BAYESIAN MULTI-SPECIES MODELLING OF NON-NEGATIVE CONTINUOUS ECOLOGICAL DATA WITH A DISCRETE MASS AT ZERO

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Bayesian multi-species modelling of non-negative continuous ecological data with a discrete mass at zero

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Abstract

Severe declines in the number of some songbirds over the last 40 years have caused heated debate amongst interested parties. Many factors have been suggested as possible causes for these declines, including an increase in the abundance and distribution of an avian predator, the Eurasian sparrowhawk *Accipiter nisus*. To test for evidence for a predator effect on the abundance of its prey, we analyse data on 10 species visiting garden bird feeding stations monitored by the British Trust for Ornithology in relation to the abundance of sparrowhawks.

We apply Bayesian hierarchical models to data relating to averaged maximum weekly counts from a garden bird monitoring survey. These data are essentially continuous, bounded below by zero, but for many species show a marked spike at zero that many standard distributions would not be able to account for. We use the Tweedie distributions, which for certain areas of parameter space relate to continuous non-negative distributions with a discrete probability mass at zero, and are hence able to deal with the shape of the empirical distributions of the data.

The methods developed in this thesis begin by modelling single prey species independently with an avian predator as a covariate, using MCMC methods to explore parameter and model spaces. This model is then extended to a multiple-prey species model, testing for interactions between species as well as synchrony in their response to environmental factors and unobserved variation.

Finally we use a relatively new methodological framework, namely the SPDE approach in the INLA framework, to fit a multi-species spatio-temporal model to the ecological data.

The results from the analyses are consistent with the hypothesis that sparrowhawks are suppressing the numbers of some species of birds visiting garden feeding stations. Only the species most susceptible to sparrowhawk predation seem to be affected.

Publications and collaboration

Some of the work presented in Chapter 3 has been included in the following publication:

Swallow, B., Buckland, S. T., King, R. and Toms, M.P. (2015) ‘Bayesian hierarchical modelling of continuous non-negative longitudinal data with a spike at zero: an application to a study of birds visiting gardens in winter’, *Biometrical Journal* (online early)

The co-authors Buckland and King provided a supervisory role to the work, whilst Toms works for the data provider.

The work in Chapter 6 was joint work with C. M. Jones-Todd. The model formulation and interpretation of results was carried out by myself whilst the code was written and run by CMJT.

Declarations

1. Candidates declarations:

I, Ben Swallow, hereby certify that this thesis, which is approximately 40,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in September 2011 and as a candidate for the degree of PhD in statistics in September 2011; the higher study for which this is a record was carried out in the University of St Andrews between 2011 and 2015.

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I am also grateful to three anonymous referees, and three editors for their comments on a manuscript based on the results from one of the anlayses that forms part of thesis. As a consequence this analysis and Chapter 3 as a whole has improved. The thesis was also part funded by the National Centre for Statistical Ecology via a NERC/EPSRC grant, for which I am thankful.

Thank you.

‘J’étais en ce temps-là un peu comme serait une hirondelle, née d’hier, très haut à l’angle d’un toit, qui commencerait à ouvrir de temps à autre au bord du nid son petit oeil d’oiseau et s’imaginerait, de là, en regardant simplement une cour et une rue, voir les profondeurs du monde et de l’espace, - les grandes étendues de l’air que plus tard il lui faudra parcourir. Ainsi, durant ces minutes de clairvoyance, j’apercevais furtivement toutes sortes d’infinis, dont je possédais déjà sans doute, dans ma tête, antérieurement à ma propre existence, les conceptions latentes.’

Pierre Loti, *Le Roman d’un enfant.*.

Contents

Chapter 1

Ecological motivation

1.1 Monitoring bird populations

Ecological communities are subject to the influence of many factors, both environmental and human-driven. In order to assess the implications of these factors and put into place effective conservation measures where necessary, it is essential to monitor ecological populations and detect changes at the earliest possible stage. The results of this monitoring also need to be fed back to interested parties, whether politicians, conservation organisations or the general public, so that legal requirements can be met and that severe declines in biodiversity can be halted or reversed. The continued monitoring can then assess whether any conservation methods put into place are producing the desired results.

The UK government is committed to a variety of national, European and international agreements concerning the conservation of biodiversity. Specifically the European Union (EU) Birds directive (2009) outlines a framework for wild bird conservation in Europe, in particular the creation, maintenance and re-establishing of habitats for all wildly-occurring species of birds. On a national scale, there are many pieces of legislation that govern how biodiversity must be conserved and regulated.

The importance of the monitoring of birds is heightened by the fact that they are often used as indicator species for the environment as a whole. Using birds as indicator species arises because of their tendencies to occupy a wide range of habitats, be comparatively easy to survey and often be near or at the top of the food chain (Bibby et al., 2000; Gregory and van Strien, 2010). The latter in particular makes them susceptible to environmental change and hence can act as an early signal that there are problems affecting the wider environment on a local or even national scale.

Effective and appropriately designed monitoring schemes are vital if the species in need of conservation are to be identified. There are many stages in a bird's life cycle that could be the cause of changes in abundance and hence an ability to isolate the stages that are most affected will allow more direct and potentially more successful conservation measures to be put in place. The monitoring of bird populations can be carried out in many different ways, but it is essential that said monitoring is carried out over a prolonged period of time. This will allow long-term trends to be analysed and isolated from short-term declines caused by, for example, unusual weather patterns. In addition to human-driven environmental factors, such as global warming, intensification of agricultural methods and over-exploitation of resources, other natural factors also need to be considered (Bibby et al., 2000). For example the increase in the number of predators in an area has been shown to have an adverse effect on the abundance and reproductive success of the red grouse *Lagopus lagopus scoticus* (New et al., 2012), whilst the presence of deer have been shown to have a negative effect on some species of woodland birds (Newson et al., 2012). Similar effects have been suggested for other species, such as sparrowhawks *Accipiter nisus* on many small songbird species (Bell et al., 2010; Chamberlain et al., 2009; Newson et al., 2010; Thomson et al., 1998).

In the UK, the British Trust for Ornithology (BTO) is charged with carrying out much of the survey work into the effects of environmental change on bird populations, movements and ecology. Founded in 1933, it set out to achieve the potential of using co-operative birdwatching to inform conservation. As such, the BTO's success in collecting long-term and wide-scale data sets is largely due to its collective of volunteers, who in combination with professional ecologists unite professional and citizen science on a scale that otherwise would not be possible. The use of volunteers to carry out these surveys has obvious practical and economic benefits. In contrast to other conservation bodies in the UK, for example the Royal Society for the Protection of Birds (RSPB), the BTO is an independent charitable research institution whose goal is to advise interested parties on the state of the UK's wild bird populations, not to campaign for conservation nor to operate nature reserves (BTO website, 2014 [1]).

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[1] `http://bto.org/about-bto`

The BTO runs multiple short- and long-term studies, each survey being purpose-designed to target the species and parameters of interest. Surveys range from large-scale multi-species schemes such as the Breeding Bird Survey (BBS) and Constant Effort Site (CES) ringing scheme, to single species surveys (for example the current Woodcock survey in partnership with the Game and Wildlife Conservation Trust). As with the latter survey, the BTO often collaborates with other research organisations to provide impartial data on a wide range of topics, including productivity, survival, movement and overall abundance of birds in the UK.

As some bird populations continue to decline, many organisations are beginning to see the need to work on an international scale. The recent negative trend in summer migrant birds to the UK, coupled with little success in linking these declines to environmental changes in the UK, has led to research being conducted abroad, namely western Africa. This emphasises the importance of monitoring birds on a suitable time and spatial scale.

The decline in bird species is also clearly something that has hit a chord with the general public, not just with conservationists. The RSPB currently has over a million members, including 195,000 youth members (RSPB website 2015 [1]). There is, therefore, a great expectation that information be provided to the general public on matters relating to the environment and that appropriate measures are implemented to counteract those declines.

1.2 Songbird populations

Of particular current concern is the declines of many small songbirds in the UK over the past few decades (Baillie et al., 2014). Many surveys have plotted the continued decline of these species, in particular those associated with farmland habitats (e.g. Baillie et al. (2014); Crick et al. (2002); Fewster et al. (2000); Fuller et al. (1995)). Of the songbirds it is the farmland specialists in particular that have shown the most severe declines, with generalists appearing to fare marginally better (Gregory et al., 2004; Mennechez and Clergeau, 2006). The house sparrow *Passer domesticus* and starling *Sturnus vulgaris* are of particular concern with the former having decreased in England by approximately 68% and the latter by around 88% over the past c.40 years

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[1] `https://www.rspb.org.uk/about/`

(Baillie et al., 2014). Simultaneously, however, other species are remaining stable or even increasing. Why it is that two of the species are faring so poorly is unsurprisingly causing much debate. Intensification of farming methods has been shown to be a leading cause of decline in rural habitats (Robinson et al., 2005a,b), although numerous possible additional causes of these declines have been proposed (e.g. Newton, 2004). The declines seen in urban populations of house sparrow, in particular, have attracted research interest but consensus has yet to be reached as to the underlying causes. Amongst potential contributory drivers of population change in urban populations of house sparrow, those linked to productivity (e.g. Morrison et al., 2014; Peach et al., 2014; Vincent, 2005) and survival (e.g. Bell et al., 2010; Newson et al., 2010) have drawn particular attention, with the latter stimulating debate across a wider audience.

These declines are an issue that few people will be ignorant of as it is a phenomenon that has reached the headlines of the tabloids (e.g Daily Mail, 09/03/10[1]), news websites[2], not to mention scientific research organisations (BTO website, 2014[3]) and game and shooting advocates[4]. This range of sources shows well the scope of interested parties in the debate on causes of songbird decline. It has become a very contentious issue as the birds concerned are often species that the general public have a direct relationship with. Members of the public investing money in feeding birds in their garden also have an interest in what other factors may be causing declines in the species that they are aiding. Equally, human-wildlife conflict has led to the legal and illegal culling of numerous species of predator that are believed to threaten particular aspects of land-use or ecology, particularly in recent years in relation to predators of red grouse *Lagopus lagopus scoticus* and other game birds. Raptors are often the first to be blamed for declines despite a scarcity of evidence to show direct effects of raptors on the populations of their prey.

Due to the difficulty in conducting experimental studies over a wide geographical area, the large proportion of previous studies have used either small time series of data and localised scales, or taken advantage of observational studies to test hypotheses (Nicoll and Norris, 2010). Unsurprisingly then, many previous studies have been unable to find consistent and universally satisfactory answers to the question of causes of these

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[1] `http://www.dailymail.co.uk/sciencetech/article-1256478/Where-songbirds-Ask-hungry-sparrowhawk.html`

[2] `http://www.bbc.co.uk/news/uk-13587950`

[3] `http://www.bto.org/news-events/press-releases/are-predators-blame-songbird-declines`

[4] `http://www.shootingtimes.co.uk/features/535206/Saving_our_songbirds.html`

declines. Why it is that some species are responding differently continues to attract research interest. Whilst intensification and other changes in agricultural practices are likely causes of declines in rural farmland (Fuller et al., 1995), additional causes in these areas and other habitats still need to be assessed. Population changes of similar or greater magnitude have also been observed in urban habitats, where intensification of farming evidently cannot be blamed. It is possible that urban populations of house sparrows, for example, could have been buffering rural populations, as the declines observed in urban gardens occurred at a later stage whilst on average being of a similar magnitude (Robinson et al., 2005a). However, it perhaps seems more likely that other factors may be simultaneously causing these declines across habitat types.

One of these potential causes continues to encourage heated debate among interested parties. The numbers of one of the avian predators frequently seen to prey on songbirds, the Eurasian sparrowhawk (henceforth sparrowhawk), have increased significantly in a similar time-frame as the declines observed in songbird numbers. As such, this thesis concentrates on this single avian predator species and aims to test for evidence to suggest that the increase in its abundance and distribution could feasibly be a cause of the songbird declines.

1.3 The Eurasian sparrowhawk

Before we discuss previous analyses of sparrowhawk predation on songbird populations, it is useful to briefly outline aspects of the sparrowhawk's ecology and historical population trends that are likely to have an effect on any of their prey species. This will help in understanding why it is that sparrowhawks have been postulated as a possible causal factor in the changes observed in their prey populations.

The sparrowhawk is a widespread bird of prey, one of the smallest in Europe, with an estimated continental population of 340,000 - 450,000 (BirdLifeInternational, 2004; Cramp and Perrins, 1979), of which approximately 35,000 pairs are found across the UK (Baillie et al., 2014). Together with the common buzzard *Buteo buteo* and common kestrel *Flaco tinnunculus* it is one of the commonest raptors in Europe. Their prey consists almost entirely of birds, making them unusual among other birds of prey who tend to feed on multiple taxa. Raptors are unusual in general in that sexual size dimorphism is in reverse with females being larger than the males, with the sparrowhawk being particularly extreme in this respect (Newton, 1986). This large difference in size means that males and females are capable of taking prey of different sizes with males rarely taking prey larger than thrushes and females able to take prey as large as collared doves *Streptopelia decaocto* and woodpigeons *Columba palumbus* (Cramp and Perrins, 1979).

The British breeding population is sedentary, only moving short distances outside of the breeding range, while in winter the population is boosted with migrants arriving from the continent (Cramp and Perrins, 1979). They are now a common site at bird feeders across the country, often seen taking small birds in a flash of high-speed action lasting little more than a few seconds. The high-profile nature of their occurrence in gardens, coupled with their population increase and range recolonisation, has led some to believe they are (at least in part) responsible for the simultaneous decline seen in the populations of many small songbirds. There is no doubt that there is some degree of temporal synchrony between these two events; however any satisfactory true causal link between them remains elusive.

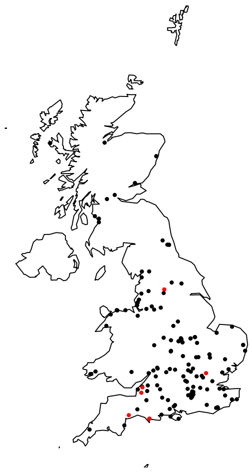
1.3.1 Historical population trends - organochlorine pesticides

The sparrowhawk has had a mixed history as a breeding bird in the UK. It is impossible to consider the fortunes of the sparrowhawk, both within and outwith the UK, without discussing the major effect of certain pesticides on populations across the species' whole range. This topic has been discussed extensively (e.g. in Newton, 1986). In summary, the numbers of sparrowhawks suddenly started to show a significant decline from the beginning of the 1950s, although it was not until around a decade later (when numbers had dropped to a noticeably low level) that birdwatchers and conservationists began to take notice. Sparrowhawks were far from the only species concerned, with other raptors and many seed-eating birds also being severely affected. The decline was noticed across the country; however it was particularly marked in the east where the sparrowhawk was previously more widespread and where arable farming was more prevalent. Population declines in the west were likely less than 50% in most areas, whilst some eastern populations were reduced to extinction.

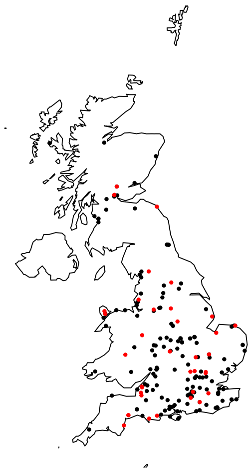
The first effects of the pesticides on birds began to be noticed in the 1950s when thousands of birds, mainly seed-eaters, were found dead in fields across Britain. Analyses of the corpses revealed organochlorine pesticide residues in their body tissues. Over the next few years it became evident that populations of raptors were also in rapid decline. The chemicals affected both productivity and survival, leading populations to drop more drastically than would be expected if even no young were produced (Newton, 1986).

Little information is available on the decline as the effects were only noted after they had happened. Once the true effects of the pesticides had been identified, successive reductions in the use of these pesticides were introduced during the 1960s and 70s. Populations of the sparrowhawk then slowly began to recover, again mainly in a west to east direction. The species recovery was at first most prevalent outside of farmland but by the early 1980s arable populations were also starting to show signs of recovery. Baillie et al. (2014) shows that by the mid-1990s the UK population had stabilised although there is some evidence of a small reduction in the overall population since 2005.

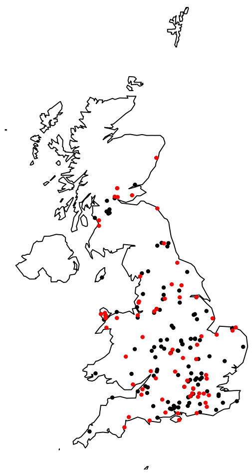
Figure 1.2 shows the spread of sparrowhawks back to areas they previously occupied through successive five-year periods from 1970-2005. These data are from sites monitored by the BTO's Garden Bird Feeding Survey (see section 1.5 for more details on this survey and the data it collects). The proportion of red dots, showing sparrowhawk presence at the sites, has clearly increased over the last four decades. The spread is generally from the west towards the east, with little in the way of change evident after the early 1990s. It is difficult to determine any north-south trends due to the lower number of surveyed sites in the north of the UK.



