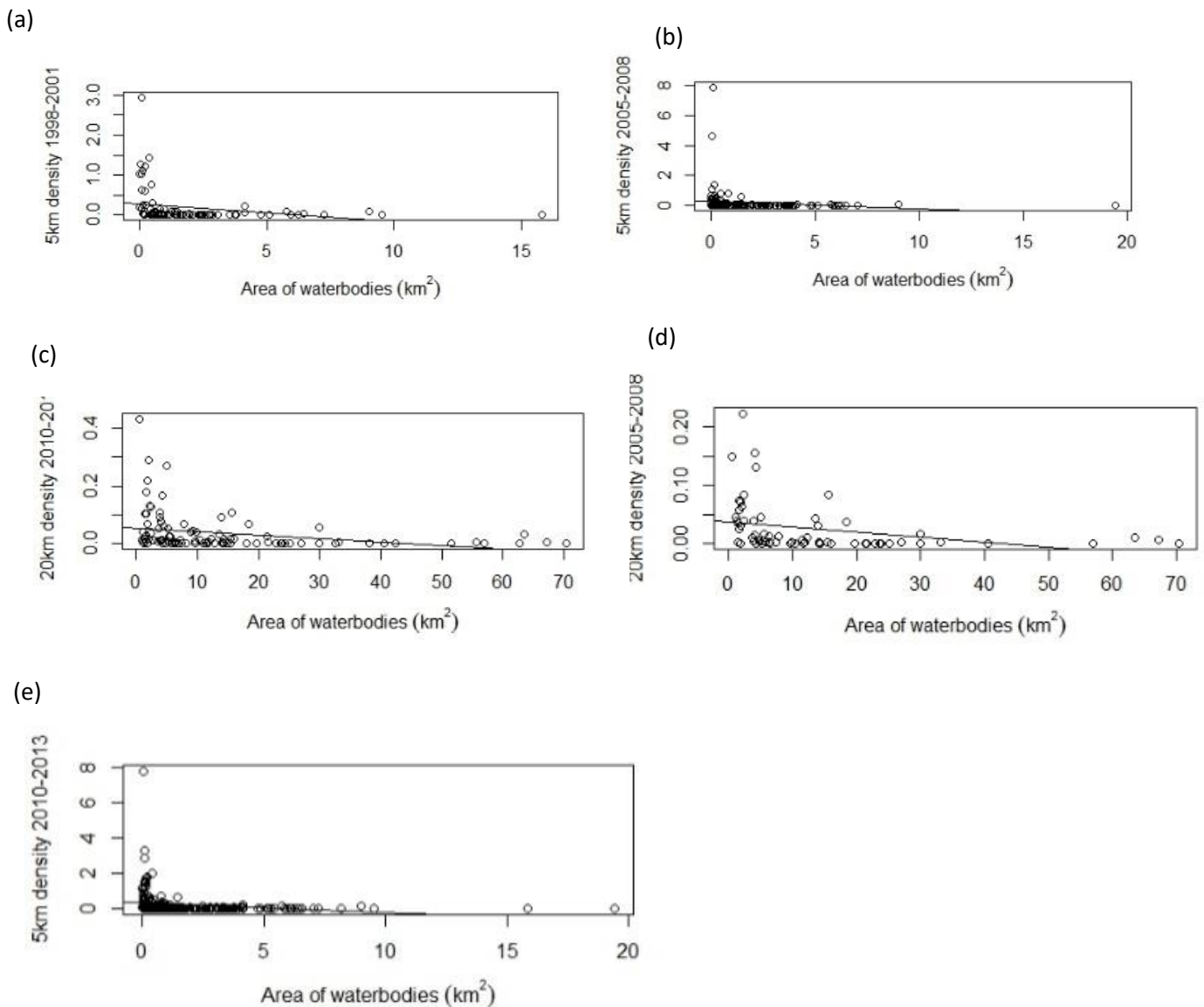


Figure 6: Plots of 5km density in the first (1998-2001) (a), second (2005-2008) (b) and third (2010-2013) (c) time periods and of 20km density in the second (d) and third (e) time periods, against the area of waterbodies within a grid cell, all fitted with regression lines

As the area of a waterbody increases, the available area of water for waterbirds to use proportionally decreases. This is because the middle of the waterbody is too deep for most species to feed in, thus a larger area of waterbody results in a smaller area, proportionally, that is usable by waterbirds. Therefore, the apriori hypothesis linked to this variable was an expected negative relationship between waterbodies and density. When looking at the density analysis waterbodies were significant

at all three time periods at the 5km resolution, and the latter two time periods at the 20km resolution, as can be seen in Figure 6. At all time periods that waterbodies were significant, they were negatively associated with density.

When considering the presence/absence data, the area of waterbodies wasn't significant at either resolution across any of the three time periods in both the single and multi-predictor models. This suggests that area of waterbodies is not an important predictor of the presence of Egyptian Goose. A potential reason for the change in significance between the density and the presence/absence analyses is that the proportionally decreased area of available useable waterbody will limit densities, as previously discussed, however, this does not translate to a similar limiting effect on the presence of individuals within a grid cell.

Rainfall

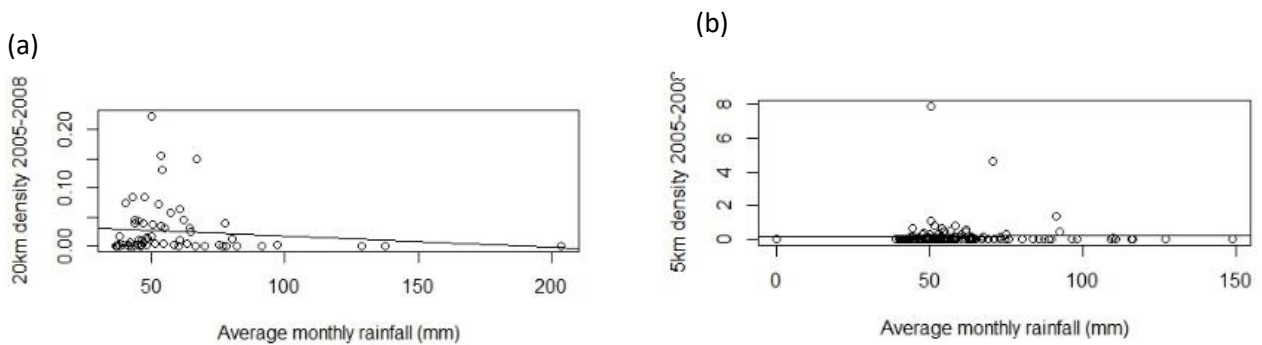


Figure 7: Plot of 20km density in the second time period (2005-2008) (a), and 5km density in the second time period (b) against the average monthly rainfall for grid cells, both fitted with regression lines

Previous studies have suggested that there may be a positive correlation between increased levels of rainfall and counts in the Egyptian Goose (e.g. Eltringham, 1974). The main factor is thought to be the increased agricultural productivity that arises as a result of increased rainfall. This factor could increase the potential for population growth of the Egyptian goose. This hypothesis is supported when considering the density analyses at the 5km resolution, where there is a positive relationship between rainfall and density in the second time period. However, when looking at the 20km resolution, this trend is reversed, and there is a significant negative relationship between rainfall and density, as can be seen in Figure 7.