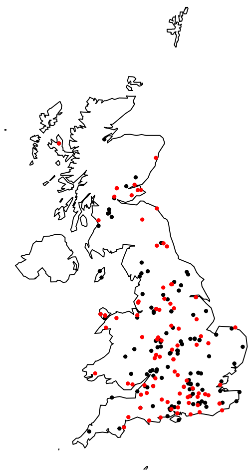
1970-74



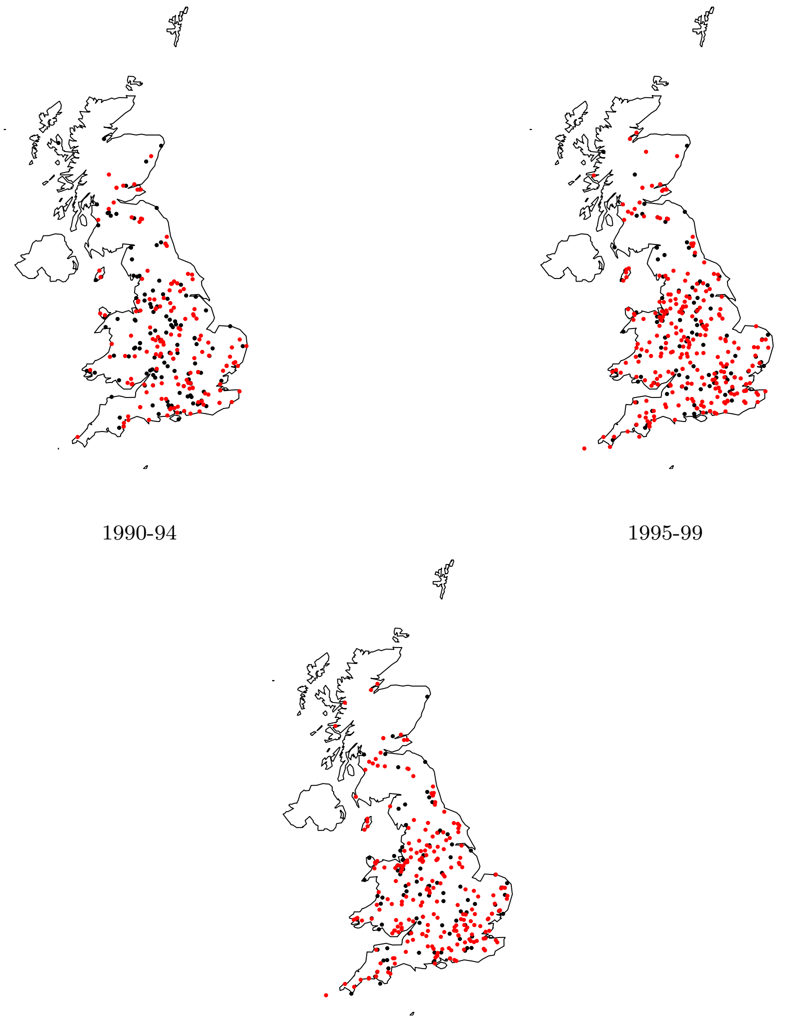
1975-79



1980-84



1985-89



1990-94

1995-99

2000-05

Figure 1.2: Maps showing the spread of sparrowhawks across the UK. Black dots represent sites where no sparrowhawks were seen at any point during the indicated five-year period (data from the BTO Garden Bird Feeding Survey). Red dots represent sites where at least one sparrowhawk was seen during that five-year period. Note also a difference in the number of sites surveyed in each plot (n=140, 190, 185, 210, 277, 365 and 323 respectively.) Proportion of sites where sparrowhawks were present are 0.05, 0.19, 0.37, 0.42, 0.53, 0.71 and 0.68 respectively.

1.4 Previous studies of sparrowhawks on songbirds

Several previous authors have analysed relationships between the increase in sparrowhawks and changes in abundance of their prey species. Here we outline some of the more relevant studies to enable later discussion and comparison with any results presented in this thesis.

As outlined in this chapter, it is of great importance to conduct continued monitoring of small birds that have shown large declines over the past few decades. A balanced analysis of the data already collected, spanning the time period of sparrowhawk decline and recolonisation, is also required in order to try to find the likely causes of the declines seen in many species of small birds. The covering of relevant time periods will allow stronger conclusions to be drawn on the effect of sparrowhawks additional to those exerted by other environmental factors. Previous approaches have often failed to incorporate a sufficient number of additional covariates to account for alternative factors that may also be affecting songbird populations.

Nicoll and Norris (2010) conducted a meta-analysis of published analyses of predator effects on their prey species and found that the probability of detecting a predator impact was strongly, positively related to the quality and quantity of data being analysed. Although for long-term studies the authors often have little choice in terms of the data sets available, it does highlight the need for careful consideration of both the data and the model formulation being used. Any results must be placed in context and considered in light of any shortcomings that the data may have.

Any evidence in favour of effects of sparrowhawks on survival or productivity then needs to be extended to prove effects at the population level, as effects on survival could just relate to the "doomed surplus" (Gibbons et al., 2007; Newton, 2004). This concept of a "doomed surplus" is one which suggests that the prey taken by sparrowhawks is prey that, in the absence of sparrowhawks, would otherwise have succumbed to other threats. The sparrowhawks merely change the dynamics of mortality in the species they prey on.

In particular, the analyses conducted in this thesis will try to extend previous analyses to make conclusions more robust. Thomson et al. (1998) analysed rates of songbird change from Common Bird Census (CBC) data and searched for statistical relationships between presence or absence of both magpies *Pica pica* and sparrowhawks and 23 potential prey species using a Poisson log-linear model. Collared doves were also included to test for spurious correlations with non-predatory birds. Density dependence was included in their model by including a standardised measure of songbird abundance on each CBC plot, which they describe as a parsimonious way of accounting for density dependence in the model. The analyses found no overall effect of either sparrowhawks or magpies on songbird population trends, but did not account for other environmental covariates that could also be driving the observed changes. Spatial autocorrelation that is inherent in these types of data was also not accounted for. In addition, using the presence or absence of predators as the response variable may underestimate the effect on songbirds when more than single predators are present.

Newson et al. (2010) also conducted analyses of breeding data relating to predator effects on songbird abundance. A suite of different predators, including both avian predators and grey squirrels, and environmental covariates were included in the model to ensure as many environmental factors could be accounted for as possible. Data from the BBS and CBC were used to conduct the analyses and no evidence was found of effects of predators on the majority of prey species analysed. Of the significant negative relationships found, some were deemed biologically implausible although a couple could relate to causal relationships. The analyses also found a large number of positive associations between predators and prey, which largely removed blame from the predators as drivers of the overall declines in songbird numbers.

Chamberlain et al. (2009) analysed data from the Garden Bird Feeding Survey (GBFS) that monitors the number of birds visiting garden feeding stations over the winter months (see Section 1.5 for more details). Their model was similar to that of Thomson et al. (1998), but specified the model in terms of change in the expected value as the response as opposed to using the observed number as in the former's analyses. In addition they included both the number of feeding units and minimum temperature as covariates in the model. Sparrowhawks were the only predator to be included in the analysis. Due to the fact that the GBFS data is collected on a weekly basis, analyses were conducted for the first, middle and last week and compared. This evidently ignores a large proportion of the data and is a relatively arbitrary choice. The effect of the number of feeding stations and minimum temperature is not declared outright, but reference to Chamberlain et al. (2005) implies that significant positive relationships were found with the number of feeding stations and significant negative relationships with minimum temperature for all species. The effect of sparrowhawks on ten species of songbird varied across weeks with both positive and negative associations found. There was some evidence to suggest that a linear relationship existed between their estimated sparrowhawk effect and the relative predation risk for a given prey species estimated by Gotmark and Post (1996).

Finally Bell et al. (2010) also analysed GBFS data for house sparrow only, and correlated decreases in house sparrow numbers with the recolonisation of some regions by sparrowhawks. However, the methods for choosing which sites were included in the analyses, namely choosing only sites with at least 10 years of consecutive monitoring, seem a little excessive and have the potential to decrease the reliability of any results obtained. In addition, no attempt to control for other variables was made and hence alternative hypotheses were not tested. It is clear that there is temporal correlation between times of observed decreases in house sparrow numbers and the time of sparrowhawk recolonisation, however without trying to account for other possible factors, any results are highly speculative and open to criticism.

Hence, overall there has been scarce statistical evidence to suggest overall negative effects of sparrowhawks on songbirds, particularly when breeding data are concerned. However, robust analyses accounting for various types of autocorrelation and environmental factors, whilst simultaneously maximising the use of all the data available, may give more robust results. These suggestions will be taken into consideration when models are developed in this thesis.

1.5 The data set: Garden Bird Feeding Survey

Garden birds are often the first birds that people are introduced to and can instil an ornithological interest in people who perhaps would not otherwise have gained one. Birds can be ever-present in even the most urban gardens and have the added bonus of often being easy to see, brightly coloured and entertaining to watch. The provision of food for birds in gardens has escalated dramatically over the last few decades. In the UK, bird feeding is now a multi-million pound industry, with current estimates suggesting around £200 million are spent each year on bird food nationally (BTO website 2015[1]). In response to the aforementioned increase in the provision of wild bird

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[1] `http://www.bto.org/volunteer-surveys/gbw/gardens-wildlife/garden-birds`

food in gardens across the UK, the BTO has charted the use of food supplements by birds in gardens since the winter of 1970/71 through the Garden Bird Feeding Survey (GBFS), allowing the monitoring of the effects of these ever-changing resources on the birds using them (from this point onwards, reference to the year 1970 will concern the winter of 1970/71 etc.). It is this data set in particular that will be analysed in this thesis. Spanning nearly 40 years, the data available give the best possible chance to test for wide-scale effects of sparrowhawks on their prey species, as it covers the time period when sparrowhawks were largely absent from large areas of the UK, and the subsequent growth and stabilisation of the UK sparrowhawk population. As the survey is carried out in gardens where food is being provided, it maximises participation and hence the geographical coverage of the survey. Corresponding continuous breeding data is largely unavailable for such a long time series. As mentioned above, Newson et al. (2010) conducted separate analysis of CBC and BBS data covering this period but the monitored sites and protocol differed between surveys making an integrated analysis difficult. Despite being an observational study, the GBFS data set is likely to be the most realistic available to find any sparrowhawk effects if they are there.

The effect of predators on passerines has generally been assumed to compensate for birds that would otherwise succumb to mortality through other means (Newton, 1998). The lack of evidence for an effect on breeding numbers is therefore perhaps not surprising. Evidence for a compensatory effect is more likely to be found through the analysis of post-breeding numbers and hence analysis of data collected over the winter may give alternative insight into the scale of predatory effects. Perrins and Geer (1980) and Newton (1998) studied the effect of an increase in a sparrowhawk population on non-breeding tits and found the seasonal pattern of mortality was altered, as was the peak in numbers. While these studies highlight local impact they fail to provide evidence of wider scale patterns, something that can only come from a much larger study. The GBFS data is such a study that can largely avoid these problems. Many species of songbird also show consistent trends in abundance in both the CBC index and probability of occurrence at GBFS sites (Chamberlain et al., 2005). Despite these close relationships for these species, it is still very difficult to extrapolate that any environmental effects on GBFS may also be affecting the overall breeding density of these species, but any results may highlight areas of further study.

1.5.1 Survey protocol

The number of participants in the GBFS is relatively small in comparison to some of the other surveys conducted by the BTO. Gardens are carefully selected from participants of another BTO survey, the Garden BirdWatch (GBW) survey, ensuring a good coverage of both urban and suburban gardens across the UK. Although some gardens have continued to conduct the survey across the full 40 years, there is a reasonably large turnover from year to year, with approximately an 8% dropout rate for the sites considered in this thesis.

The survey is restricted to approximately 250 gardens per year, with participants making weekly counts during two consecutive 13-week periods (October-December and January-March respectively). Counts relate to the maximum number of each species seen to be taking advantage of the food and/or water provided in the garden at any one time, or birds preying on the congregated small birds. Using the maximum number of each species seen at one time prevents counting the same individuals twice, although the numbers are likely to be lower bounds for at least some of the species actually using the food. Participants note the maximum number of each species observed feeding or drinking at any one time (i.e. simultaneously) during the week and are encouraged to remain consistent in the time spent observing each week.

1.5.2 GBFS data

The counts of 10 potential sparrowhawk prey species were contained in the data set, corresponding to the same species analysed by Chamberlain et al. (2009). In addition to the number of sparrowhawks observed, data on blue tit *Cyanistes caeruleus*, great tit *Parus major*, coal tit *Periparus ater*, house sparrow, greenfinch *Carduelis chloris*, chaffinch *Fringilla coelebs*, robin *Erithacus rubecula*, blackbird *Turdus merula*, starling and collared dove were also available. In addition to the numbers of birds of each species observed, the data set used in this thesis also contained the following variables: northing and easting (six-figure grid references that were converted to spatial location variables for each of the sites surveyed), suburban or rural (a two-level factor variable concerning the level of urbanisation at each site) and the number of sparrowhawks observed for each site and year combination.

Figure 1.3: Averaged annual trends across all sites for the ten species analysed in the thesis and sparrowhawk between 1970/71 and 2005/06.

Figure 1.3 shows the average number of each of the ten prey species and sparrowhawks observed across all GBFS sites between 1970 and 2005. There are clearly very different trends observed in the populations of the species considered, with many staying relatively stable in the long-term. House sparrow and starling, however, have shown severe declines of over 50% across this period. There was a particularly steep drop in numbers for theses two species, followed by a relatively stable 15 year period, before a severe decline in both species since 1990. Numbers of these two species have declined across the wider countryside and this is not just an anomaly of this data (Crick et al., 2002). Due to the consideration that the species was so abundant, and considered an agricultural pest in the early part of the 20th Century, the declines in house sparrows in particular were not noticed for considerable time. The increase in sparrowhawk abundance is less clear due to the scale but numbers have increased from an average of exactly zero in 1970 to 0.15 in 2005.

Each site is monitored up to 26 times each year, giving a large amount of data requiring a potentially very complex correlation structure of weeks within sites within years. In addition, not all 26 counts are successfully made at each site in every year. As such, modelling all the raw data would require a three-way correlation structure together with non-trivial handling of missing observations. Given the volume of data, this was considered to be too large a task to be feasably accomplished and hence we follow the methods of Bell et al. (2010) in taking an annual average across the 26 weeks for each site. The raw data is therefore converted into an annual average of weekly maxima. Although this has the potential to introduce bias if the number of observations over which we take an average is small, or if there is some pattern to the missing data, exploratory analysis of the data suggested this is unlikely to be a problem here. Of all the site-year combinations, approximately 60% relate to an average over all 26 weekly maximum counts, whilst over 95% of the average counts were averaged over at least 23 weeks. There was also no obvious pattern in which weeks and sites were missed. The combination of relatively few missed counts and the lack of pattern should, therefore, introduce negligible bias to the results.

The year-on-year turnover of sites is fairly high with few sites spanning the full time period, although the number of sites monitored each year has remained fairly consistent. On average there is an 8% yearly drop-out rate for the years 1970-2005, with sites being replaced by suitable sites in a similar area and habitat type. For the modelling process used in this thesis, we select only sites with at least three consecutive years of data.

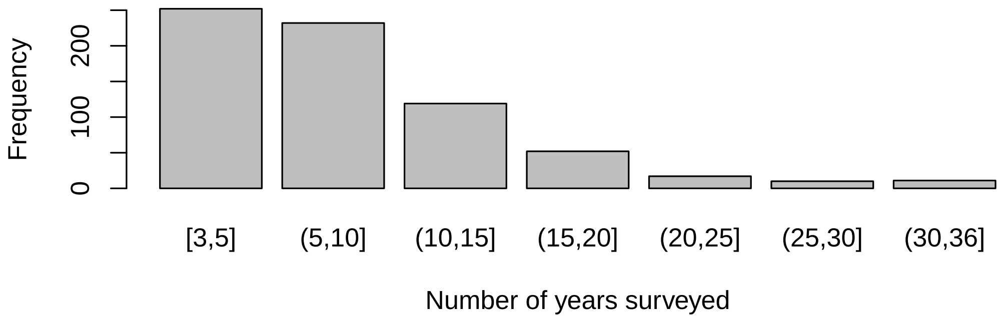

Figure 1.4: Distribution of number of consecutive years each site is monitored. Sites where monitoring is interrupted are considered separate sites before and after the break.

Although this choice of 3 is somewhat arbitrary, it reduces the potential of low precision introduced from estimating a comparatively large number of parameters from a very small amount of data. Low precision in the estimation of some parameters may lead to bias in others where the magnitude of effects of certain covariates may be diluted by imprecise estimation of other parameters. This problem will be discussed in more detail later in the thesis where relevant. Bell et al. (2010) restricts the analysis of the GBFS data to only sites with at least 10 years of continuous monitoring. We feel this is too draconian and reduces the analysis unnecessarily to a much smaller number of sites. Any geographical pattern to these sites, which is not checked by Bell et al. (2010), could introduce structural bias to the results.

Very few sites spanned the full period (only two out of the sites analysed (Figure 1.4)) whilst some dropped out before returning later on or missed single years. For the sake of the modelling process the sites with disjoint observation intervals, providing each distinct period covered at least three years, were defined as different sites for each interval. The intervening years could have been considered as missing data and estimated as part of the modelling process but this was the case for sufficiently few sites that it was not considered to be worthwhile. This gives us a total of $n_{obs} = 6185$ observations across $n_{site} = 693$ sites for the entire period (Figure 1.5).

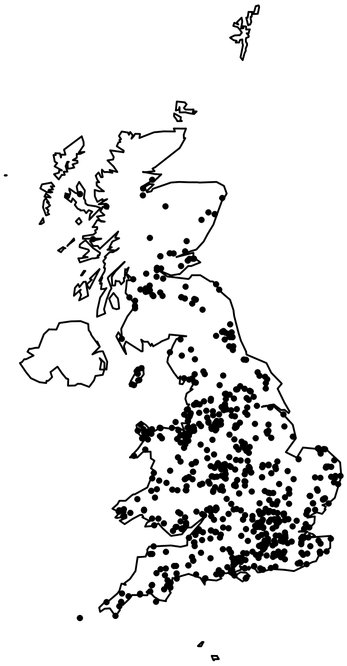

Figure 1.5: Spatial distribution of all surveyed sites included in the analyses.

Table 1.1: Percentage of all site-by-year observations that are exact zeros.

Species	Percentage of exact zeros	Number of unoccupied sites
Blackbird	0.6	0
Blue tit	0.1	0
Collared dove	20.1	72
Chaffinch	3.9	7
Coal tit	18.6	40
Greenfinch	4.7	5
Great tit	3.4	3
House sparrow	7.5	12
Robin	0.7	1
Starling	7.9	15

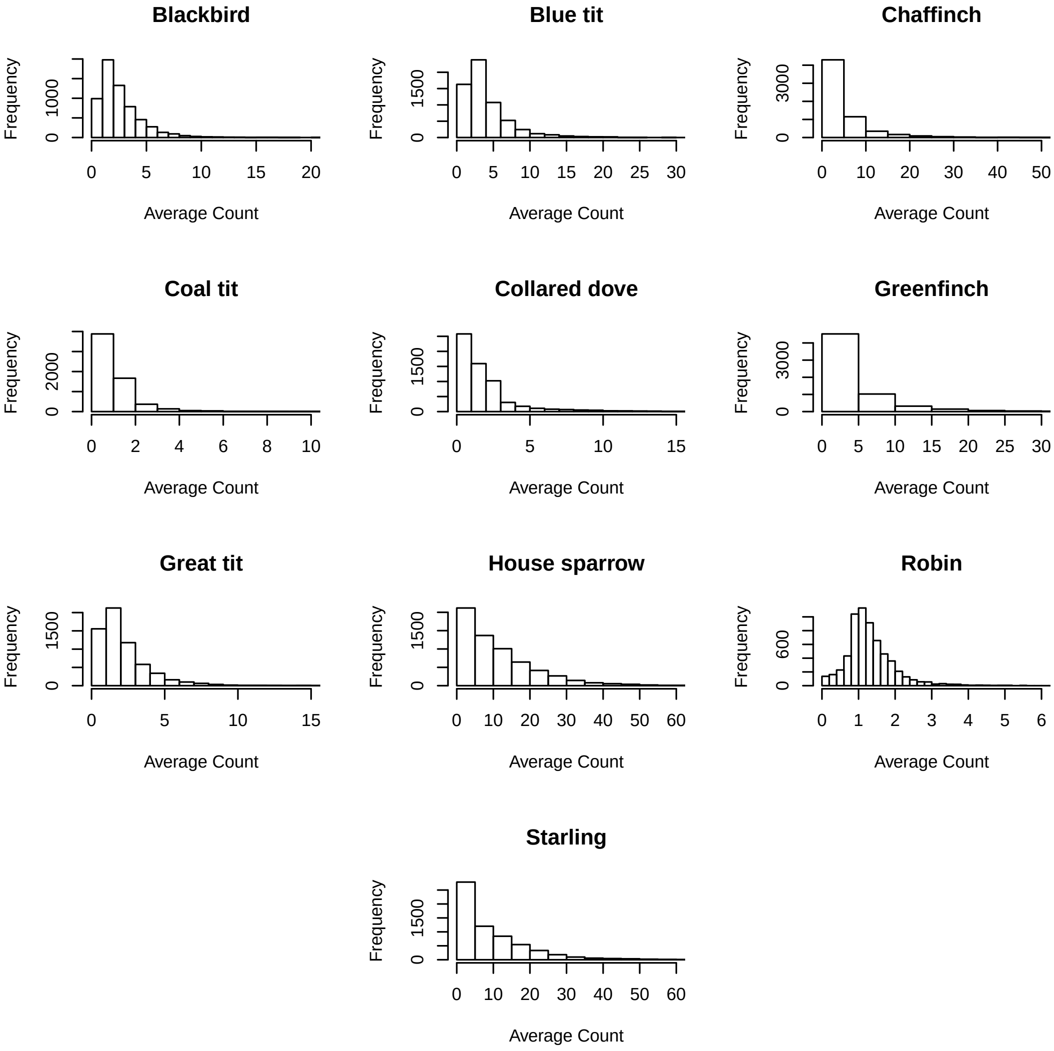

Figure 1.6: Histograms of the annual means of weekly maxima for the 10 songbird species analysed in this thesis. The histograms have been righ-truncated so that the shapes of the distributions can be seen more easily.

Of the 10 prey species for which data were available, even after having averaged over the 26 weekly counts, there were still a large number of sites with mean counts of exactly zero (Table 1.1, Figure 1.6). For most of the species, these were spread across sites and very few sites never observed those species. In this case, the zeros are most likely sampling zeros at sites with a generally low, but non-zero, abundance of that species. However, some species, such as collared dove and coal tit, were not recorded at any point at a larger number of sites (Table 1.1).

1.5.3 Environmental covariate data

In addition to the GBFS data set, extra environmental data were obtained in order to help control for climatic changes in space and time. We use data obtained from the Met Office gridded online data sets from the UKCP09[1], which records observations of climatic variables at various temporal scales at a network of meteorological stations across the UK. These observations are then subjected to an interpolation process that estimates the variables at a finer spatial scale, up to 5km x 5km resolution. Full details of this process can be found in Perry and Hollis (2005). In this thesis we use the days of ground frost monthly data set, that is the number of days in that month when the grass minimum temperature is below 0 °C. We then summed over the months in which the GBFS is conducted, namely October to March, giving a single value of the total number of ground frost days per site per year. The nearest square from the gridded data set to each of the 693 site grid references was selected using the `nearest` function in the `R` package `GenKern` (Lucy and Aykroyd, 2013).

1.6 Thesis Outline

The aim of this thesis is to develop Bayesian hierarchical methods for analysing changes in the number of birds visiting garden bird feeding stations across the UK, tailored to the nature of the GBFS. Despite being designed to be specifically applied to the GBFS data set, these methods could easily be adjusted to be used with alternative data sets and ecological processes. We then apply these methods to the GBFS data to help make inference on the environmental factors affecting the species of interest.

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[1] `http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/`

The factors underlying the changes in populations of songbirds are likely to be complex and subject to many different inter-related factors. Many previous studies of this or similar data sets have only concentrated on small aspects of the factors driving the population dynamics. The methods developed here set out to maximise the use of the data available and give the most comprehensive understanding of the mechanisms underlying these populations.

In Chapter 2 we outline some of the statistical theory that is relevant throughout the thesis, including the essentials of Bayesian inference and some of the non-standard techniques used to analyse the GBFS data set. Chapter 3 introduces the modelling technique using independent models to analyse changes in garden bird abundance as a function of environmental covariates. Often analyses are conducted using a single model formulation, assuming covariates enter the model in a specific way. It may not, however, give comparable results if a different model formulation with different parametric form is used. Chapter 4 therefore proposes an adapted model using a change-change approach, i.e. change of abundance is modelled as a function of *change* in covariates, allowing different hypotheses to be tested and contrasted with the results from Chapter 3.

Most analyses of this kind concentrate on a single species, or model different species independently of each other. However, species are usually part of a community or ecosystem that will be simultaneously susceptible to the same environment and factors therein. The extension of methodology to incorporate a multi-species approach is much needed in ecological statistics, and hence we also develop and extend current methods to model multiple species simultaneously, checking for how those species respond similarly or differently to various external factors and how unexplained variation is synchronous or asynchronous between species. Chapter 5 extends the methods of Chapter 3 to a multi-species approach and extends current methods for testing for synchrony across species in relation to environmental covariates. Following on from this, in Chapter 6, we propose methods for simultaneously modelling changes in multiple-species' distribution in both space and time using recent developments in the stochastic partial differential equation (SPDE) approach, fitted using the integrated nested Laplace approximation (INLA) methodology.

The final two chapters aim to provide an overall conclusion to the methods and results presented in the preceding chapters. In Chapter 7 we attempt to place the results of theses analyses in an ecological context and discuss their wider implications, as well as discussing similarities and differences between these results and other previous studies. Chapter 8 places the results of theses analyses in a statistical context and outlines and proposes potential future directions for the work discussed in this thesis.

Chapter 2

Statistical Theory

Throughout this thesis we make use of numerous statistical methodologies to conduct our analyses. In this chapter we outline the generalities of these statistical methods to avoid repetition in future sections. Initially we summarise the Bayesian statistical theory and the computational Markov chain Monte Carlo (MCMC) algorithms employed to implement the Bayesian approach in the analyses conducted in the subsequent chapters as well as the relatively new alternative Integrated Nested Laplace Approximation (INLA) which can be used for estimating parameters in certain types of model. We then discuss methods for analysing non-negative continuous data where exact zeros occur with non-zero probability.

2.1 Bayesian statistics: why and how

In this thesis we will adopt a Bayesian approach to inference on the model parameters of interest. The following sections will outline why the decision to conduct analyses in the Bayesian paradigm was made. Bayesian statistics has many advantages over frequentist statistics. Bayesian paradigm parameters are assumed to have distributions, rather than fixed values, and as such provide a more natural interpretation in terms of probability. Uncertainty about parameter values can easily be included explicitly in the estimation process rather than relying on asymptotic assumptions, as is done in a frequentist setting. In addition, Bayesian inference enables inclusion of prior information in the analysis if this is available. Often when conducting applied analyses, particularly so in ecology, experts in the field will have at least some prior knowledge of the likely values for the parameters of interest prior to any analysis being conducted. These advantages, however, do not come without cost. As discussed below, the methods for parameter estimation are often computationally intensive and, as based on simulation, frequently take a long time to complete.

2.1.1 Bayes' theorem

We let $\boldsymbol{\theta}$ denote the set of model parameters and $\boldsymbol{y}$ the observed data. We initially start with some prior beliefs $p(\boldsymbol{\theta})$, independent of the data. These prior beliefs are then updated through the likelihood $f(\boldsymbol{y}|\boldsymbol{\theta})$ giving the posterior distribution $\pi(\boldsymbol{\theta}|\boldsymbol{y})$ once data has been collected. The posterior distribution is given by

$$\pi(\boldsymbol{\theta}|\boldsymbol{y}) = \frac{f(\boldsymbol{y}|\boldsymbol{\theta})p(\boldsymbol{\theta})}{f(\boldsymbol{y})}. \tag{2.1}$$

The normalising constant $f(\boldsymbol{y})$ is independent of the parameter(s) of interest and frequently intractable or tedious to calculate. It is therefore often left out of the equation and equation 2.1 is rewritten as:

$$\pi(\boldsymbol{\theta}|\boldsymbol{y}) \propto f(\boldsymbol{y}|\boldsymbol{\theta})p(\boldsymbol{\theta}). \tag{2.2}$$

2.1.2 Bayesian hierarchical models

Hierarchical, or multilevel, models are used when information is available at different levels of observations, for example observations conducted at multiple times within a site. We would expect these times within sites to be related or connected in some way and hence the modelling framework should reflect that dependence. These types of models are essentially equivalent to mixed-effects models in a frequentist framework and this name is often used interchangeably for them, despite all parameters in a Bayesian framework technically being random quantities. In this instance the 'fixed effects' relate to regression parameters with additional 'random effects' often following a zero-mean normal distribution.

Mathematically, let $\boldsymbol{\theta}$ correspond to the 'fixed effect' parameters and $\boldsymbol{\phi}$ the 'random' terms. The posterior distribution for this model would then be of the following form

$$\pi(\boldsymbol{\theta}, \boldsymbol{\phi}|\boldsymbol{y}) \propto f(\boldsymbol{y}|\boldsymbol{\theta}, \boldsymbol{\phi}) f(\boldsymbol{\theta}|\boldsymbol{\phi}) p(\phi). \tag{2.3}$$

Hence the structure becomes hierarchical, with the distribution of the random effects itself being dependent on unknown *hyperparameters*.

2.1.3 Monte Carlo Integration

When modelling ecological processes cases regularly occur where a very large number of parameters need to be estimated. Posterior distributions in these cases can be very complex and evaluating integrals can become very difficult or impossible to achieve explicitly. Traditionally, summary statistics of these distributions are often used, which require integration of the posterior density. Explicitly we may wish to estimate the marginal posterior expectation of a parameter θ, expressed by

$$\mathbb{E}(\theta) = \int \theta \pi(\theta|\boldsymbol{y}) \mathrm{d}\theta. \tag{2.4}$$

To obtain an estimate for this integral, the method of *Monte Carlo integration* can be used to estimate the interval by generating a sufficiently large sample from the distribution of interest. We define the observation drawn from the distribution θ_i^t to be the value of parameter θ_i at iteration t. This sample is then used to calculate an empirical estimate of the expectation. Given a sample $\theta^1, \theta^2, ..., \theta^n \sim \pi(\theta|\boldsymbol{x})$, we can estimate the expectation of equation 2.4 by,

$$\mathbb{E}(\theta) \approx \frac{1}{n} \sum_{i=1}^{n} \theta^i.$$

The Law of Large Numbers states that

$$\frac{1}{n} \sum_{i=1}^{n} \theta^i \to \theta \quad \text{as} \quad n \to \infty.$$

In the case where the θ_i are not independent, it is likely to be less efficient and require a larger sample size to reach the same degree of Monte Carlo error. It is easy to extend this to any function of the parameter $v(\theta)$. To estimate the posterior mean of $v(\theta)$, we take the sample mean of observations of $v(\theta^i)$ by

$$\overline{v} = \frac{1}{n}\sum_{i=1}^{n} v(\theta^i).$$

Posterior variances can similarly be estimated using the sample variance.

2.1.4 Markov chain Monte Carlo inference

The simplest method for obtaining samples from the posterior distribution of interest is to sample directly from it. This, however, is only realistically feasible in very contrived cases where the distribution is of known form. In most applications it is not possible to sample directly from the posterior distribution as it is not of a standard form. Instead we use a Markov chain Monte Carlo (MCMC) algorithm to obtain inference on the parameters of interest.

A Markov chain is a stochastic sequence of numbers, where each value of the sequence is dependent *only* on the previous value of the sequence, i.e.

$$\theta^{n+1} \sim \mathcal{K}(\theta^{n+1}|\theta^{n}).$$

The transition kernel $\mathcal{K}$ uniquely describes the dynamics of the chain.

Under certain conditions, the distribution of the Markov chain will converge to a stationary (or target) distribution, independent of the initial values of the chain. If this stationary distribution is set equal to the posterior distribution of interest $\pi(\boldsymbol{\theta}|\boldsymbol{x})$, we can run the Markov chain until it reaches the stationary distribution, after which any realisations of the chain can be considered a *dependent* sample from the posterior distribution of interest. We can then use the method of Monte Carlo integration outlined above to obtain Monte Carlo estimates of the parameters of interest. The combination of these two methods is called Markov chain Monte Carlo. Only values obtained post-convergence (the point the chain has reached the stationary distribution) can be used. Any realisations prior to this point are referred to as “burn-in” and are discarded before Monte Carlo estimates are calculated. Given the joint posterior distribution, we can obtain marginal posterior distributions for each parameter by integration. This is not done mathematically but rather computationally.

There are two commonly used MCMC samplers that are exploited to varying degrees in this thesis. The Gibbs sampler and the Metropolis-Hastings algorithm are now outlined.

2.1.5 Gibbs sampler

The first method for obtaining samples is to use the full conditional distribution of π to sample directly from the joint distribution. Given a parameter vector $\boldsymbol{\theta} = (\theta_1, \theta_2, ..., \theta_p)$ with joint posterior distribution $\pi(\boldsymbol{\theta})$ (for simplicity we remove the condition on the data $\boldsymbol{y}$), the Markov chain is constructed as follows:

STEP 1. Initialise the chain.

Set $\boldsymbol{\theta}^0 = (\theta_1^0, \theta_2^0, ..., \theta_p^0)$

STEP 2. At iteration $t+1$ update parameters in turn.

$$\begin{array}{ccc}
\theta_1^{t+1} & \text{is sampled from} & \pi(\theta_1|\theta_2^t, ..., \theta_p^t) \\
\theta_2^{t+1} & \text{is sampled from} & \pi(\theta_2|\theta_1^{t+1}, \theta_3^t, ..., \theta_p^{t+1}) \\
. & . & . \\
. & . & . \\
. & . & . \\
\theta_p^t & \text{is sampled from} & \pi(\theta_p|\theta_1^{t+1}, ..., \theta_{p-1}^{t+1})
\end{array}$$

STEP 3. Repeat until T iterations have been performed.

2.1.6 The single-update Metropolis Hastings Algorithm

STEP 1: Initialise the chain.

Set $\boldsymbol{\theta}^0 = (\theta_1^0, \theta_2^0, ..., \theta_p^0)$

STEP 2: Propose updated value for the first parameter, θ_1

At iteration $t+1$, given current parameter value θ_1^t a candidate parameter value ϕ_1 is generated from the distribution $q\left(\phi_1|\theta_1^t\right)$

STEP 3: Accept or reject proposed value

Calculate the acceptance probability,

$$\alpha(\boldsymbol{\theta}, \boldsymbol{\phi}) = \min\left(1, \frac{\pi(\phi_1) q\left(\theta_1^t|\phi_1\right)}{\pi(\boldsymbol{\theta}_1^t) q\left(\phi_1|\theta_1^t\right)}\right) \tag{2.5}$$

With probability $\alpha(\boldsymbol{\theta}, \boldsymbol{\phi})$ set $\boldsymbol{\theta}^{t+1} = \boldsymbol{\theta}$

STEP 4: Repeat STEP 2 for parameters 2:$\boldsymbol{p}$

Update all other parameters that are being updated with the M-H algorithm as above.

STEP 5: Repeat STEP 1 and STEP 2 until T iterations have been performed.

The above algorithm is a single-update procedure where at each iteration all parameters are updated separately. An alternative is to use a block-update where sets of parameters are updated (or not) in a single step. This method can be very useful if parameters are highly correlated. It does however require the specification of a multi-dimensional proposal distribution. It is also possible to use a single-update Metropolis-Hastings algorithm in which each parameter in STEP 2 is updated in turn using a univariate proposal distribution.

The Gibbs update algorithm outlined above is a special case of the Metropolis-Hastings algorithm, where the proposal distribution is set equal to the posterior conditional distribution. In this case the acceptance probability of equation 2.5 simplifies to one.

2.1.7 Checking convergence

To ensure that parameter estimates are independent of the starting values and that the Markov chain has reached the stationary distribution, any iterations prior to this point, commonly referred to as ‘burn-in’, must be discarded. The choice of what proportion of the iterations to discard must be made. No convergence diagnostic can prove convergence; it can only identify when it is not the case.

Visual checking

The easiest way to assess convergence of individual parameters is to look at trace plots showing the value of the parameter at each iteration. It is then often possible to see when the parameter has converged on the stationary distribution when they converge on values around a constant mean. Although a very simple method for determining convergence, it is not always the most robust method. Sometimes a more formal approach is necessary.

Brooks-Gelman-Rubin statistic

The Brooks-Gelman-Rubin (BGR) statistic (Brooks and Gelman, 1998) is one such formal method and the most commonly used. This approach is based upon an analysis of variance type approach where separate runs of the chain are conducted with overdispersed starting values. For a chain containing $2n$ iterations, the first n iterations are discarded. The statistic is then the ratio of the width of the 80% credible interval of the pooled chains to the mean width of the 80% credible intervals of the individual chains, for the remaining n iterations i.e.

$$\hat{R} = \frac{\text{width of 80\% credible interval of pooled chains}}{\text{mean of width of 80\% credible interval of individual chains chains}}. \tag{2.6}$$

Convergence can then be assumed when $\hat{R} \approx 1$.