Rainfall was found to be non-significant for presence/absence across all of the multi-predictor models at 5km, but was negatively significant in the second and third periods at 20km. It was also negatively significant at every period at the 20km resolution in the single-predictor models, with explanatory power (R^2) increasing through time.

The explanation for negative relationships remains uncertain. The Egyptian Goose may have spread out from stately home sites that are not climatically optimal for the species, in which case range expansion might be expected to progress in a way that favours colonisation of more climatically favourable sites. Nevertheless, it is probably too early to conclude much about this as the population expansion is likely to be far away from reaching any kind of equilibrium. Related to this issue, rainfall could be acting as a surrogate predictor for a spatial component of range expansion, as there is a strong correlation between longitude and the location of this species. Rainfall increases from East to West in England, and since the Egyptian Goose has expanded its range and population predominantly from the East, the negative correlation could be an artefact of this dispersal and range expansion process resulting in greater levels of occupancy in the East.

Occupancy

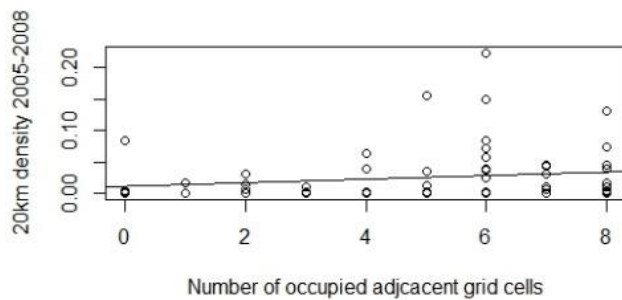


Figure 8: Plot of 20km density at the second time period (2005-2008) against the number of occupied adjacent grid cells, fitted with a regression line

The hypothesis for this variable was that grid cells that had higher levels of occupancy of neighbouring cells would have correspondingly higher densities than those that did not.

Rainfall was found to be non-significant for presence/absence across all of the multi-predictor models at 5km, but was negatively significant in the second and third periods at 20km. It was also negatively significant at every period at the 20km resolution in the single-predictor models, with explanatory power (R^2) increasing through time.

The explanation for negative relationships remains uncertain. The Egyptian Goose may have spread out from stately home sites that are not climatically optimal for the species, in which case range expansion might be expected to progress in a way that favours colonisation of more climatically favourable sites. Nevertheless, it is probably too early to conclude much about this as the population expansion is likely to be far away from reaching any kind of equilibrium. Related to this issue, rainfall could be acting as a surrogate predictor for a spatial component of range expansion, as there is a strong correlation between longitude and the location of this species. Rainfall increases from East to West in England, and since the Egyptian Goose has expanded its range and population predominantly from the East, the negative correlation could be an artefact of this dispersal and range expansion process resulting in greater levels of occupancy in the East.

Other non-conclusive variables

The apriori hypothesis regarding landcover was that there would be a positive correlation with urbanisation, grassland and arable land. However, there was no consistent link proven between either density or presence/absence and these landcover designations. Despite this it is obvious that the Egyptian Goose still nests in tree-hole cavities in grassland, and is often seen in urban areas. To definitively prove whether there is a link between these landcover designations and either density or present/absence would require further study. It could be that the Egyptian Goose is generalist enough in its habitat requirements that any signal is too weak to be detected through this method of analysis.

The lack of a consistent signal from temperature from this analysis does not preclude there being a link between lower temperatures and lower densities and/or counts. It could be that as average minimum monthly temperatures continue to increase, especially in winter, any signal that is present will grow stronger. However, further analysis would be required to determine whether this is the case.

Finally, whilst protected areas have been previously hypothesised to be supporting populations of Egyptian Geese, there was no consistent signal that this was the case. Whilst Hiley, Bradbury and Thomas (2013) suggested that there was a link, their definition of protected area was much narrower than the one used in this project. Therefore, whilst it could be possible that Egyptian Geese are using the protected areas, they could be enough of a generalist species that any signal is getting lost as a result of other landcover types. Alternatively, it could be that the broader definition of protected areas used in this study weakens any signal to the extent where it is lost. As previously stated though to prove a link definitively further study would have to be undertaken.

Limitations and further study

There were some limitations to this study and to the analysis that we undertook. These were that, especially at the 20-km resolution, the earlier time periods were zero-inflated for density, and thus removing the zeros reduced the sample size significantly. This made testing the number of predictor variables that we did problematic as the ratio of grid cells (samples) to predictors was lower than is desirable for statistically robust conclusions to be drawn. There are also problems associated with the usage of the stepwise modelling technique, as were discussed by (Whittingham *et al.* 2006). The limitations of this technique can be summarised as: potential bias in parameter estimation, an inherent problem of multiple hypothesis testing and a reliance on a single best model.

Another limitation was that the eutrophication data was only available for the third time period, and thus we could not include it in analyses for earlier periods. This meant that it wasn't possible to assess the relative influence of these variables across the time periods selected for the study.

In hindsight, and if we had more time, we would have treated certain environmental variables differently. For example, in addition to testing the importance of area of stately homes in a given grid cell as a predictor of the presence/absence and density of Egyptian Goose within that grid cell, we could have tested the distance a grid cell was from the nearest stately home known to have had long-term (historical) populations of Egyptian Goose present, hence the role of stately homes as source populations. We could also have tested the utility of total perimeter distance of waterbodies within a grid cell, as an alternative to total waterbody area, as a predictor of density and presence/absence. We could also have quantified connectivity of grid cells to neighbouring grid cells in terms of shared waterways (rivers and canals) for use as a test of waterway connectivity as a predictor of range expansion.

With the benefit of more time it would also have been informative to look at spatio-temporal variation in the rate of change of Egyptian goose population numbers, explore the which grid cells in each time period were where the rate was highest, and identify the environmental drivers that best predicted this variation.

Another potential recommendation for future research would be to resample to a third spatial sampling resolution, possibly 1x1km, in an attempt to further explore how understanding of range and population expansion is influenced by different spatial scales of analysis.

It could have been beneficial to test the environmental variables within the backwards removal models by Akaike Information Criterion (AIC), rather than P value. AIC is generally used to predict the quality and goodness of fit of models, as a replacement for the base P value. If this project were to be run again, it would certainly boost the confidence in the final model outputs if they were tested using AIC instead of P value. Using AIC is useful because it can take into account sample size, by increasing the relative penalty for model complexity with small datasets, this could have been very useful in this project, given the previously discussed problems with small datasets (Burnham and Anderson, 2002).

Conclusions

This study has furthered the knowledge of the trajectory and drivers of the range and population expansion of the Egyptian Goose across the UK. Previous studies of range expansion of the species in the UK were limited in their spatial scale, largely also because the range expansion of the species had not advanced to the wider geographic extent included in this study. The larger spatial extent of this study and the fact that it includes a more advanced stage of range expansion therefore contributes to its novelty. The opportunity to look at environmental associations at different stages of the range expansion have allowed novel insights to be made.