2.2 Data Augmentation

Bayesian statistics has the additional benefit over frequentist statistics in that missing data can easily be incorporated into the modelling framework. A data augmentation approach is a simple extension that can be used in Bayesian analyses to extend Bayes' Theorem over both model parameters and unobserved data (Tanner and Wong, 1987). As such the missing data is treated in the same way as unknown model parameters and the posterior distribution is specified jointly over both these unknown data and model parameters. Let $\boldsymbol{z}$ be a vector of missing data. For observed data $\boldsymbol{y}$ and unobserved data $\boldsymbol{z}$, the joint posterior distribution of parameters and unobserved data is given by:

$$\pi(\boldsymbol{\theta}, \boldsymbol{z}|\boldsymbol{y}) \propto f(\boldsymbol{z}, \boldsymbol{y}|\boldsymbol{\theta})p(\boldsymbol{\theta}).$$

We may then be interested in the posterior distribution $\pi(\boldsymbol{\theta}|\boldsymbol{y})$, which is simply the marginal posterior distribution having integrated out the unobserved data. Formally,

$$\pi(\boldsymbol{\theta}|\boldsymbol{y}) = \int \pi(\boldsymbol{\theta}, \boldsymbol{z}|\boldsymbol{y})d\boldsymbol{z}.$$

The same approach can be used if we are interested in predicting future outcomes. Specifying the predicted data as unobserved or missing, these values can be updated using the MCMC framework.

2.3 Model discrimination

The general form of the Metropolis-Hastings algorithm outlined above assumes a fixed model and then enables estimation of the parameters within that model. However, when analysing ecological data, a range of models may be considered plausible. Of particular interest to this thesis is the overall effect of covariates on changes in garden bird counts, that is a range of models with different combinations of covariates. There are several different ways to approach the problem of model uncertainty. Below we outline two of these such approaches.

2.3.1 Information criteria

When conducting model selection in a classical framework, the Akaike Information Criterion (AIC) is often used to compare competing models and is a trade-off between-model fit (through the deviance) and complexity (the number of parameters). Within the Bayesian framework, however, the parameters no longer have a fixed value but rather a distribution. An alternative to the AIC has been proposed for use in Bayesian model selection - the Deviance Information Criterion (DIC) (Spiegelhalter et al., 2002).

The DIC for a given model m is defined by

$$DIC = -2\mathbb{E}_{\pi}(\log f_m(\boldsymbol{y}|\boldsymbol{\theta})) + p_D(m);$$

where $f_m(\boldsymbol{y}|\boldsymbol{\theta})$ is the likelihood function under model m and $p_D(m)$ is the effective number of parameters and is defined as

$$p_D(m) = -2\mathbb{E}_{\pi}(\log f_m(\boldsymbol{y}|\boldsymbol{\theta})) + 2\log f_m(\boldsymbol{y}|\mathbb{E}_{\pi}(\boldsymbol{\theta})).$$

The model with the lowest DIC statistic is then chosen as the preferred model.

The disadvantage of the information criteria is that they must be calculated for each possible model individually and then compared across models. This is not a particular problem when only a small number of possible models are to be considered feasible. However, when more than a few models are potentially feasible, the use of information criteria requires many different models to be fitted independently and compared. When more than a few models are considered feasible *a priori*, this can potentially become highly computationally intensive. They are also conditional on the correct set of potential models being specified as only these can be compared.

Celeux et al. (2006) studied the performance of the DIC in the presence of missing data and found that it was frequently inadequate for evaluating the complexity and fit of a model. Since its original proposal, the DIC has received much criticism. Recently Spiegelhalter et al. (2014) outlined the criticisms that have been put forward and discussed some possible imporvements to the DIC. Following Spiegelhalter et al. (2014), the main criticisms of the DIC in addition to those of Celeux et al. (2006) can be summarised as follows:

- The effective number of parameters is not invariant to reparameterisation, even if the priors specified on those parameters are equivalent. In certain cases a negative effective number of parameters can be obtained.
- A lack of statistical consistency.
- It is not based on a formal predictive critereon, instead using plug-in predictions rather than the full predictive distributions.

Alternatives to the DIC that are more appropriate for complex models have been suggested, such as the WAIC (Watanabe, 2013). Alternatives to information critereon are predominately used in this thesis, hence we do not discuss them to any further degree here.

2.3.2 Posterior model probabilities and Bayes Factors

An alternative approach to compare competing models is to consider posterior model probabilities. A simple extension of the Bayes' Theorem to incorporate model uncertainty as well as parameter uncertainty can be used by considering the model itself to be an unknown parameter. Through the use of Bayes' Theorem we can incorporate any prior information on the relative importance of the models.

The extension of Bayes' Theorem is formulated as follows:

$$\pi(\boldsymbol{\theta}_m, m|\boldsymbol{y}) \propto f_m(\boldsymbol{y}|\boldsymbol{\theta}_m, m)p(\boldsymbol{\theta}_m|m)p(m)$$

where $\boldsymbol{\theta}_m$ are the parameters in model m and $p(m)$ is the prior probability of model m. The prior distributions $p(\boldsymbol{\theta}_m|m)$ on the parameter can be specified independently for each model, although usually if a parameter is present in more than one model the same prior will be specified on that parameter in all models.

Once posterior model probabilities have been calculated, Bayes factors can then be computed to compare two models or hypotheses against each other. Formally, the Bayes factor of model m_1 against m_2 is defined as

$$B_{12} = \frac{\pi(m_1|\boldsymbol{y})/\pi(m_2|\boldsymbol{y})}{p(m_1)/p(m_2)}.$$

Table 2.1: Guide to Bayes factor interpretation, from Kass and Raftery (1995).

Bayes Factor	Evidence against H_0
< 3	Not worth mentioning
3 - 20	Positive evidence
20 - 150	Strong evidence
> 150	Very strong evidence

That is the ratio of posterior odds to prior odds. Kass and Raftery (1995) give a guide to the interpretation of Bayes factors. Their table is reproduced in Table 2.1. In general we follow the rule of thumb that a Bayes factor ≥ 3 corresponds to positive evidence in support of one model or hypothesis over another.

2.3.3 Reversible Jump MCMC

When more than a few models are *a priori* feasible, a more complex algorithm is required to cover uncertainty across model space. Given a set of potential models, we now need to be able to estimate the posterior model probabilities of each of the competing models. The reversible jump algorithm is an extension of the Metropolis-Hastings algorithm outlined in section 2.1.6 which allows movements between models of different dimensions. The standard case of the reversible jump algorithm used in the thesis is a method for covariate selection and can be defined as follows. We denote $\boldsymbol{\theta}_m \in \boldsymbol{\Theta}$ to be the subset of regression covariate parameters in model m. At each iteration, a single regression parameter is proposed to be added or removed from the model, depending on whether or not it is in model m.

STEP 1. Update model parameters

Suppose that at iteration t the Markov chain is in model m with covariate parameter vector $\boldsymbol{\theta}_m$. Update all regression parameters in $\boldsymbol{\theta}_m$ and any additional model parameters using the random walk Metropolis algorithm, or, in the case of conjugate parameters, the Gibbs algorithm, conditional on model m.

STEP 2. At iteration t, propose move to neighbouring model

Select one of the regression parameters at random. Propose to move to a new neighbouring model m' with probability $p(m'|m)$ and associated regression parameter vector $\boldsymbol{\theta}'_{m'}$.

STEP 3. At iteration t, accept or reject model update

If the proposed parameter is not currently in the model, then $\boldsymbol{\theta}^t_m = \{\boldsymbol{\delta}\}$ and $\boldsymbol{\theta}'_{m'} = \{\boldsymbol{\delta}', \kappa'\}$,

i. Set $\boldsymbol{\delta}' = \boldsymbol{\delta}$ and $\kappa' = u$, where $u \sim q(u)$.

ii. Calculate acceptance probability in $\min(1, A)$, where,

$$A = \frac{\pi(\boldsymbol{\theta}'_m, m'|\boldsymbol{y})p(m|m')}{\pi(\boldsymbol{\theta}_m, m|\boldsymbol{y})p(m'|m)q(u)} \left| \frac{\partial\left(\boldsymbol{\delta}', \kappa'\right)}{\partial(\boldsymbol{\delta}, u)} \right|.$$

iii. With probability $\min(1, A)$ set $(\boldsymbol{\theta}^{t+1}_m, m^{t+1}) = (\{\boldsymbol{\delta}', \kappa'\}, m')$, else $(\boldsymbol{\theta}^{t+1}_m, m^{t+1}) = (\boldsymbol{\delta}, m)$.

Else if we propose the reverse move from model m' to model m, $\boldsymbol{\theta}'_{m'} = \{\boldsymbol{\delta}', \kappa'\}$ and $\boldsymbol{\theta}_m = \{\boldsymbol{\delta}\}$,

i. Remove κ' from the model (equivalently set $u = \kappa'$) and calculate A as above.

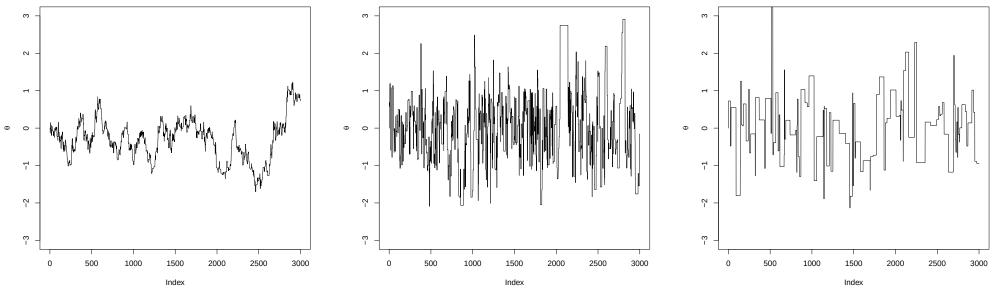
ii. With probability $\min(1, A^{-1})$ set $(\boldsymbol{\theta}^{t+1}_m, m^{t+1}) = (\boldsymbol{\delta}, m)$, else $(\boldsymbol{\theta}^{t+1}_m, m^{t+1}) = (\{\boldsymbol{\delta}', \kappa'\}, m)$.

Using the identity function as the bijective function means that the Jacobian reduces to unity,

$$\left| \frac{\partial\left(\boldsymbol{\delta}', \kappa'\right)}{\partial(\boldsymbol{\delta}, u)} \right| = \begin{vmatrix} \frac{\partial \boldsymbol{\delta}'}{\partial \boldsymbol{\delta}} & \frac{\partial \boldsymbol{\delta}'}{\partial u} \\ \frac{\partial \kappa'}{\partial \boldsymbol{\delta}} & \frac{\partial \kappa'}{\partial u} \end{vmatrix} = 1.$$

Equal prior probabilities are specified on the covariates being present or absent i.e. $p(m|m') = p(m'|m) = 1$ and hence A can be simplified to,

$$A = \frac{\pi(\boldsymbol{\theta}', m'|\boldsymbol{y})}{\pi(\boldsymbol{\theta}, m|\boldsymbol{y})q(u)}.$$



$\sigma^2 = 0.01$ $\sigma^2 = 1$ $\sigma^2 = 100$

Figure 2.1: Trace-plots of Metropolis-Hastings algorithms with varying proposal variances.

2.4 Improving mixing in chains

A common problem that can often occur when conducting Bayesian inference using MCMC methods is mixing of the chains. This relates to the how well the chain generates and accepts proposed parameter values. If the proposal distribution q is chosen poorly then the acceptance probability may be too low. This leads to low efficiency and chains that get stuck at the same value for large portions of the chain. Conversely, if parameter values too close to the current value are proposed, then the chain will move very slowly and it will take a long time to span posterior space and reach convergence. In this case, post burn-in samples will also have very high auto-correlation meaning once more the efficiency of the algorithm is poor. Figure 2.1 shows mixing for MCMC chains for differing proposal distributions, where the posterior distribution of interest is a standard normal distribution. Ideally, a traceplot similar to plot (b) is desirable. Many different methods for dealing with this problem have been suggested. Two of these methods are used in the thesis and an outline of their use is given below.

2.4.1 Hierarchical centring

A common problem with repeated measure multilevel models such as those fitted in this thesis is the highly computationally intensive nature of the parameter estimation process, particularly when using MCMC methods (Browne, 2004; Browne et al., 2009). In particular, the constructed Markov chains are often highly correlated, leading to slow convergence and/or poor coverage of parameter space, usually leading to high Monte

Carlo error. To improve the efficiency of the MCMC algorithm we use hierarchical centring (Gelfand et al., 1995), a reparameterisation algorithm developed for nested random effect models where the original parameters in the model are replaced with less correlated ones. The aim of this method is to remove correlation between the parameters associated with fixed effects in the linear predictor that are constant within random effect clusters and the zero-mean random effects (Browne, 2004; Browne et al., 2009). Formally, let η be the expected value of a model with link function $g(\mu)$. Then, the model without hierarchical centring can be written as:

$$\eta = g(\mu)$$

where

$$\mu = \beta_0 + \sum_{i=1}^{k} x_k \beta_k + b_j, \qquad b_j \sim N(0, \sigma_b^2). \tag{2.7}$$

The simple reparameterisation in this instance is to centre the random effects on this (these) parameter(s), such that the zero means are replaced with a function of the original cluster level predictors and fixed effects "pulled" from the linear predictor. In the above example, it could be that the intercept and covariate x_1 are constant within each grouping unit j, whilst $x_2, ..., x_k$ are not. In which case, Equation 2.7 then becomes

$$\mu = \beta_0 + \sum_{i=2}^{k} x_k \beta_k + b_j, \qquad b_j \sim N(\beta_0 + \beta_1 x_1, \sigma_b^2).$$

Oedekoven et al. (2014) extend this reparameterisation method for the use in a RJMCMC (2.3.3), where it was found to improve model mixing and movement over model and parameter space. Poor mixing in between-model moves can arise for multiple reasons, including poor specification of proposal distributions (see Section 2.4.2 below). These problems can be particularly severe in random effect models as the random effect coefficients can begin absorbing the effect of a fixed effect if it is not currently in the model (Oedekoven et al., 2014). Proposed moves to models with this covariate in the model are then unlikely to be accepted if they have already been accounted for by the random effects. During a between-model move, the distribution of the random effects would normally remain the same, whilst the formula for the mean of the response distribution changes. When using hierarchical centring, between-model moves adding or removing covariates used in the centring now affects the distribution of the random effects and not the response distribution, whilst moves to add or remove other covariates remain the same. In both scenarios, only the random effect coefficients affect both parts of the likelihood. Therefore, using centring the likelihood of the response distribution remains unchanged for both within- and between-model moves when the centred covariates are concerned. The mean of the normal density will produce higher likelihood values when the random effect coefficients are close to the mean and hence including a covariate in the model when it should be there will on average improve the overall likelihood by making the individual coefficients closer to their assumed mean.

2.4.2 Proposal variance pilot-tuning

Markov chain Monte Carlo algorithms require the definition of a distribution $q(.)$ to generate proposal values for the parameters of interest. Although arbitrary, the efficiency of the chain is highly dependent on the specification of this distribution. To improve the mixing and efficiency of the algorithm, we follow Sherlock et al. (2010), using Algorithm 2 of the sequential tuning approach outlined. We denote θ_i the parameters to be updated via the random walk Metropolis algorithm and $\theta_i^{(t)}$ the value of the parameter at the current iteration. The variances λ_i^2 of the proposal distribution $q(\theta_i^{(t)}, \lambda_i^2)$ are tuned independently for each parameter. For a Gaussian proposal and target distribution, the optimum acceptance probability is between 0.4 and 0.45 (Sherlock et al., 2010). The target distributions in this application are, however, not Gaussian so we found that tuning the proposals to give acceptance probabilities between 0.1 and 0.8 gave the best mixing. In general, the sequential tuning algorithm used here works on the basis that if the proposal variance is too small, acceptance probabilities tend to be high (and hence the chain will move slowly around parameter space). Conversely, variances that are too large will produce acceptance probabilities that are smaller and hence the chain will get stuck at the same value for longer periods.

During the burn-in phase, for parameter θ_i:

STEP 1. Propose updated model parameters

At iteration t of the MCMC algorithm, with current parameter value $\theta_i^{(t)}$, generate new parameter value ϕ from $q(\theta_i^{(t)}, \lambda_i^{(t)2})$.

STEP 2. Calculate and save acceptance probabilities

Calculate the acceptance probability,

$$\alpha(\theta_i^{(t)}, \phi) = \min\left(1, \frac{\pi(\phi|.)q(\theta_i^{(t)}, \lambda_i^{(t)2})}{\pi(\theta_i^{(t)}|.)q(\phi, \lambda_i^{(t)2})}\right).$$

where $\pi(\phi|.)$ is the posterior conditional distribution of parameter ϕ, conditional on the other parameters in the model and the data.

STEP 3. Accept or reject proposed parameter values

Set $\theta_i^{(t+1)} = \phi$ with probability $\alpha(\theta_i^{(t)}, \phi)$, else $\theta^{(t+1)} = \theta_i^t$.

STEP 4. If acceptance probability $\alpha(\theta_i^{(t)}, \phi) \notin (a, b)$ tune proposal variance accordingly

1. If $\alpha(\theta_i^{(t)}, \phi) < a$ set $\lambda_i^{(t+1)2} = \lambda_i^{(t)2}/x_a$.
2. If $\alpha(\theta_i^{(t)}, \phi) > b$ set $\lambda_i^{(t+1)2} = x_b\lambda_i^{(t)2}$,

for $x_a, x_b > 1$. a, b, x_a and x_b are chosen by further pilot tuning. Several different runs of the algorithm with different combinations of these parameters were run and the acceptance probabilities monitored.

STEP 5. Increase iteration by one and repeat from STEP 1.

Set $t = t + 1$ and return to step 1 until $t =$ burn-in.

2.5 Goodness of fit and the Bayesian p-value

When a model has been fitted we generally wish to assess whether it is a good fit to the data. Having adopted a Bayesian approach to obtaining inference in this thesis, we check for evidence of poor fit of the models using the Bayesian p-value (Gelman et al., 2014). This statistic is a measure of the fitted model's posterior predictive ability. In essence, it involves simulating data of the same dimension as that of the observed data for each iteration of the MCMC post burn-in and then calculating the discrepancy between these simulated datasets and the observed data at each iteration. To measure the discrepancy between the two, a suitable statistic must be chosen that measures some form of difference between the two. This is carried out over all models. We then calculate the proportion of the simulated datasets that equal or exceed its realised value. If the model fits well and is indeed similar to the data-generating process then we would expect the fitted model to generate data consistent with the observed data.