The rate of occupancy of new areas has been shown to increase through time, at a new faster rate in the latter and more recent periods of the expansion phase. In the first instances of range expansion, and for the first 10 years, there is a faster rate of grid cell occupancy than there is of wetland occupancy. This suggests that populations of the Egyptian Goose are colonising grid cells, and moving on without colonising all of the available wetland area. This suggests that range expansion may spread from wetlands in one grid cell to wetlands in a neighbouring grid cell more rapidly in many cases than spread between wetlands within the same grid cell in the early stages of expansion. However, this trend is reversed in the latter stages of expansion, coinciding with an increase in the rate at which both wetland area and grid cells are occupied. This then suggests that whilst there are still meta-populations colonising new areas of the country, there are also meta-populations filling out the already colonised grid cells, and that this appears to be happening at a faster rate than new grid cells are being occupied.

This project has shown that waterbodies has a consistent negative relationship with density of Egyptian Geese across two distinct spatial resolutions, and it has been theorised that this could be due to the area of a wetland including a proportion of area that is not used. It has been theorised that whilst there has been shown to be a historic link between Egyptian Goose and stately homes by previous studies, that there is a still potential link between stately homes densities. There was shown to be a positive relationship at the 20km resolution, in latter periods, although this relationship was not mirrored by a similar relationship at the finer resolution.

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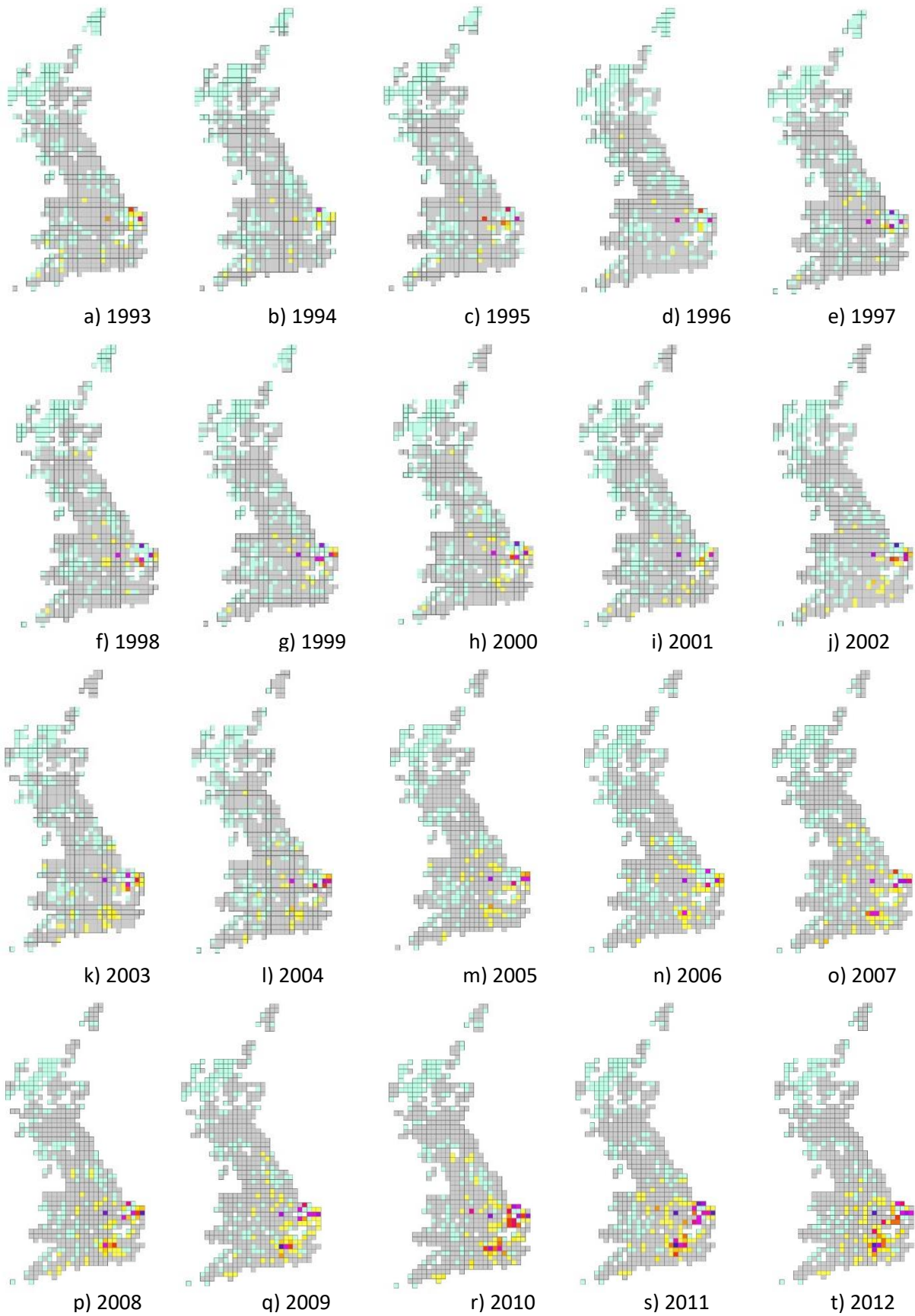
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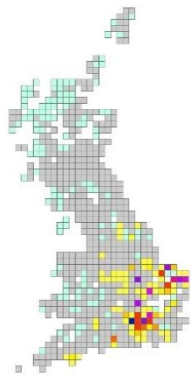
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Appendix I

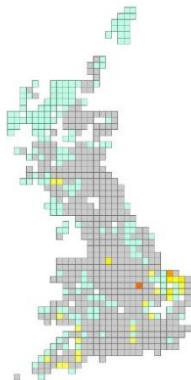
Figure S1 – Autumn Counts



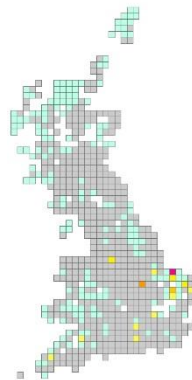


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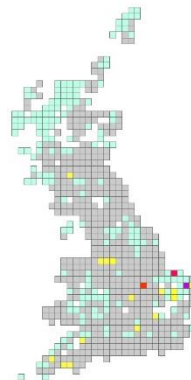
Figure S2 – Winter Counts



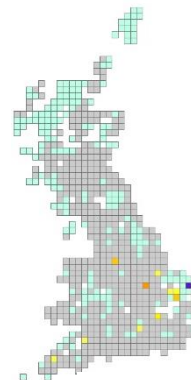
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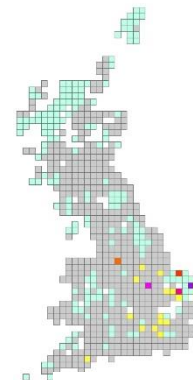
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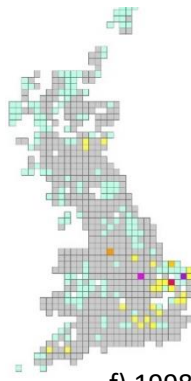
c) 1995