The Bayesian posterior predictive p-value is the test quantity

$$p_B = \Pr(T(y^{\text{rep}}, \theta) \geq T(y, \theta) | y),$$

where T is the chosen discrepancy statistic and y^{rep} the replicated datasets simulated from the model. The test quantile $T(y, \theta)$ is scalar summary of data and parameters chosen to compare data to predictive simulations. The deviance is commonly used as a measure of model fit and is frequently chosen for the test quantile for Bayesian p-value calculation. Models with p-values in either the upper or lower tail are considered to show evidence of a poor fitting model. As such, we use a 5% rejection region in both tails i.e. a rejection region of $p_B \notin [0.05, 0.95]$, a reasonable range suggested by Gelman et al. (2014). A model with an associated Bayesian p-value outside of this region would warrant further checking and scrutiny.

There has been some discussion recently as to the ability of the posterior predictive p-value to provide evidence that a model is indeeed a good fit, or whether it can merely highlight poor fitting models (e.g. Gelman, 2013). It is therefore suggested that further checks of fitted against observed values are important. Alternatives and extensions to the posterior predictive p-values have been suggested and are discussed by Steinbakk and Storvik (2009).

2.6 Integrated Nested Laplace Approximation

Until recently, MCMC has dominated the Bayesian methodology literature as the most commonly used method for the estimation of parameters in hierarchical models. Due to the fact that MCMC uses stochastic simulation, it can become very slow and computationally intensive to estimate parameters in complex hierarchical Bayesian models. An alternative to MCMC, which can be applied to a particular set of models, was proposed by Rue et al. (2009) and has previously been applied to ecological applications, amongst others (e.g. Illian et al., 2013). This alternative methodology, Integrated Nested Laplace Approximation (INLA), has been designed to produce fast, accurate approximations for a large class of models, namely latent Gaussian models. These models, which are also fitted in a Bayesian setting, consist of three levels: the observations, an underlying latent structure and a vector of hyperparameters.

The observations (denoted $\boldsymbol{y}$) are assumed to follow some probability distribution, with

$$f(\boldsymbol{y}|\boldsymbol{\eta}) = \prod_{k \in \mathcal{K}} f(y_k|\eta_k),$$

where $\mathcal{K}$ is an index for grid cells and $\boldsymbol{\eta}$ is the latent Gaussian field. Conditional on the latent field $\boldsymbol{\eta}$, the observations are assumed to be independent.

The latent field itself is a latent Gaussian random field, which is included to reduce spatial autocorrelation and relates to observed and unobserved covariates.

$$f(\boldsymbol{\eta}|\boldsymbol{\theta}) = N(\mathbf{0}, \boldsymbol{\Sigma}(\boldsymbol{\theta}))),$$

with hyperparameters $\boldsymbol{\theta}$ having prior distributions $p(\boldsymbol{\theta})$. In INLA the (continuous) Gaussian random field is approximated by a discrete Gaussian Markov random field (GMRF) on a spatial grid. The use of this discrete approximation takes advantage of the sparse precision matrix of the GMRF $Q(\boldsymbol{\theta}) = \boldsymbol{\Sigma}^{-1}(\boldsymbol{\theta})$ where values in the grid depend only on the spatial neighbours.

We are then usually interested in calculating the posterior marginal distributions for the latent variables and the hyperparameters. That is

$$
\begin{aligned}
\pi(\eta_k|\boldsymbol{y}) &= \int f(\eta_k|\boldsymbol{y},\boldsymbol{\theta})f(\boldsymbol{\theta}|\boldsymbol{y})d\boldsymbol{\theta} \\
\pi(\theta_j|\boldsymbol{y}) &= \int \pi(\boldsymbol{\theta}|\boldsymbol{y})d\boldsymbol{\theta}_{-j}.
\end{aligned}
$$

INLA approximates $\pi(\eta_k|\boldsymbol{y},\theta)$ and $\pi(\boldsymbol{\theta}|\boldsymbol{y})$ and then uses numerical integration to integrate out $\boldsymbol{\theta}$ and compute $\pi(\eta_k|\boldsymbol{\theta})$. $\pi(\theta_j|\boldsymbol{y})$ is similarly calculated by using numerical integration to integrate over $\boldsymbol{\theta}_{-j}$ from the approximation to $\pi(\boldsymbol{\theta}|\boldsymbol{y})$.

The approximation to $\pi(\boldsymbol{\theta}|\boldsymbol{y})$ is done as follows, where $u^*(\boldsymbol{\theta})$ is the posterior mode of the full conditional:

$$
\pi(\boldsymbol{\theta}|\boldsymbol{y}) \approx \frac{f(\boldsymbol{\eta},\boldsymbol{\theta},\boldsymbol{y})}{\tilde{f}_G(\boldsymbol{\eta}|\boldsymbol{y},\boldsymbol{\theta})} \,|_{\boldsymbol{\eta}=u^*(\boldsymbol{\theta})} \,.
$$

$\tilde{f}_G(\boldsymbol{\eta}|\boldsymbol{y},\boldsymbol{\theta})$ is the Gaussian approximation to the full conditional of $\boldsymbol{\eta}$.

The `R` package `INLA` (Rue et al., 2014) can be used to fit a set of different spatial and spatio-temporal models using the INLA framework defined above.

2.7 Modelling non-negative continuous data with a discrete mass at zero

The nature of the data outlined in the previous chapter necessitates a model which will allow a distribution that is non-negative continuous and bounded below by zero, which for many species is characterised by a discrete mass at the origin. It may be possible in some situations to explain this non-zero probability at zero with a particular covariate if mass of probability is particularly associated with a particular phenomenon. However this is likely to be the case only in a minority of applications. Instead, models that can formally account for the reduced variability are necessary. There are two main approaches to this. The first approach, the delta model, uses a mixture of two separate models; one for the presence or absence of a species and a continuous distribution to model the positive observations. The second approach models both zeros and positive observations together in a single distribution.

2.7.1 Delta model

The delta model outlined by Aitchison (1955) assumes that there is a non-zero probability π such that a random variable Y takes the value zero, and hence a probability $1-\pi$ that Y is non-zero. Conditional on being non-zero, Y is assumed to follow some positive continuous distribution, most frequently the log-normal or gamma distributions. The distribution of Y is hence:

$$\begin{aligned} P(Y=0) &= \pi,\ \ 0 \leq \pi \leq 1 \\ P(Y|Y>0) &= (1-\pi)g(y) \end{aligned}$$

where $g(y)$ is a probability density function with non-negative continuous support. Frequently the log-normal distribution is used for $g(y)$ (e.g. Foster and Bravington, 2013). Following Aitchison (1955) and Foster and Bravington (2013), the delta log-normal model is specified as follows:

$$\begin{aligned} \text{logit}(\mathbb{E}(\mathbb{I}(y_i > 0))) &= \boldsymbol{w}_i^\top \boldsymbol{\beta} \\ \mathbb{E}(\log(y_i)|y_i > 0) &= \boldsymbol{x}_i^\top \boldsymbol{\tau} \end{aligned}$$

where $\boldsymbol{w}_i$ and $\boldsymbol{x}_i$ are vectors of covariates for the presence/absence and density likelihoods respectively, with associated parameter vectors $\boldsymbol{\beta}$ and $\boldsymbol{\tau}$.

Practically, this is equivalent to fitting a binary model to the entire data and a log-normal model to only the positive observations. The delta model has the advantage of allowing covariate dependence in both parts of the model, namely the logistic and the gamma/log-normal parts. This is particularly useful if the zeros are a special case and different ecological mechanisms are suspected to be generating them. However, if the processes governing the zeros and positive values are not considered to be different, the delta models create an unnatural discontinuity at zero whilst also being relatively sensitive to standard sampling assumptions (Lecomte et al., 2013). It is also difficult to include random effects in this type of model. Min and Agresti (2005) discuss random effect models for zero-inflated count data, which could easily be extended for the use with the delta model but we tend not to use these models in this thesis unless unavoidable.

This type of model has been applied previously to ecological data, particularly fisheries data (e.g. Hvingel et al., 2012; Stefánsson, 1996)

2.8 The Tweedie distributions

The second general approach to modelling this mixture of discrete and continuous data of this type is to use a distribution that is flexible enough to account for the discrete mass at zero directly. One such class of distributions exists, but its use has been somewhat restricted due to the difficulty in computing the likelihood.

The Tweedie distributions are a family of probability distributions which encompass both continuous distributions (such as the normal and gamma) and discrete distributions (such as the Poisson) in addition to compound Poisson-gamma distributions, which have positive mass at zero and are continuous everywhere else. In general the variance of the Tweedie distributions obey a fixed mean-variance relationship of the form:

$$Var(Y) = \phi\mu^p$$

for $\mu = \mathbb{E}(Y)$ and constants ϕ and p.

Following Dunn and Smyth (2005), the Tweedie family are a special case of an exponential dispersion model, the latter a type of exponential family of the form:

$$f(y; \mu, \phi) = a(y, \phi) \exp\{\frac{1}{\phi}[y\theta(\mu) - \kappa(\theta(\mu))]\}. \tag{2.8}$$

For a Tweedie distribution θ and κ take the form:

$$\theta(\mu) = \begin{cases} \frac{\mu^{1-p}}{1-p} & p \neq 1 \\ \log\mu & p = 1 \end{cases} \tag{2.9}$$

and

$$\kappa(\theta(\mu)) = \begin{cases} \frac{\mu^{2-p}}{2-p} & p \neq 2 \\ \log \mu & p = 2 \end{cases} \tag{2.10}$$

2.8.1 Special cases of the Tweedie distributions

Table 2.2: Special cases of the Tweedie distributions for fixed values of ϕ and p.

p	ϕ	Distribution
0	σ^2	Normal
1	1	Poisson
1	$\neq 1$	Quasi-Poisson
$1 < p < 2$	> 0	Compound Poisson-gamma
2	> 0	Gamma
3	> 0	Inverse normal

The Tweedie class of distributions, although having no overall closed likelihood, do contain several common distributions as special cases. Specifically the combinations of values of p and ϕ corresponding to special cases can be found in Table 2.2. The normal, Poisson, gamma and inverse normal are all special cases of the Tweedie distributions. This range of distributions alone shows the flexibility of the family, containing as it does both discrete and continuous distributions.

In this thesis, we will be particularly interested in the cases where $1 < p < 2$, that is the compound Poisson-gamma distributions. Smyth (1996) and Dunn and Smyth (2005) show an equivalence between the Tweedie distributions when $1 < p < 2$ and a mixture distribution of the following form:

$$y_{i,j} \sim \sum_{i=1}^{n_i} w_{i,j} \tag{2.11}$$

where

$$n_i \sim P(\lambda_i)$$

and

$$w_{ij} \sim \Gamma(\alpha, \beta_i). \tag{2.12}$$

Here, there is a direct relationship between the parameters of the two different parameterisations. That is,

$$\lambda_i = \frac{1}{\phi}\frac{\mu_i^{2-p}}{2-p}, \qquad \alpha = \frac{2-p}{p-1}, \qquad \text{and} \qquad \beta_i = \phi(p-1)\mu_i^{p-1}.$$

This relationship has advantages over other parametrisations as it has direct interpretations for many applications in which these types of Tweedie distributinos can be used. The Poisson-gamma formulation has also been exploited when calculating likelihoods due to its simpler likelihood form (e.g. Dunn, 2014; Foster, 2014).

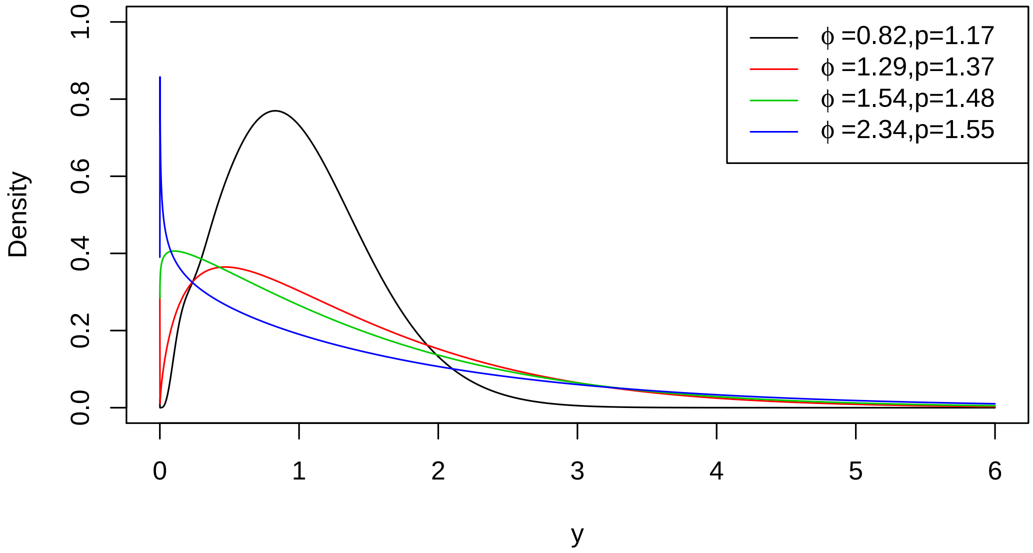


Figure 2.2: Example Tweedie densities for a fixed value of $\mu = 1$.

Some examples of the types of distributions that can be fitted for a fixed value of $\mu = 1$ and $p \in (1, 2)$ are shown in Figure 2.2. Varying μ will provide an even greater variety of shapes of distributions. In addition, the degree of zero-inflation is also highly variable so even if data are not evidently zero-inflated, the Tweedie distributions may still be relevant.

2.8.2 Density estimation

As mentioned in the previous section, there is no closed-form expression for the likelihood of the Tweedie distributions when they do not correspond to one of the special cases from Table 2.2. Thus computationally-intensive approximations are required in order to estimate the likelihood for a given set of parameters $\{\mu, \phi, p\}$. The difficulty in calculating the likelihood of the Tweedie distributions is one of the main reasons for their lack of use, despite their wide applicability and flexibility as a family of distributions.

There is a reasonably large and increasing volume of literature dedicated to the estimation of Tweedie densities. As it does not form a large part of this thesis, we do not discuss it at great length here. Tweedie density estimation has been disccussed extensively elsewhere (e.g. Dunn and Smyth, 2005; Foster and Bravington, 2013; Smyth, 1996) and interested readers are guided to these references for further details. Tweedie densities throughout this thesis were estimated using the `R` package `fishMod` (Foster, 2014).

2.8.3 Previous applications of the Tweedie distributions

The Tweedie distributions have found several areas of application, despite being generally underused. The flexibility that their three parameters enable, and their inclusion of many standard distributions as special cases, make them widely-applicable to numerous different areas of research. The majority of papers where they have been used have been in the fisheries biomass literature, although even here they are not used extensively (e.g. Candy, 2004; Foster and Bravington, 2013; Shono, 2008). Similarly, compound Poisson distributions were also used in equivalent applications by Ancelet et al. (2010) and Lecomte et al. (2013). Other areas include the application of climate data, particularly rainfall (e.g. Dunn, 2004; Hasan and Dunn, 2010), and insurance claims (Smyth and Jørgensen, 1994).

Compared to the delta models, the ability to account for serial correlation in observations is much easier. The inflation of zero observations in this case can also directly be accounted for without the need to treat them as special cases. All of these applications have used the Tweedie distributions to capture distributions that are continuous and non-negative but with a discrete mass at zero, i.e. corresponding to a restricted subset of parameter space for p. Little work has been done using these distributions for alternative combinations of parameters, probably due to the fact that alternative and simpler distributions are available for these types of data.

The majority of these applications have exploited the compound-Poisson specification of the distribution as the response variables in each case can easily be separated into frequencies (N_i) and summands (w_{ij}). For example, biomass can be split into the number of fish caught (the Poisson part of the likelihood) and the weights of individual fish (the gamma part). Similarly with insurance claims, this becomes the number of claims and the amount per claim respectively. In the case of other applications, however, this reparameterisation might not always have the required interpretation and as such the standard Tweedie parameterisation in terms of μ, ϕ and p may be more appropriate.

Chapter 3

Independent models for the GBFS data

3.1 Introduction

In this chapter we outline the first model used to analyse changes in songbird populations using data from the GBFS. As discussed in Section 1.5.2, the data relate to an annual mean of weekly maxima and are hence continuous but for some species the probability of an exact zero is highly inflated. The empirical distributions are also variable in terms of shape, scale and kurtosis and hence the Tweedie distributions are ideal for flexibly fitting models across all species. Our first approach will model the mean maximum annual abundance of a single species as a function of a combination of environmental factors. We are specifically interested in finding whether there is evidence to suggest that sparrowhawks are having a negative impact on the numbers of any of the species of interest, but control for additional variables that are likely to be affecting the number of the 10 potential prey species outlined in Section 1.5.2. Here we build on work by previous authors to use a more extensive and flexible approach to the modelling of these garden bird data.

An additional question concerned whether site-specific random effects should be included in the model. Linear mixed or hierarchical models that account for relatedness between observations collected in space and time were until recently underused in ecology (Buckley and Rees, 2003). It seems plausible that variation between individual sites that is not accounted for by the covariates is likely to be greater on average than that within sites across all years. We therefore use site-specific random effects to account for this spatial dependence.

3.2 The model

In this section we outline the model used in this chapter. Firstly we outline some notation used in the model specification. Mathematically, let y_{it} denote the mean maximum number of a given prey species at site i in year t $(i = 1, ..., n_{site}; t \in \boldsymbol{t}_i)$, where n_{site} is the total number of distinct sites and $\boldsymbol{t}_i$ is the set of years in which observations are carried out at site i. We denote $t = 1$ to be the first year that a given site is monitored. Therefore the exact year that this refers to will vary depending on when that site enters the survey. Furthermore, let $\boldsymbol{x}_i$ denote a vector of covariates that are time invariant and $\boldsymbol{v}_{it}$ a vector of time-varying covariates corresponding to a given site i with associated regression parameter vectors $\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$ respectively. If $\mathbb{E}\left(y_{it}|\boldsymbol{x}_i, \boldsymbol{v}_{it}, \epsilon_i\right) = \mu_{it}$ is the expectation of the mean of weekly maxima then

$$y_{it} \sim Tw\left(\mu_{it}, \phi, p\right) \tag{3.1}$$

where

$$Var(y_{it}) = \phi\mu_{it}^p$$

and

$$\mu_{it} = \mu_{it-1}\exp\left(\alpha + \boldsymbol{x}_i^\top\boldsymbol{\beta} + \widetilde{y}_{it-1}^\top\nu + \boldsymbol{v}_{it}^\top\boldsymbol{\gamma} + \epsilon_i\right). \tag{3.2}$$

Equivalently,

$$\log\left(\frac{\mu_{it}}{\mu_{it-1}}\right) = \alpha + \boldsymbol{x}_i^\top\boldsymbol{\beta} + \widetilde{y}_{it-1}^\top\nu + \boldsymbol{v}_{it}^\top\boldsymbol{\gamma} + \epsilon_i. \tag{3.3}$$

The $\boldsymbol{\epsilon}_i$ denote site-specific random effects such that

$$\epsilon_i \sim N\left(0, \sigma^2\right) \quad \text{for} \quad i = 1, ..., n_{site}, \tag{3.4}$$

where σ^2 denotes the random effect variance.

This model specifies the rate of change in the log of average prey species count as a linear function of the covariates, as previously used for example by Thomson et al. (1998) and Freeman and Newson (2008). The use of a change model removes any dependence on the initial size of the population, considering only how that population changes over time. This reduces the chance of spurious correlations between the abundance of the predators and prey that may be driven by concurrent processes (Newson et al., 2010). We would generally expect sites with greater numbers of a prey species to be capable of supporting or even attracting larger numbers of predators. Using the change in expected value as the response variable in this case minimises the risk of detecting this spurious correlation.

There are biological arguments in support of including lagged or unlagged values for the covariates in Equation 3.3. Newson et al. (2010) fitted both lagged and unlagged versions of their model and selected the preferred model using AIC. For all of the species in this chapter where information was available (that is all except collared dove), the results suggested the model without a lag was most appropriate (Newson et al., 2010, Table S1 Supporting information). For that reason we only fit models where the covariate considered relates to the value for the corresponding year of observation. As the species under consideration in this chapter are relatively stochastic most effects of predators would be expected to be fairly quick acting on the populations of their prey species.

In addition to including sparrowhawk as a covariate in the model, previous studies on changes in songbirds in relation to avian predators have also suggested the inclusion of collared dove as a “pseudo-predator” (e.g. Newson et al., 2010; Thomson et al., 1998). Collared doves have collonised the UK in a similar time-frame to the observed increases in sparrowhawks, although from an inverse direction (that is east to west). As we would not expect to see negative effects of collared doves on other songbirds from an ecological perspective, if negative effects were found this would call into question any significant sparrowhawk effects if they were found.

3.2.1 Density dependence

Density dependence is known to be a phenomenon that affects the breeding densities of many species of birds as populations tend to remain largely stable over long periods of time when not severely affected by external factors (Newton, 1998). This implies that they are regulated in some way, either through births, deaths, immigration or emigration. This regulation is usually referred to as density dependence and is defined generally as “when the population growth rate, or constituent gain rates (e.g. birth and immigration) or loss rates (death and emigration), vary causally with population size or density”(Hixon, 2009).

Little previous work has been done on density dependence in garden birds over the winter. Evidently, the definition of density dependence usually applied to demographic parameters is not directly applicable here as the data relate to counts of birds that are attracted to a specific location outside of the breeding season. Species can, and often do, visit the feeding stations from a wide geographical area (Chamberlain et al., 2009), and the feeding itself can even determine the status of the populations (Fuller et al., 2008). However, in the close vicinity of the feeding stations, these birds will still be subject to similar constraints of competition for resources and space, predation and parasitisation amongst others as they would be during the breeding season. In this analysis, density dependence is therefore assumed to act on a local level in the close vicinity of the feeding station or garden at which the survey is conducted.

Despite there being evidence that birds can travel large distances to visit the sites where food is provided, the number of birds visiting and feeding at a given site is likely to be limited. The degree of limitation will be controlled in particular through the finite amount of food and space available at each site. More territorial or competitive species are likely to be more limited in the total number of conspecifics that will be tolerated at one time. As participants can only count the number of each species seen directly feeding on provisioned food at any one time, specifying density dependence in this format seems a sensible proposition. There could well be, and most likely are, additional birds waiting to feed that will be missed or unable to be counted under the survey protocol. Whilst this can only give a vague representation of what are probably quite complex intra-species interactions, it may provide some recommendations for areas of further research into some of the within-site processes that are taking place.

Following Dennis and Taper (1994), we test for density dependence by including a year-lagged measure of the abundance of each prey species in their respective model as an additional covariate ($\widetilde{y}_{it-1}$), with associated regression parameter ν. We only expect a first-order Markovian structure and assume no further dependence on any previous years. This Markov property, that the population at time t depends only on the population size at time $t-1$, is a general assumption that has been applicable in many ecological applications (Dennis and Taper, 1994; Thomson et al., 1998). The species of interest here are relatively consistent between years, whilst being relatively short-lived compared to other species of birds, and as such a first-order dependency structure should be realistic.

Wolda and Dennis (1993) discuss the use of this type of approach to detect density dependence and conclude that significant results are consistent with the idea of density-dependent regulation, but could also be attributed to a number of other hypotheses appropriate to the application. Conversely a non-significant result, as with any covariate analysis, does not indicate a lack of density dependence but could just indicate in this case that the time series was not long enough for the density-dependent factors to become statistically significant. As such, interpretation of density dependence (or a lack thereof) must be conducted within the confines of the ecological application it is being applied to. The analyses conducted by Wolda and Dennis (1993) also found that the probability of finding statistically significant density dependence increased with greater measurement error in the data. This is something that must also be considered in this application.

As a second purpose, the inclusion of the density dependence term acts as an AR(1) process, accounting for temporal correlation in species trends. As the random effects are only species-specific, it is important to account for any further temporal correlation within sites that is not accounted for by the other covariates.

3.2.2 Effects of other environmental covariates

We know that the temporal change in abundance of each of the species is not constant across the UK and hence we use spatial variables in the model corresponding to general trends in populations that are not specific to the measured covariates. For example, this could represent general trends in land-use across the UK such as types of farming practice that may be prevalent in certain regions but not others. To test for evidence of effects of environmental factors on changes in the number of birds visiting garden bird feeding stations, we include the following covariates in the model: northing (x_{i1}), easting (x_{i2}) and level of urbanisation (rural = -1 and suburban/urban = 1) (x_{i3}) with associated parameter vector $\boldsymbol{\beta}$. We also include time-varying covariates of averaged sparrowhawk count (v_{i1t}), averaged collared dove count (v_{i2t}) and average number of days frost across the relevant months (v_{i3t}) with associated parameters $\boldsymbol{\gamma}$. The averaged counts of sparrowhawk and collared dove relate to similar variables as those used as the response variable in these analyses. That is they are within year averages of the maximum number of those species observed at the corresponding sites and years. In the collared dove analysis, a measure of collared dove abundance is already included via the density dependence covariate. As such, the additional covariate v_{i2t} is not included in this particular analysis.

Table 3.1: Environmental covariates and their associated parameters.

Covariate	Notation	Associated parameter
Intercept	-	α
Northing	x_{i1}	β_1
Easting	x_{i2}	β_2
Sub/rur	x_{i3}	β_3
Dens. dep.	$\widetilde{y}_{it-1}$	ν
Sparrowhawk	v_{i1t}	γ_1
Collared dove	v_{i2t}	γ_2
Ground frost	v_{i3t}	γ_3

Some of the covariates used (particularly the time-varying covariates) are estimates from other models or (minimal) estimates of the number of other species present in the area. In particular, the ground frost covariate is interpolated from a much coarser grid of measurements and the sparrowhawk and collared dove covariates relate to the mean of weekly maxima observed through the GBFS survey. As such, we accept that the magnitude of effects and their significance associated with the regression covariates estimated from the model could potentially be underestimated (Carroll et al., 2006; Newson et al., 2010). However, although we have no way of quantifying this, the method is consistent across the analysis and hence should not introduce significant bias in this case.

All covariates were normalised to ensure correct specification of prior distributions and also to ease interpretation of any estimated covariate effects. By normalising the covariates, differences in the magnitude of covariate parameter estimates can be considered to represent differences in the relative sizes of the effects.

The $\boldsymbol{x}_i = \{x_{i1}, x_{i2}\}$ covariates relate to spatial northing and easting values for the site respectively and as the sites remain constant in position throughout the survey period are time invariant. Any relationships between the number of birds visiting garden feeders and these variables may indicate further additional relationships with covariates that are not included in this analysis. The restriction of these trends to be purely linear across northing and easting will only pick up the most general of trends, however the other covariates in the model should account for additional variation and attribute it more directly to specific factors. The ground frost covariate is an average number of days of ground frost obtained from the Met Office's UKCP09 gridded datasets (`http://ukclimateprojections.metoffice.gov.uk/`). These data are a measure of the number of days of ground frost for each 5km square across the UK, interpolated from Met Office observation stations. Further details of the interpolation process can be found in Perry and Hollis (2005) and in Section 1.5.3. The nearest monitoring point to each GBFS survey site was selected before averaging over the months of the survey (i.e. October to March inclusive) for each site and year in the GBFS dataset. This was done using the function `nearest` from the `GenKern` library (Lucy and Aykroyd, 2013). All covariate parameters are assumed to be constant across both space and time, and no interactions between covariates are considered. A summary of the covariates used and their associated parameters can be found in Table 3.1.

Overall, the effect of a specific covariate across all species can be calculated using a weighted mean (Newson et al., 2010). The authors use the reciprocal of the variance of the parameter as the weight of the contribution for each species. We modify the weighted mean proposed in the aforementioned paper to use the associated Bayes factor to determine the contribution of each species' coefficient value instead. Species that show a stronger relationship with a given covariate therefore contribute more to the weighted mean than those with non-significant relationships. That is for a parameter θ,

$$WM_\theta = \frac{\sum_s \frac{n_{mod}}{n_{tot}} \bar{\theta}_s}{n_{sp}}, \tag{3.5}$$

where n_{mod}, n_{tot} and n_{sp} are the number of iterations where the covariate is in the model, the total number of iterations and the number of prey species respectively.

3.2.3 Estimating the expected value in year zero

Equation 3.3 models the change in the expected value between years $t-1$ and t as a function of the environmental covariates. Inevitably in using this type of model the model must be initialised with the expected value in the first year, which itself must depend on the previous year. By modelling change in the prey species, we require the specification of μ_{i0}, the expected number of birds at site i in year zero, i.e. the year prior to data being collected at site i. Various authors have tried to address this problem, with each method having at least some limitations. The simplest method to deal with this is to replace the μ_{it} of Equation 3.2 with the observed number of birds, y_{it} (Thomson et al., 1998). This does, however, cause two problems. Firstly, it reduces the amount of data available as the analysis can only start in the second year (with the first year used to start the recursive process off). Although for large datasets this will likely have little effect on the results, discarding data unless absolutely necessary is undoubtedly less than optimal. Secondly, and of more concern, it cannot be used when zero observations occur as any observation at a site after a zero observation has occurred must also be exactly zero for the rest of the survey period, irrespective of covariate values, preventing the realistic possibility of site recolonisation. This causes an additional problem when using the Tweedie distributions as they are only defined for $\mu > 0$. Freeman and Newson (2008) maintain the use of the expected values over the observed value and reparameterise the model to a recursive form with the expected value in year 1 included as a fixed site-dependent offset. This can then be estimated within the model fitting process.

We follow a similar framework to the modelling approach of Freeman and Newson (2008) and specify the expected value in year t to be a function of the expected value in year $t-1$. However, using a Bayesian approach we can extend the modelling process and treat $\boldsymbol{\mu}_0$ as a vector of additional parameters to be estimated through MCMC simulation, that is using the data augmentation approach outlined in Section 2.2. This method essentially estimates the zero year observation from the rest of the data and uses this to initialise the remainder of the years. The methodology then allows zero observations and the first observation at each site to contribute to estimating the remaining regression parameters. This method can also be used when values of covariates are missing or for missing years of observations during the survey. The data augmented μ_{i0} are also used as the density-dependence covariate for the initial year of observations.

Skrondal and Rabe-Hesketh (2014) discuss methods to deal with a similar 'initial conditions problem' for probit models. They discuss two approaches to the problem, a joint model of the initial and subsequent responses and a model for the subsequent responses conditional on the initial response. Both of these approaches require approximations to the true specified model. As it is not clear in this instance what the model should be for the initial response, the approach outlined above seems to be the most sensible.

A graphical representation of the model showing dependencies between each of the parameters and the data is shown in Figure 3.1.

3.2.4 Improving mixing of the MCMC algorithm

Hierarchical centring

To help improve mixing of the Metropolis-Hastings algorithm we implement the hierarchical centring reparameterisation outlined in Section 2.4.1. In our application, the grouping unit for the random effects is site, so any covariate that is constant within each site can be included in the centring. That is, the intercept, northing and easting covariates whose values are constant within random effect groups (the intercept is also constant across sites). This simple reparameterisation replaces the zero mean of the random effects from Equation 3.4 with the sum of the site level fixed effects "pulled" from the linear predictor. We can therefore rewrite Equations 3.3 and 3.4 as

$$\log\left(\frac{\mu_{it}}{\mu_{it-1}}\right) = \widetilde{y}_{it-1}^{\top}\nu + \boldsymbol{v}_{it}^{\top}\boldsymbol{\gamma} + \epsilon_i$$

where

$$\epsilon_i \sim N\left(\alpha + \boldsymbol{x}_i^{\top}\boldsymbol{\beta}, \sigma^2\right) \quad i = 1, ..., n_{site}$$

respectively. The use of this method should reduce autocorrelation in the constructed Markov chain, aiding mixing in both within- and between model moves (Oedekoven et al., 2014).

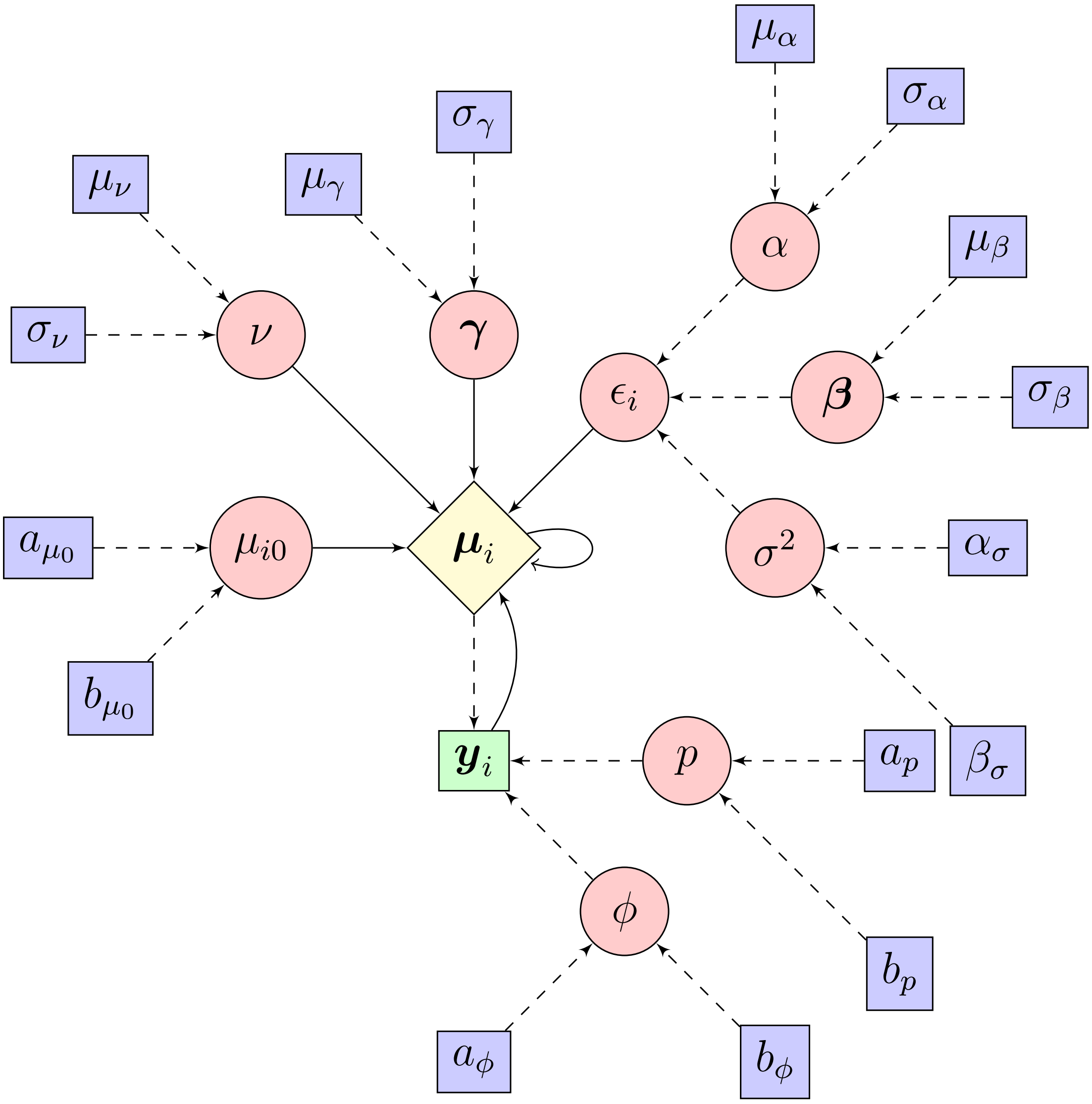


Figure 3.1: Directed acyclic graph of the hierarchical model of Equation 3.1. Square blue nodes correspond to fixed parameters of prior distributions. Red circular nodes are parameters to be estimated from the model. The solid arrows represent deterministic relationships, whilst the dashed arrows relate to stochastic dependencies.

Adaptive algorithm

Secondly, we use the adaptive tuning method outlined in Section 2.4.2 to modify the proposal variances for each parameter independently during the burn-in phase of the MCMC algorithm. Initially we tuned the variances whenever the acceptance probability was outside of the interval $(0.4, 0.5)$, an optimum region of acceptance for a single parameter Gaussian target and proposal (Sherlock et al., 2010). Sherlock et al. (2010) recommend for random walk algorithms with a large number of parameters the algorithm should be tuned to to give acceptance probabilities of approximately 0.234 and this was also tried for comparison. In our analyses, the optimal results in terms of the appearance of trace plots were found when only tuning proposal variances outside of the interval $(0.1, 0.8)$. Due to the large number of parameters, tuning too many variances in one iteration generally caused proposal variances to approach zero very quickly and hence the algorithm became very inefficient. The x_a and x_b from Section 2.4.2 were chosen as 1.5 and 2 respectively for the regression parameters and 2 and 2 for all other parameters, again after several runs with varying values to find the best combinations.