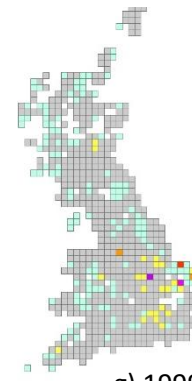
d) 1996



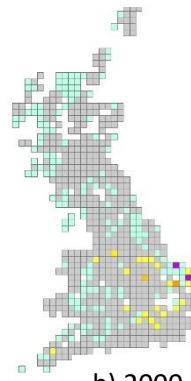
e) 1997



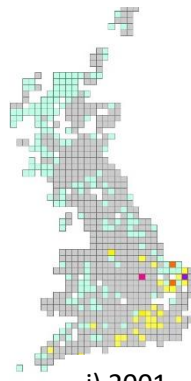
f) 1998



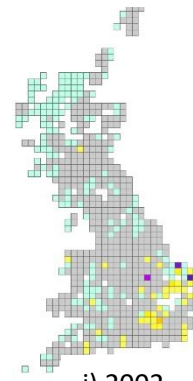
g) 1999



h) 2000



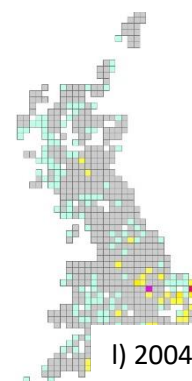
i) 2001



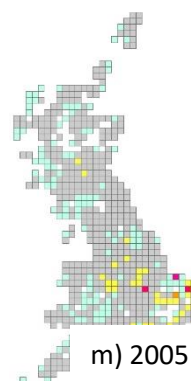
j) 2002



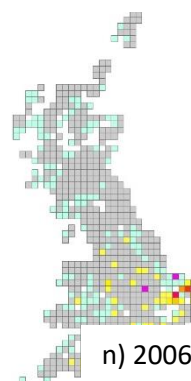
k) 2003



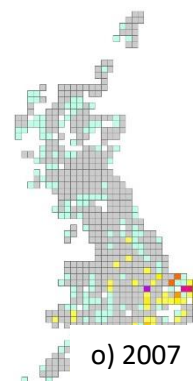
l) 2004



m) 2005



n) 2006



o) 2007

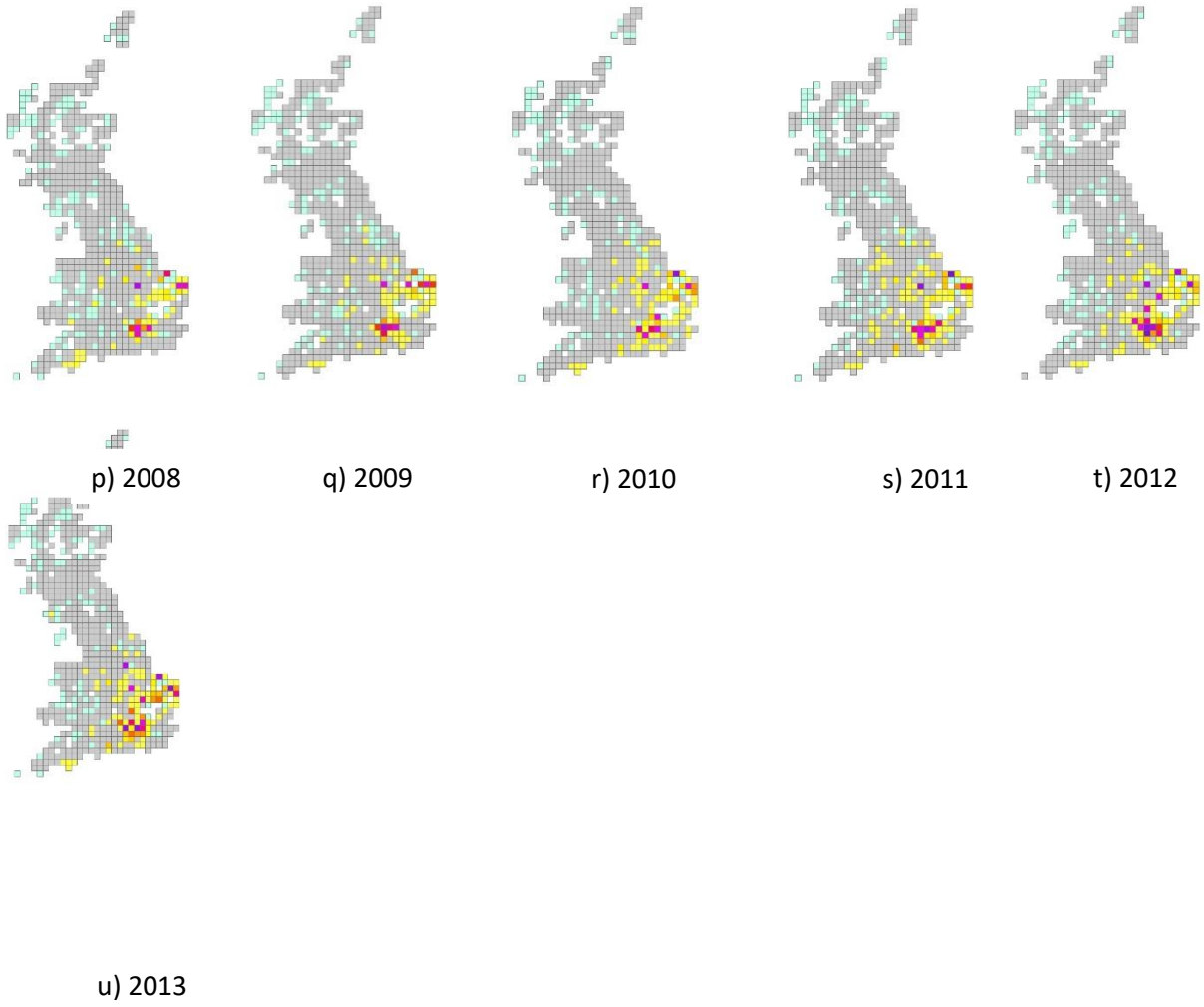
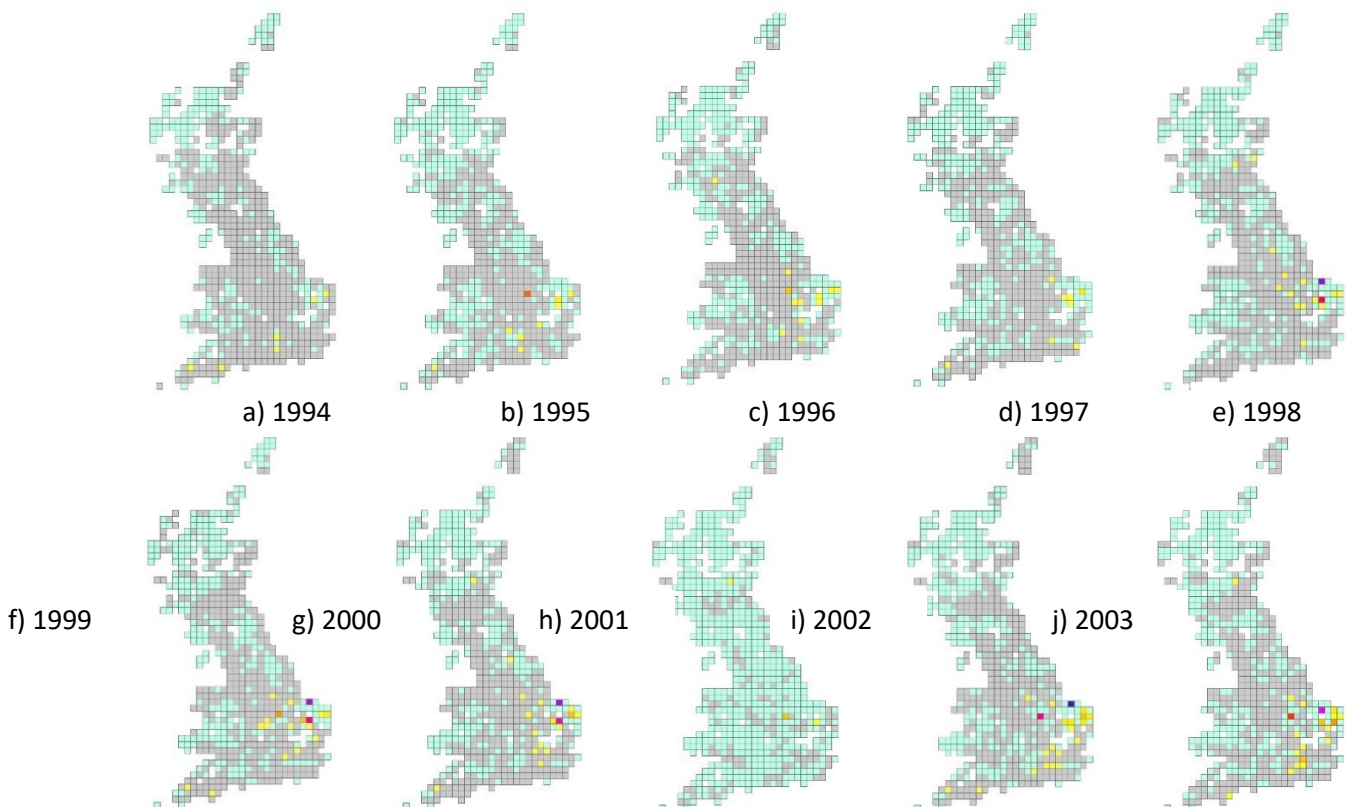


Figure S3 – Spring Counts



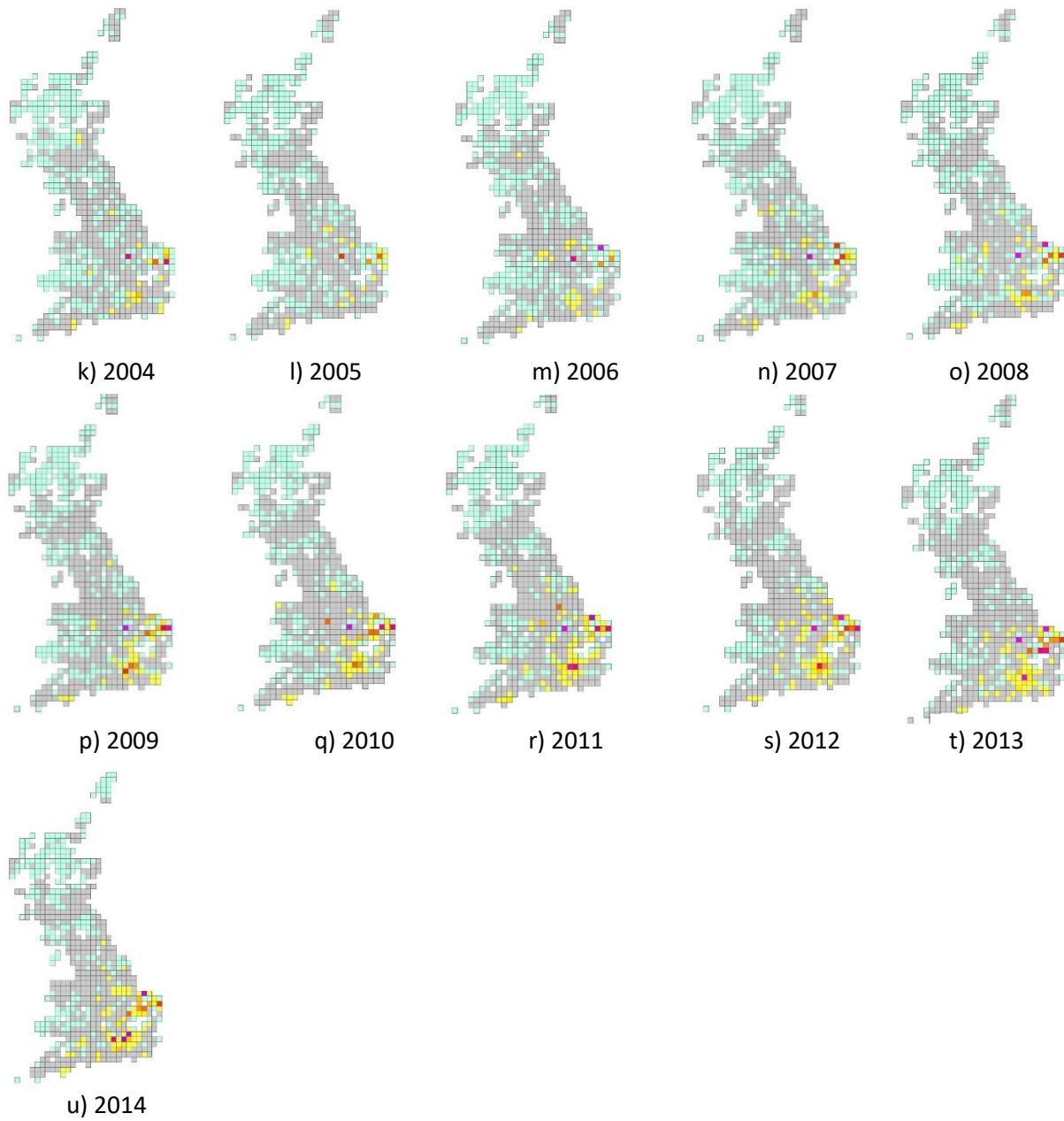
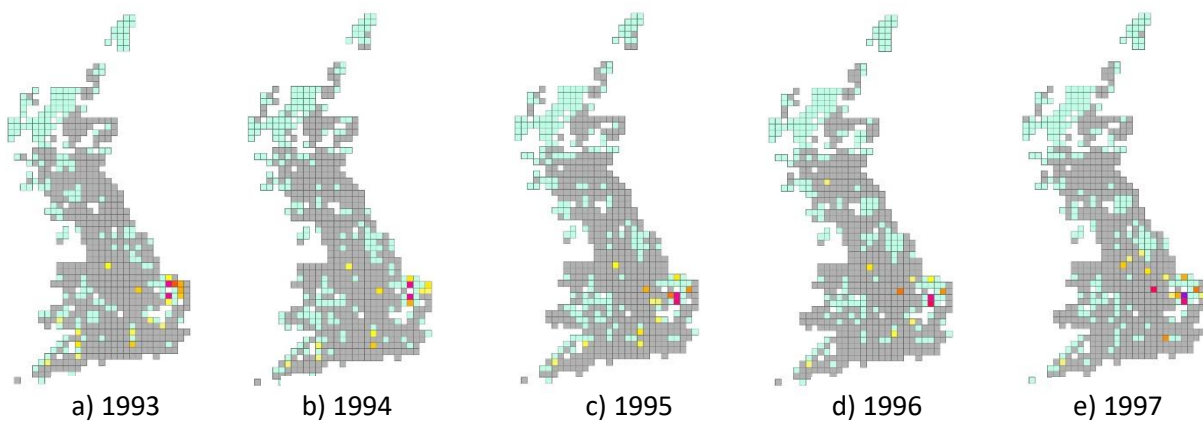
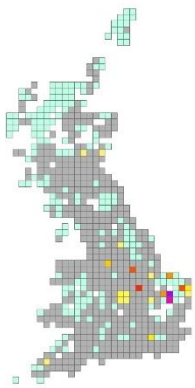
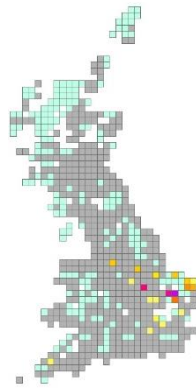