3.2.5 Priors

Table 3.2: Prior distributions specified on parameters in Equation 3.2.

Parameter	Prior
α	$N(0, 10^{-2})$
β_j	$N(0, 10^{-2})$
ν	$HN^{-}(0, 10^{-2})$
γ_j	$N(0, 10^{-2})$
μ_{i0}	$U[0, 200]$
ϕ	$U[0, 5]$
p	$U[1, 2]$
σ^2	$\Gamma^{-1}(10^{-3}, 10^{-3})$

Conducting the analysis within a Bayesian framework, we must specify prior distributions on all model parameters. Little information is known *a priori* for most parameters so we generally use diffuse priors where possible. Table 3.2 outlines the prior distributions specified on the model parameters. For the regression parameters, a little more information is available from the ecologists. Populations are on the whole stable, with any decreases being relatively constant in nature. In general for the regression covariate parameters in this model, we have no *a priori* reason to favour positive or negative values. As such, zero-mean symmetric distributions are specified on these parameters. Note that density dependence is formulated in such a way that it must be negative, hence the half normal prior specified on this parameter. The variance of these priors, $\sigma^2 = 10^{-2}$, puts most of the prior weight on parameters that generated stable or constantly increasing/decreasing population projections. Variances greater than this gave rise to parameter combinations that led to exponential decay or growth in counts. As this is known not to be the case from previous analyses and regular monitoring of the species' populations, the prior variances were limited accordingly. These priors are therefore relatively flat over the region of parameter space expected to be covered by the parameters. The same priors are specified on parameters across all models. We also specify equal prior probabilities of a covariate being included in the model. That is for regression covariate parameter θ_i, $p(\theta_i = 0) = p(\theta_i \neq 0) = 0.5$.

We restrict the Tweedie distribution index parameter p to be between 1 and 2 as these correspond to the compound Poisson-gamma distributions outlined in Section 2.8, which are continuous and non-negative with a discrete mass at zero. Aside from this, we have no further information on p so use a uniform prior on this interval. It is less clear what a suitable prior distribution is for the dispersion parameter ϕ. We follow Zhang (2013) and use a uniform prior on the interval $[0, 5]$ as no additional information is available on this.

The specification of a flat uniform prior on the data augmented $\boldsymbol{\mu}_0$ is specified as we have no prior information as to the values of these parameters. Care must be made when applying this methodology as for smaller runs of data, some bias could be introduced into the results. We have restricted the data to only include sites with at least 3 consecutive years of observations precisely to avoid this issue. Our method merely predicts the expected number in the previous year given the rest of the data.

3.2.6 Posterior conditional distribution for σ^2

Using a conjugate inverse gamma prior distribution for σ^2 means that the full posterior conditional distribution can be specified for this parameter. This also enables the Gibbs sampler (see Section 2.1.5) to be used in the MCMC update procedure for this parameter. We assume the hierarchical model outlined in Equations 3.1-3.3, with the ϵ_i assumed to follow a zero-mean normal distribution with variance σ^2. For a given fixed value of $\boldsymbol{\epsilon}$,

$$\pi(\sigma^2|\boldsymbol{\epsilon}) \propto \prod_{i=1}^{n_{site}} \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{(\epsilon_i - 0)^2}{2\sigma^2}\right) \times (\sigma^2)^{-(\alpha_\sigma+1)} \exp\left(-\frac{\beta_\sigma}{\sigma^2}\right)$$

$$\propto (\sigma^2)^{-(n_{site}/2+\alpha_\sigma+1)} \exp\left(-\frac{\frac{1}{2}\sum_{i=1}^{n_{site}}(\epsilon_i)^2 + \beta_\sigma}{\sigma^2}\right)$$

$$\Rightarrow \sigma^2|\boldsymbol{\epsilon} \sim \Gamma^{-1}\left(\frac{n_{site}}{2} + \alpha_\sigma, \frac{\sum\limits_{i=1}^{n_{site}} \epsilon_i^2}{2} + \beta_\sigma\right).$$

When using hierarchical centring, the zero mean is replaced by the sum of the site-specific only regression parameters multiplied by their respective regression parameters, that is

$$\sigma^2|\boldsymbol{\epsilon} \sim \Gamma^{-1}\left(\frac{n_{site}}{2} + \alpha_\sigma, \frac{\sum\limits_{i=1}^{n_{site}} \left(\epsilon_i - (\alpha + \boldsymbol{x}_i^\top \boldsymbol{\beta})\right)^2}{2} + \beta_\sigma\right).$$

There has been a trend recently towards using diffuse uniform priors for the random effect variance (see Gelman (e.g. 2006)) due to some sensitivity to results that can be observed depending on the choice of α_σ and β_σ. The results in this thesis were not found to vary greatly when a uniform distributions was used.

3.2.7 Covariate dependence

We do not expect all the covariates in the model to necessarily affect all of the species. We therefore wish to select different subsets of covariates for each species that show a statistically significant relationship with the change in the average count of that species. The MCMC algorithm is fitted independently to each species, enabling a different subset of covariates to be significant predictors of changes in each of them.

We extend the Metropolis-Hastings algorithm using reversible jump algorithm to allow movement between models with differing numbers of covariates. This will then allow us to choose different subsets of covariates for each species to gain a better understanding of how the numbers of each species are changing and what are potential drivers of these changes in numbers. The algorithm used for within and between model moves is outlined in Section 2.3.3. The feasibility of using information criteria in this case is low due to the number of possible combinations of covariates. It would be necessary to fit the model for each combination of covariates, that is 128 different models for the seven covariates used, and calculate the DIC for each of these. Arguably, some form of search algorithm could be used in this case to reduce the number of potential models fitted to the data.

Posterior model probabilities can be used to compare the support for models with different combinations of covariates included. However when there are more than a few different covariates, the number of different models with posterior support can be relatively high. We therefore use Bayes factors relating to posterior inclusion probabilities, that is the proportion of iterations post burn-in where a given covariate is in the model. For a given covariate parameter θ_i, we wish to test

$$H_0 : \theta_i = 0 \quad \text{vs} \quad H_1 : \theta_i \neq 0.$$

Bayes factors greater than one in this case would suggest greater support for a covariate being included in the model. Values greater than 3 are considered to give evidence of a significant relationship with that species (Kass and Raftery, 1995). In practical terms, we calculate posterior model probabilities by calculating the proportion of time that each of the 7 covariates discussed in Section 3.2.2 is included in the model. The Bayes factor for this covariate is then the ratio of the proportion of iterations that the covariate is in the model to those where the covariate is excluded from the model.

The choice of proposal distribution for the between model moves once again needs to be specified to optimise efficiency of the chain. There are various ways that this can be achieved. We follow the suggestions of King et al. (2010, pp. 181-182) by initially running the saturated model, that is the fixed full model with all covariates included and no reversible jump step. Posterior means and variances of each of the parameters are then usually reasonable proposal means and variances of the proposal distributions for the corresponding parameters when the reversible jump step is added to the model algorithm. This assumes that parameter values are fairly consistent amongst models, which we assume is a valid assumption in this case.

3.3 Model results

The analyses were run on models both with and without random site effects, the results of which can be found in Tables 3.3 - 3.7. Initially 20,000 iterations were conducted in the saturated model with the first 5,000 iterations discarded as burn-in. The results of this analysis were then used to determine the parameters of the RJ proposal distributions. For a given parameter θ the proposal distribution was defined as follows:

$$q(u) \sim N(\overline{\theta}_{MH}, \overline{s}(\theta_{MH})^2),$$

where $\overline{\theta}_{MH}$ is the mean of the posterior sample from the analysis conducted in the saturated model and $\overline{s}(\theta_{MH})^2$ the variance obtained from the same sample. Using these proposal distribution parameters, no obvious problems with mixing and movement between models was apparent when models were run in the smallest and largest models as they gave similar posterior estimates.

Table 3.3: Posterior means and Bayes factors in parentheses for the regression parameter for all independent species model without random effects. Significant covariates with BF$\geq$ 3 are highlighted in bold. Collared dove is not included as a covariate when analysing changes in collared dove numbers.

Species	**Intercept**	**North**	**East**	**Rur/sub**	**Dens. dep.**	**S/whawk**	**C. dove**	**Frost**
Collared Dove	0.0154	0.0014	**0.0042**	-0.0028	-0.0018	-0.0045	-	0.0038
	-	(< 0.1)	(4.1)	(0.2)	(0.1)	(0.3)	-	(0.3)
Blackbird	0.0072	0.0006	-0.0004	-0.0013	-0.0013	-0.0005	**0.0038**	0.0011
	-	(< 0.1)	(< 0.1)	(< 0.1)	(0.2)	(< 0.1)	(> 10)	(< 0.1)
Robin	0.0007	0.0002	-0.0005	-0.0005	**-0.0017**	0.0006	0.0017	-0.0007
	-	(< 0.1)	(< 0.1)	(< 0.1)	(3.9)	(< 0.1)	(0.3)	(< 0.1)
Blue tit	-0.0183	0.0009	-0.0015	0.0009	-0.0010	**-0.0025**	-0.0017	-0.0001
	-	(< 0.1)	(0.1)	(< 0.1)	(< 0.1)	(3.9)	(< 0.1)	(< 0.1)
Coal tit	0.0006	**0.0044**	-0.0033	0.0000	-0.0019	0.0015	0.0017	0.0003
	-	(> 10)	(0.1)	(< 0.1)	(0.1)	(< 0.1)	(< 0.1)	(< 0.1)
Great tit	-0.0122	0.0002	-0.0007	0.0007	-0.0017	-0.0017	-0.0005	-0.0008
	-	(< 0.1)	(< 0.1)	(< 0.1)	(1.1)	(< 0.1)	(< 0.1)	(< 0.1)
House sparrow	-0.0410	0.0025	-0.0018	-0.0027	-0.0002	**-0.0084**	0.0019	**0.0049**
	-	(0.3)	(< 0.1)	(1.0)	(< 0.1)	(> 10)	(< 0.1)	(> 10)
Starling	-0.0365	-0.0002	0.0002	**-0.0033**	-0.0002	**-0.0137**	**0.0052**	**0.0044**
	-	(< 0.1)	(< 0.1)	(4.0)	(< 0.1)	(> 10)	(> 10)	(4.8)
Chaffinch	0.0091	0.0002	0.0014	-0.0016	-0.0013	-0.0013	**0.0040**	0.0022
	-	(< 0.1)	(< 0.1)	(< 0.1)	(0.1)	(< 0.1)	(> 10)	(0.2)
Greenfinch	0.0006	0.0021	-0.0028	-0.0024	-0.0009	-0.0006	0.0015	-0.0011
	-	(0.1)	(0.3)	(0.2)	(< 0.1)	(< 0.1)	(< 0.1)	(< 0.1)

Table 3.4: Posterior means of the Tweedie variance parameters for the independent species models without random effects (standard deviations in parentheses).

Species	ϕ	p
Collared Dove	0.7444 (0.0132)	1.3855 (0.0061)
Blackbird	0.2471 (0.0053)	1.3176 (0.0156)
Robin	0.0832 (0.0016)	1.0701 (0.0081)
Blue tit	0.2006 (0.0054)	1.4946 (0.0178)
Coal tit	0.3900 (0.0080)	1.2936 (0.0061)
Great tit	0.2399 (0.0042)	1.2119 (0.0076)
House sparrow	0.9357 (0.0163)	1.3894 (0.0061)
Starling	0.8899 (0.0147)	1.4336 (0.0064)
Chaffinch	0.4989 (0.0086)	1.4292 (0.0082)
Greenfinch	0.6882 (0.0115)	1.4860 (0.0077)

Table 3.5: Posterior means and Bayes factors in parentheses for the regression parameter for all independent species mixed-effects models. Significant covariates are highlighted in bold. Collared dove is not included as a covariate when analysing changes in collared dove numbers

Species	Intercept	North	East	Rur/sub	Dens. dep.	S/whawk	C. dove	Frost
Collared Dove	0.0185	-0.0016	0.0099	-0.0091	**-0.0466**	-0.0043	-	0.0096
	-	(< 0.1)	(0.2)	(0.2)	(>10)	(< 0.1)	-	(0.3)
Blackbird	0.0110	0.0049	-0.0069	-0.0077	**-0.0328**	**0.0103**	**0.0153**	**0.0119**
	-	(0.1)	(0.4)	(1.0)	(>10)	(>10)	(>10)	(>10)
Robin	0.0044	0.0012	-0.0046	**-0.0095**	**-0.0291**	0.0049	0.0030	0.0009
	-	(< 0.1)	(0.4)	(>10)	(>10)	(2.7)	(0.2)	(< 0.1)
Blue tit	-0.0205	-0.0011	-0.0044	**-0.0074**	**-0.0142**	**-0.0077**	-0.0017	**0.0077**
	-	(< 0.1)	(0.1)	(3.1)	(>10)	(>10)	(< 0.1)	(>10)
Coal tit	-0.0118	0.0125	**-0.0168**	0.0006	**-0.0243**	**0.0135**	0.0069	0.0034
	-	(1.3)	(7.1)	(< 0.1)	(>10)	(>10)	(< 0.1)	(< 0.1)
Great tit	-0.0099	-0.0007	-0.0010	**-0.0090**	**-0.0188**	0.0000	-0.0018	0.0045
	-	(< 0.1)	(< 0.1)	(>10)	(>10)	(< 0.1)	(< 0.1)	(0.3)
House sparrow	-0.0744	-0.0122	**-0.0254**	-0.0140	-0.0003	**-0.0385**	0.0011	**0.0451**
	-	(0.3)	(> 10)	(1.2)	(< 0.1)	(>10)	(< 0.1)	(>10)
Starling	-0.0594	-0.0080	-0.0008	0.0008	-0.0014	**-0.0332**	**0.0080**	**0.0429**
	-	(0.2)	(< 0.1)	(< 0.1)	(< 0.1)	(>10)	(>10)	(>10)
Chaffinch	0.0045	0.0041	**-0.0141**	**-0.0155**	**-0.0249**	0.0035	**0.0088**	**0.0290**
	-	(< 0.1)	(7.4)	(>10)	(>10)	(0.1)	(>10)	(>10)
Greenfinch	-0.0243	0.0027	**-0.0200**	-0.0145	**-0.0199**	-0.0044	-0.0051	0.0104
	-	(< 0.1)	(>10)	(2.4)	(>10)	(0.3)	(0.2)	(0.4)

Table 3.6: 95% highest posterior density intervals (HPDIs) for the mixed effects models from Table 3.5.

Species	**Intercept**	**North**	**East**	**Rur/sub**
Collared Dove	(0.0071,0.0304)	(-0.0146,0.0112)	(-0.0010,0.0204)	(-0.0221,0.0021)
Blackbird	(0.0053,0.0164)	(-0.0013,0.0121)	(-0.0126,-0.0013)	(-0.0133,-0.0016)
Robin	(0.0006,0.0084)	(-0.0023,0.0044)	(-0.0083,-0.0006)	(-0.0136,-0.0056)
Blue tit	(-0.0251,-0.0160)	(-0.0061,0.0031)	(-0.0088,0.0001)	(-0.0118,-0.0024)
Coal tit	(-0.0191,-0.0032)	(0.0026,0.0220)	(-0.0266,-0.0073)	(-0.0081,0.0078)
Great tit	(-0.0146,-0.0053)	(-0.0050,0.0048)	(-0.0058,0.0056)	(-0.0136,-0.0041)
House sparrow	(-0.0859,-0.0631)	(-0.0261,0.0014)	(-0.0375,-0.0130)	(-0.0251,-0.0025)
Starling	(-0.0692,-0.0504)	(-0.0180,0.0003)	(-0.0102,0.0071)	(-0.0082,0.0111)
Chaffinch	(-0.0035,0.0125)	(-0.0045,0.0122)	(-0.0230,-0.0060)	(-0.0233,-0.0076)
Greenfinch	(-0.0340,-0.0143)	(-0.0068,0.0131)	(-0.0302,-0.0099)	(-0.0240,-0.0046)

Species	**Dens. dep.**	**S/whawk**	**C. dove**	**Frost**
Collared Dove	(-0.0528,-0.0415)	(-0.0151,0.0025)	-	(0.0023,0.0244)
Blackbird	(-0.0385,-0.0262)	(0.0060,0.0146)	(0.0107,0.0191)	(0.0071,0.0168)
Robin	(-0.0328,-0.0250)	(0.0024,0.0081)	(0.0008,0.0053)	(-0.0011,0.0033)
Blue tit	(-0.0188,-0.0100)	(-0.0111,-0.0037)	(-0.0038,0.0007)	(0.0038,0.0114)
Coal tit	(-0.0313,-0.0161)	(0.0070,0.0213)	(-0.0009,0.0136)	(-0.0043,0.0105)
Great tit	(-0.0240,-0.0149)	(-0.0030,0.0024)	(-0.0053,0.0021)	(0.0005,0.0084)
House sparrow	(-0.0009,0.0000)	(-0.0469,-0.0302)	(-0.0029,0.0045)	(0.0370,0.0531)
Starling	(-0.0027,0.0000)	(-0.0409,-0.0255)	(0.0029,0.0127)	(0.0359,0.0498)
Chaffinch	(-0.0292,-0.0208)	(-0.0023,0.0060)	(0.0039,0.0142)	(0.0215,0.0359)
Greenfinch	(-0.0244,-0.0153)	(-0.0118,0.0044)	(-0.0085,-0.0008)	(0.0008,0.0199)

Table 3.7: Posterior means of the Tweedie variance parameters and random effect variance for the mixed-effects models with standard deviations in parentheses.