Figure S4 – Autumn Density

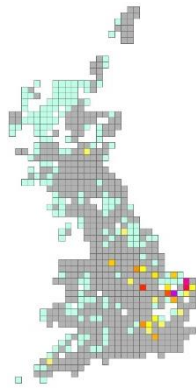




f) 1998



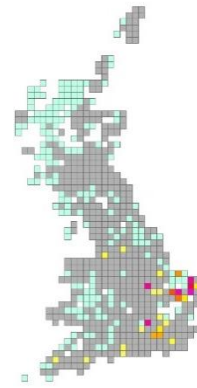
g) 1999



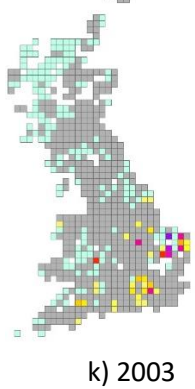
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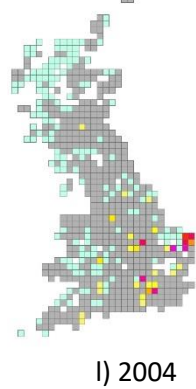
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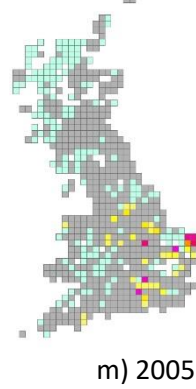
j) 2002



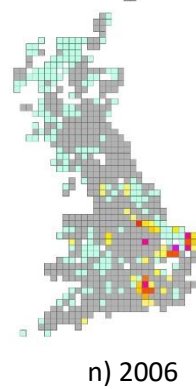
k) 2003



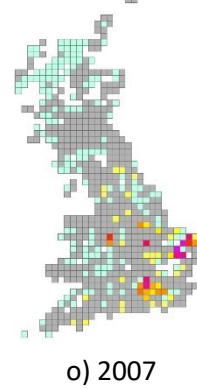
l) 2004



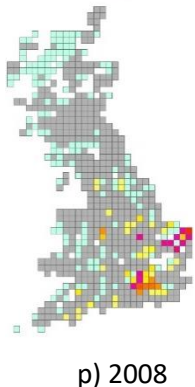
m) 2005



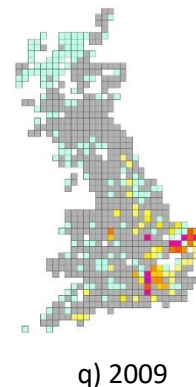
n) 2006



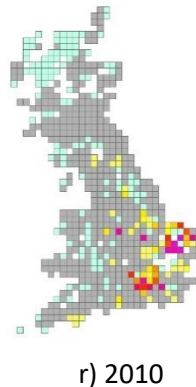
o) 2007



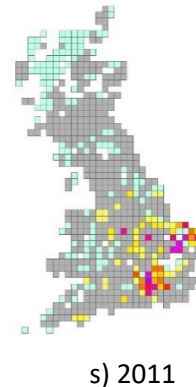
p) 2008



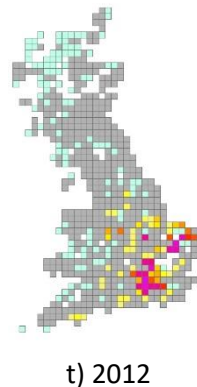
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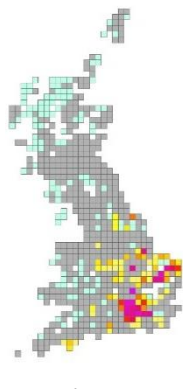
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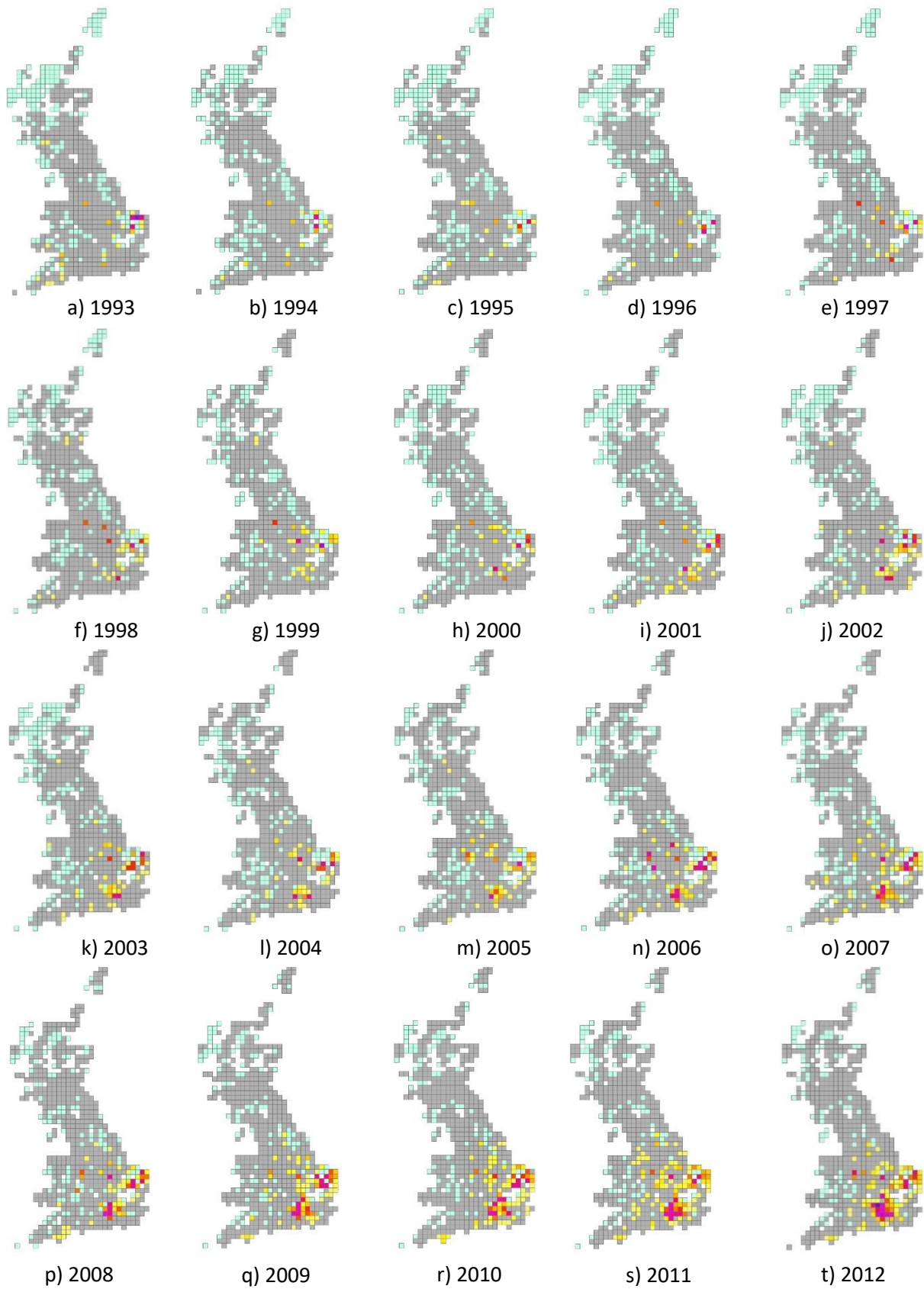


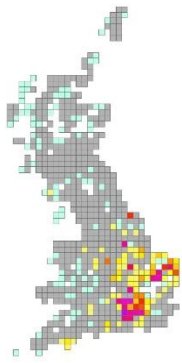
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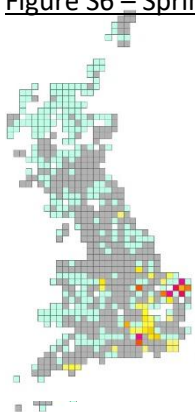
Figure S5 – Winter Density



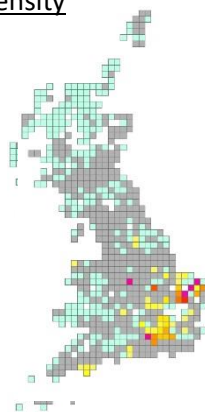


u) 2013

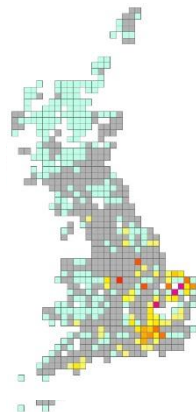
Figure S6 – Spring Density



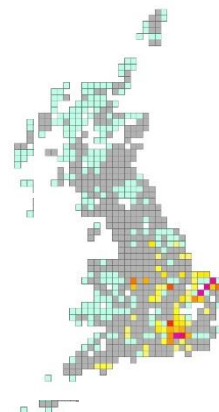
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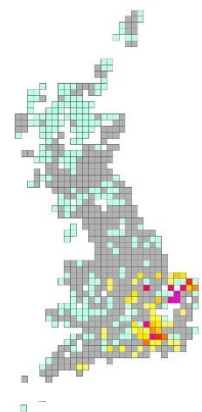
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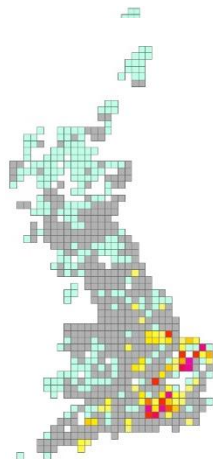
c) 1996



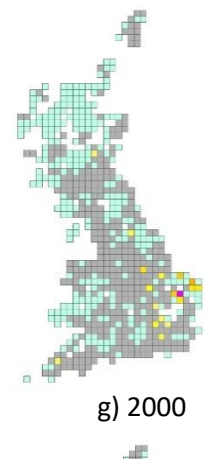
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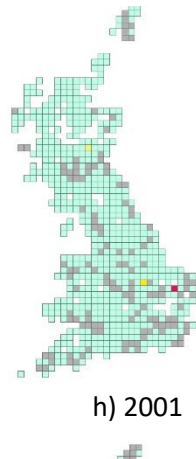
e) 1998



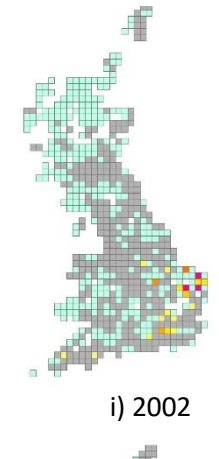
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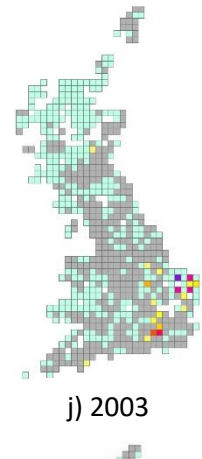
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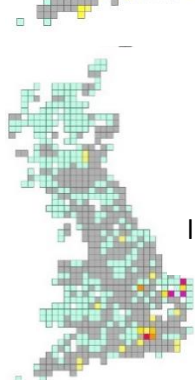
h) 2001



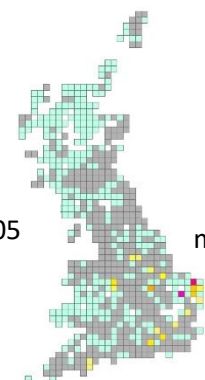
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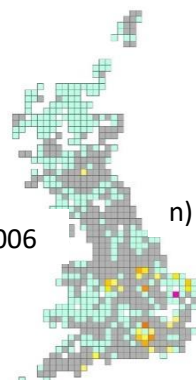
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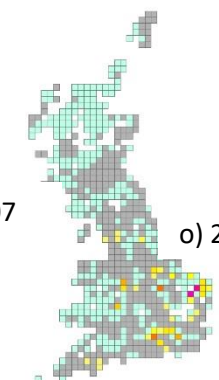
k) 2004



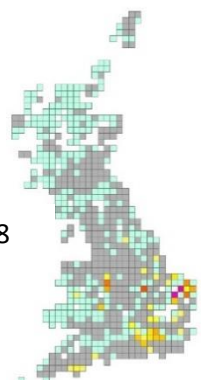
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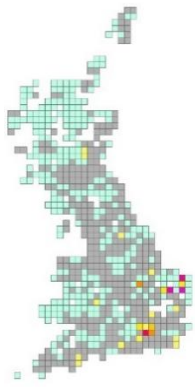
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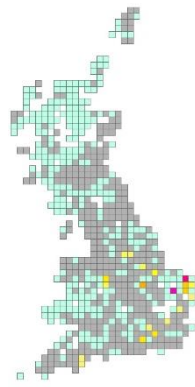
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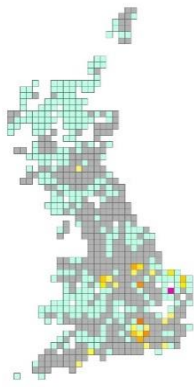
o) 2008



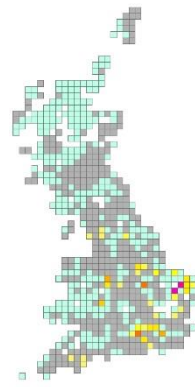
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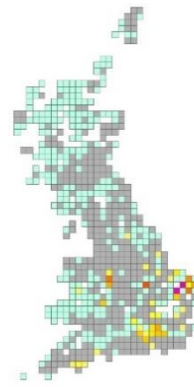
q) 2010



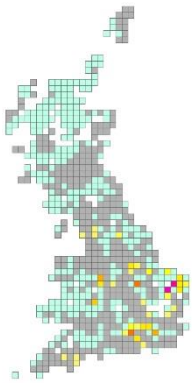
r) 2011



s) 2012



t) 2013



u) 2014

Appendix 2

Table S1. Results of the forward step check of the final poisson error GLMs at the 20km density. Results in bold are those that show significant to P>0.05

Predictors	Time period (20km)					
	1998-2001		2005-2008		2010-2013	
	P	R ²	P	R ²	P	R ²
Land area	0.834	0.178	0.987	0.455	0.132	0.423
Number of surveys	0.910	0.168	<.001	0.405	0.929	0.428
Waterbodies	0.065	0.350	<.001	0.405	<.001	0.435
Rivers and Canals	0.285	0.139	0.057	0.416	0.002	0.435
Eutrophied rivers	-	-	-	-	0.527	0.433
Eutrophied lakes	-	-	-	-	0.346	0.430
Arable landcover	0.069	0.282	0.885	0.455	0.213	0.426
Grassland landcover	0.271	0.206	0.445	0.448	0.919	0.435
Urban landcover	0.099	0.350	0.284	0.442	0.219	0.425
Urban grassland landcover	0.000	0.491	0.779	0.454	0.579	0.433
Temperature	0.792	0.171	0.659	0.452	0.231	0.426
Rainfall	0.727	0.172	0.037	0.405	0.387	0.430
Protected areas	0.131	0.223	<.001	0.405	0.222	0.427
Stately homes	0.528	0.179	0.001	0.405	<.001	0.435
Country Parks	0.293	0.194	0.565	0.450	0.400	0.431
Time since occupation	0.288	0.172	0.368	0.444	0.011	0.435
Occupancy	0.543	0.185	0.029	0.405	0.906	0.411
X coordinate	0.541	0.180	0.209	0.438	0.906	0.411
Y coordinate	0.153	0.230	0.323	0.442	0.002	0.435

Table S2. Results of the forward step check of the final poisson error GLMs at the 5km density. Results in bold are those that show significant to P>0.05

Predictors	Time period (5km)					
	1998-2001		2005-2008		2010-2013	
	P	R ²	P	R ²	P	R ²
Land area	0.712	0.302	0.001	0.519	0.741	0.472
Number of surveys	0.001	0.305	0.141	0.499	<.001	0.472
Waterbodies	0.013	0.305	0.006	0.519	<.001	0.472
Rivers and canals	0.830	0.304	0.355	0.512	0.124	0.458
Eutrophied rivers	-	-	-	-	0.740	0.472
Eutrophied lakes	-	-	-	-	0.131	0.463
Arable landcover	0.231	0.271	0.118	0.496	0.001	0.472
Grassland landcover	0.119	0.249	0.771	0.519	0.763	0.471
Urban landcover	0.374	0.287	0.131	0.498	0.010	0.472
Urban grassland landcover	0.412	0.290	0.240	0.506	0.747	0.472
Temperature	0.072	0.217	0.858	0.519	0.805	0.472
Rainfall	0.687	0.302	0.034	0.519	0.598	0.471
Protected areas	0.221	0.274	0.894	0.519	0.017	0.472
Stately homes	0.602	0.300	0.523	0.516	0.415	0.469
Country Parks	0.466	0.295	0.721	0.518	0.365	0.466
Time since occupation	0.966	0.305	0.757	0.518	0.398	0.468
Occupancy	0.239	0.271	0.309	0.509	0.721	0.472
X coordinate	0.816	0.304	0.002	0.519	0.026	0.472
Y coordinate	0.903	0.305	0.981	0.519	0.097	0.454

Table S3. Results of the forward step check of the final logistic regression models at the 20km density. Results in bold are those that show significant to P>0.05

Predictors						
	1998-2001		2005-2008		2009-2013	
	P	R ²	P	R ²	P	R ²
Land area	0.278	0.399	0.024	0.321	0.285	0.579
Number of surveys	0.928	0.395	0.207	0.325	0.514	0.578
Waterbodies	0.967	0.948	0.964	0.903	0.926	0.922
Rivers and canals	<.001	0.424	0.095	0.411	<.001	0.608
Eutrophied rivers	-	-	-	-	0.991	0.589
Eutrophied lakes	-	-	-	-	0.494	0.578
Arable landcover	0.005	0.424	0.162	0.325	0.306	0.579
Grassland landcover	0.363	0.397	0.213	0.334	0.028	0.608
Urban landcover	0.851	0.395	0.796	0.321	0.014	0.608
Urban grassland landcover	0.154	0.401	0.001	0.347	0.193	0.596
Temperature	0.001	0.424	0.370	0.323	0.822	0.588
Rainfall	0.783	0.395	0.002	0.347	<.001	0.608
Protected areas	0.002	0.424	<.001	0.347	0.123	0.610
Stately homes	0.131	0.436	0.124	0.326	1.000	0.588
Country Parks	0.007	0.395	<.001	0.347	0.349	0.590
Time since occupation	0.150	0.390	0.423	0.321	0.369	0.589
Occupancy	0.156	0.390	0.369	0.344	<.001	0.608
X coordinate	<.001	0.424	0.243	0.356	0.000	0.608
Y coordinate	0.167	0.390	<.001	0.347	0.006	0.608

Table S4. Results of the forward step check of the final logistic regression models at the 20km density. Results in bold are those that show significant to P>0.05

Predictors	Time period (5km)					
	1997-2001		2004-2008		2009-2013	
	P	R ²	P	R ²	P	R ²
Land area	0.374	0.603	0.629	0.341	0.773	0.386
Number of surveys	0.055	0.606	0.273	0.342	<.001	0.386
Waterbodies	0.333	0.603	0.637	0.341	0.172	0.387
Rivers and canals	0.306	0.603	0.416	0.341	0.173	0.387
Eutrophied rivers	-	-	-	-	0.005	0.386
Eutrophied lakes	-	-	-	-	<.001	0.386
Arable landcover	0.002	0.602	0.031	0.341	0.001	0.386
Grassland landcover	0.676	0.602	<.001	0.341	0.138	0.388
Urban landcover	0.501	0.602	0.920	0.341	0.402	0.386
Urban grassland landcover	0.268	0.603	0.958	0.341	0.194	0.387
Temperature	0.733	0.602	0.973	0.341	0.285	0.387
Rainfall	0.191	0.603	0.899	0.341	0.162	0.387
Protected areas	0.208	0.603	0.753	0.341	0.537	0.386
Stately homes	0.808	0.602	0.432	0.341	0.037	0.386
Country Parks	0.048	0.602	0.002	0.341	0.426	0.386
Time since occupation	0.753	0.602	0.729	0.340	0.792	0.386
Occupancy	<.001	0.602	<.001	0.341	<.001	0.386
X coordinate	0.704	0.602	<.001	0.341	<.001	0.386
Y coordinate	0.031	0.602	<.001	0.341	<.001	0.386