Species	ϕ	p	σ^2
Collared Dove	0.5393	1.3280	0.0129
	(0.0105)	(0.0059)	(0.0014)
Blackbird	0.2040	1.2434	0.0032
	(0.0041)	(0.0144)	(0.0004)
Robin	0.0638	1.0581	0.0013
	(0.0013)	(0.0059)	(0.0002)
Blue tit	0.1683	1.4424	0.0019
	(0.0051)	(0.0194)	(0.0002)
Coal tit	0.3323	1.2650	0.0040
	(0.0067)	(0.0056)	(0.0006)
Great tit	0.1994	1.1796	0.0018
	(0.0036)	(0.0070)	(0.0002)
House sparrow	0.6844	1.3484	0.0131
	(0.0128)	(0.0061)	(0.0010)
Starling	0.6982	1.3875	0.0082
	(0.0125)	(0.0063)	(0.0009)
Chaffinch	0.3815	1.3634	0.0063
	(0.0071)	(0.0079)	(0.0006)
Greenfinch	0.5212	1.4127	0.0102
	(0.0090)	(0.0074)	(0.0009)

The results tables present posterior means and Bayes factors (where appropriate). The Bayes factors for the regression parameters correspond to the two models with and without this parameter, that is the ratio of posterior support for $\theta_i \neq 0$ to $\theta_i = 0$. Following Kass and Raftery (1995) and Table 2.1 we assume parameters with Bayes factors ≥ 3 have a significant relationship with the number of a given species visiting garden feeding stations, and these parameters are highlighted in bold. Posterior means for the regression parameters were averages over all models where that covariate was present. Posterior marginal distributions for these parameters were checked to ensure they were unimodal. In addition, the posterior estimates were not used for prediction, hence it was considered that averaging over models in this case was justified.

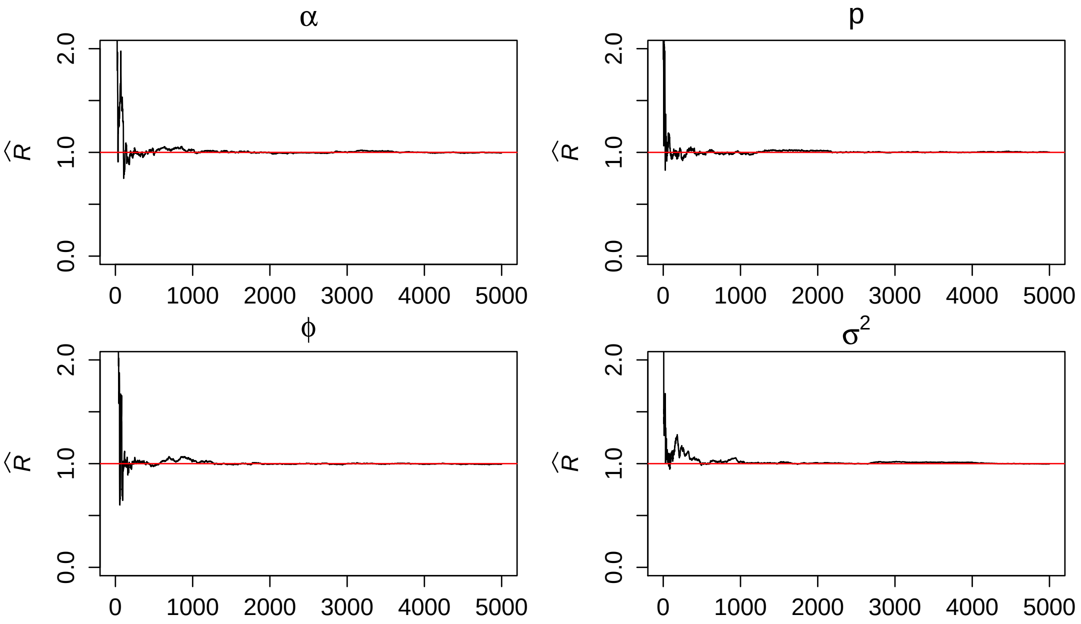


Figure 3.2: BGR plots for the house sparrow model.

Convergence was mainly assessed using visual checking of traceplots. To verify this, the BGR statistic was calculated for the house sparrow analysis to ensure the visual checking was justified. Three chains with overdispersed parameter and model starting values were run with the same number of iterations and the BGR calculated as outlined in Section 2.1.7. The results are shown in Figure 3.2 and suggest that the model has clearly converged very early on, roughly after 1,000 iterations. Therefore using a burn-in of 5,000 appears to be very conservative.

3.3.1 Inclusion of random site effects

A comparison of the results from the model without random site effects (Tables 3.3 and 3.4) with those from the same model but with random effects included (Tables 3.5 and 3.7) shows that the number of significant regression covariates increases when random site effects are included. The time-varying covariates that are significant in the simpler model are always significant in the mixed-effects model too, however the same is not the case for the site-specific covariates. This is essentially a computational issue that means we may not be exploring the posterior distribution efficiently. Using random effects with hierarchical centring clearly aids in reducing this autocorrelation between covariates and allows the effects of certain covariates to be better detected. Secondly, without random effects, strong linear assumptions are made on the relationship between changes in garden bird counts and the site-specific covariates. By including random site effects, small deviations from this at each site can be accounted for and hence underlying relationships that are present can be more easily determined by the model.

The model with random effects appears to be able to attribute a greater amount of variability to the measured covariates. The repeated observations conducted within sites should ideally also be accounted for, which the random site effects do. The mixed effects model is clearly more appropriate, and hence we concentrate on the results from theses models only for the remainder of this chapter.

3.3.2 Response to environmental covariates

There is a large amount of variability between species as to which of the covariates are significant predictors of the changes observed within that species. Density dependence seems to be the covariate most consistent across species. Interestingly, only two species do not show significant density dependence. House sparrow and starling are the two species that have declined significantly over the course of the years considered in this analysis. They are also two species which are most likely to form groups or flocks around the feeding units. The willingness of these two species to congregate in large numbers around feeding sites may be the reason why no density dependence was found in these species. Although there is evidence to suggest that birds visiting feeding stations can be attracted from a large distance away, density dependence in this instance is likely to be acting on a strictly local level, that is within the vicinity of the feeding units or the garden as a whole. With limited resources available at any one site and often concentrated in a small area, the numbers of birds counted are probably a lower bound of the number of that species in the area. Some species, such as robin, are fiercely territorial and hence only a small number of this species is likely to be seen at one time on the feeding units, unless the 'site' is particularly large. The density dependence detected will therefore most likely be a representation of how many of each species a single site can support at any one time, either due to limited resources or the territorial nature of that species. In the case of collared dove, with the largest relative estimate of density dependence, the former is probably the case. Despite not being particularly territorial, as the largest of the prey species considered in these analyses, smaller sites are likely to have a relatively low upper limit on the number of this species that can be supported. Clearly further research into this area is needed to ascertain the processes driving the observed patterns of density dependence in non-breeding abundances of garden bird species.

The prevalence of ground frost was consistently found to have a significant effect on the number of birds counted in a given site-year combination. All effects were positive, even the non-significant ones. This suggests that birds are attracted to garden feeders when temperatures drop and the ground freezes. During these conditions, natural food will become scarcer or more difficult to obtain. This highlights the importance of garden feeding for many species of birds when the weather is poor. Chamberlain et al. (2005) analysed the probability of occurrence of each species of bird analysed in this study in relation with minimum temperature and found significant negative relationships between the two. Although we used ground frost as the covariate there was a strong negative linear correlation between the two covariates and the sites and years considered in this analysis (-0.87), therefore the findings of Chamberlain et al. (2005) agree well with our findings.

The three species that showed significant negative changes at sites with a larger number of sparrowhawks were house sparrow, starling and blue tit. Newson et al. (2010) fitted log-linear models of a similar form to those fitted here with a similar wide-ranging array of covariates. Their estimates for the parameter associated with sparrowhawk abundance were negative for blue tit and starling and positive for house sparrow, but were non-significant in each case. The lack of significant relationships between breeding abundance of these species, may be consistent with the concept of a change in the seasonal pattern of mortality, which has been suggested by previous authors (e.g. Newton, 1998; Perrins and Geer, 1980). This corresponds with the concept that the environment in which a certain prey species lives is capable of sustaining a limited density of breeders of a given species, due to limited food, suitable nesting habitat, or other factors leading to competition (Newton, 1998). Any surplus birds that cannot be supported by the resources that would otherwise die from starvation are now taken by predators instead, whilst the breeding density of the species remains unchanged. Despite there being good agreement between the numbers of house sparrows and starlings counted through breeding bird surveys (such as the CBC) and the corresponding probability of detection at GBFS sites (Chamberlain et al., 2009), it is unwise to extrapolate that an effect of sparrowhawks on some species visiting garden feeding sites is consistent with an effect on the breeding densities of these species. In fact, previous analyses of large scale data from breeding bird surveys have failed to find any such effect (e.g. Newson et al., 2010).

Figure 1.3 shows that blue tit counts have on average remained relatively stable over the last 40 years when compared with those of house sparrows and starlings. Any negative impact of sparrowhawks on their population as a whole is being counteracted by other factors.

Two species, blackbird and coal tit, showed a significant positive relationship with numbers of sparrowhawks. We cannot rule out that these represent confounding variables that are causing positive associations. For example, habitat quality may be more important for these two species. The quality of food provided has no doubt increased significantly, as has the tendency for creating gardens that are attractive to wildlife. As the participants in the GBFS survey are people with a prior interest in birds, it is possible that the gardens of these participants are tended to be particularly attractive to birds. The positive effects of sparrowhawks on these species may relate to coincidental requirements of both predator and prey. Coal tits have become a more common sight at garden feeders over the course of the years in this study, and their range across the country has also increased (McKenzie et al., 2007). Another possible explanation for these positive effects could be a behavioural response of these species to greater predation pressure from sparrowhawks over the years. The coal tit analysis showed some evidence of poor fit (see Section 3.6) so some question could be raised as to the validity of the parameter estimates under this model. Further discussion of this is made in Section 4.4.

Easting and level of urbanisation were found to be significant in just under half the species. These variables represent vague trends in the populations and the significance of the parameters for some species suggest there are further specific covariates associated with these that may be driving the changes in populations. With regards to the two parameters, all significant estimates were negative suggesting numbers of the associated species are faring worse in urban environments and in the east of the country. Both these have been suggested by previous analyses of similar species. The relationships with easting may represent the prevalence of arable farming in the east of the UK. Previously analyses have shown that birds associated with farming are faring particularly poorly in relation to other habitat specialists (Chamberlain et al., 2005; Newton, 2004). Of the four species showing negative relationships with easting, three are species also associated closely with arable habitats. According to Chamberlain et al. (2005), chaffinch and house sparrow numbers at garden feeding sites correlate well with CBC indices, giving support to this hypothesis. Previous analyses have shown that bird populations of birds in urban habitats have declined at a greater rate than those in rural ones (e.g. Mennechez and Clergeau, 2006; Peach et al., 2008; Solonen, 2001). Conversely, no significant relationships with northing were found. Either the change in species counts is constant across all latitudes or other covariates are accounting for any such changes, such as ground frost which will inevitably be correlated to some degree with northing.

No significant negative associations were found with collared dove, which was included in the model as a pseudo-predator to assess the risk of detecting spurious correlations. The three positive associations found, namely in blackbird, starling and chaffinch, relate to species that, due to their size, may require larger gardens and hence positive associations between these species is not surprising. As we would not expect significant negative associations between collared doves and the other songbird species, and negative associations would call into question the significant negative associations with sparrowhawks. As this has not occurred, further support for genuine effects of sparrowhawks on their prey is given.

The use of site-specific random effects was chosen over either time-varying ones or a bivariate random effect. As the amount of food has generally increased in quantity and quality at sites over the last forty years, there may be unmodelled improvements in a site's ability to attract birds over the years (Chamberlain et al., 2005). We cannot rule out the effect of this increase on the results as the model assumes that any unexplained variation within sites will be constant across years. However, it is not clear how spurious

Table 3.8: Weighted mean for each covariate across all species in the mixed-effects models calculated according to Equation 3.5 with the number of species showing a significant effect for this parameter in parentheses.

Covariate	**Weighted mean**
Northing	0.0002 (0)
Easting	-0.0075 (4)
Sub/rur	-0.0059 (3)
Dens. dependence	-0.0211 (8)
Sparrowhawk	-0.0051 (5)
Collared Dove	0.0035 (3)
Ground frost	0.0138 (5)

negative sparrowhawk effects would be found in this instance as the species would likely be attracted to the same sites where food is increasing or improving. The density dependence effect could be argued to vary as a site becomes more suitable and hence could potentially support more birds, but if anything the effect would be underestimated rather than overestimated.

Chamberlain et al. (2004) found that species occurrence in gardens was associated with habitat from the surrounding local habitat, which may also have changed over time. Although we expect that the majority of correlation present in the data will be site-dependent rather than time-dependent, the latter may still have some effect on the results. An additional time-dependent random effect or a bivariate random effect may improve the model. However, the additional computational cost of adding either of these to the model outweighs the potential gain in model fit. The density dependence parameter will also have accounted for some of the .

Whilst the μ_{it} are inevitably correlated with the y_{it-1}, no obvious effect was observed on the other covariates if this was removed from the model. The only noticeable difference where tested was a corresponding increase in the magnitude of the site effects to account for the variation no longer explained by this covariate.

The weighted mean coefficients for each regression parameter were calculated across all species from Equation 3.5 and are presented in Table 3.8. Whilst it would be inadvisable to use these coefficients in prediction, they can indicate the average effect across species of the covariates considered relative to each other. On average northing, collared dove and ground frost are positively related to changes in garden bird counts whilst easting, urbanisation, density dependence and sparrowhawk numbers all have negative associations. The magnitude of the average effect correlates well with the number of species in which that the covariate was found to be significant.

Concentrating on the mean sparrowhawk effect, although negative, this is a relatively small overall effect, corresponding to a less than 0.5% reduction in the rate of change in mean weekly counts attributed to sparrowhawks. Using the average annual number of sparrowhawks across all sites from the observed data, the overall expected prey population by 2005 would be roughly 98.8% of that in 1970 based on the weighted mean average. This was calculated using the following projection formula assuming that the population is at 100% at time zero:

$$\pi_T = \prod_{i=1}^{T} \pi_{i-1}(\exp(-0.0051 \times SH_i)),$$

where SH_i is the average sparrowhawk count across all sites between in year i.

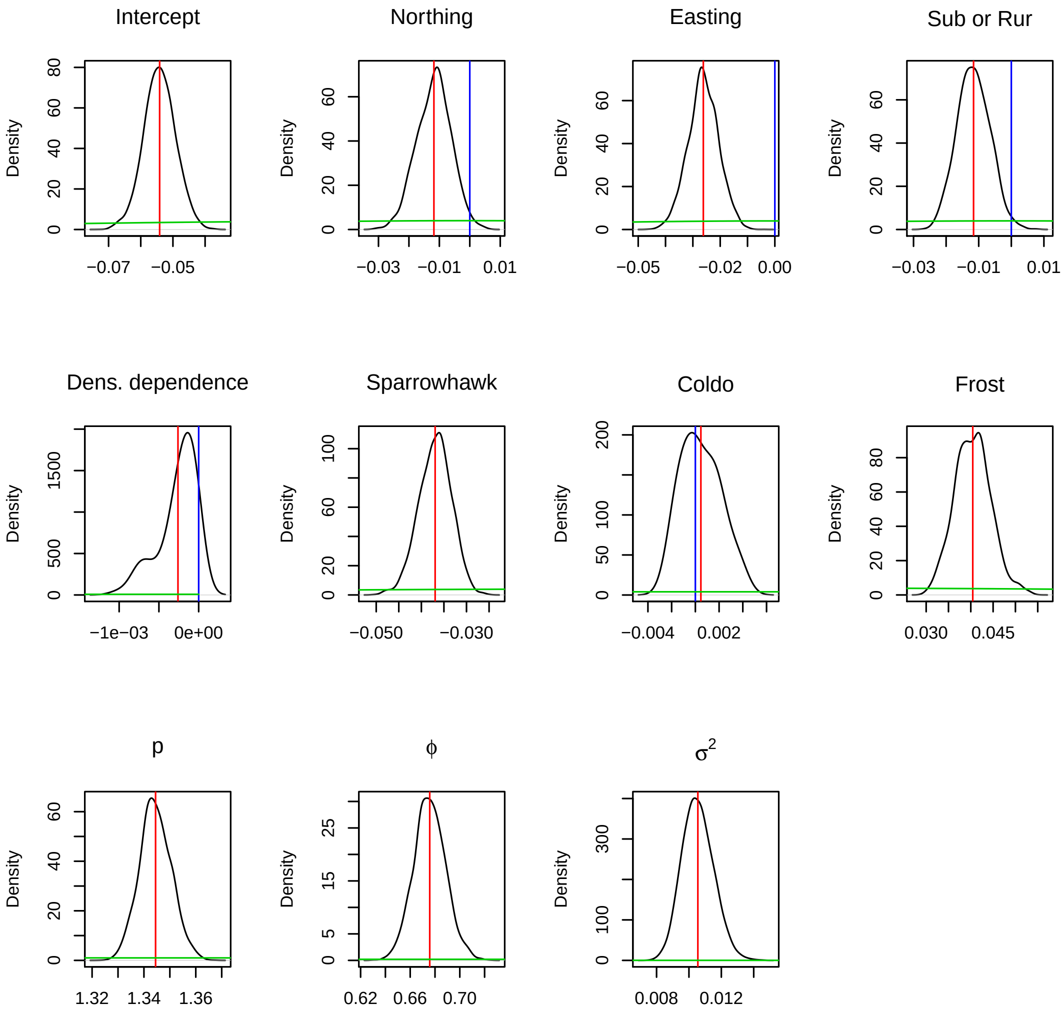


Figure 3.3: Posterior distributions for the house sparrow analysis with random effects (black), posterior mean(red) and corresponding prior distributions (green). Blue lines at $x = 0$ where zero is a plausible value.

Figure 3.3 shows the prior and marginal posterior distributions (conditional on the parameter being in the model) for each of the parameters from the house sparrow mixed-effects analysis. Over the region of posterior parameter space, the prior distributions are relatively flat. The posterior distributions are largely symmetrical about the posterior mean, with the posterior distributions spanning zero for those regression parameters not considered to be significant predictors of changes in house sparrow averaged counts. This is supported by the 95% HPDIs in Table 3.6, which unsurprisingly tend to contain zero if and only if the parameter is non-significant.

As discussed by Scott and Berger (2010), Bayesian variable selection can account for multiple testing providing the prior inclusion probability is not fixed. When comparing hierarchical methods with fixed prior inclusion probabilities on simulated data with 10 real variables, and increasing numbers of false variables generated from N(0,1) distributions. Even with 10 “noise variables”, only 2 false positives were observed when fixed prior probabilities were used. Scott and Berger (2010) recommend the use of Beta distribution for p, the probability of including a given covariate. As only a relatively small number of variables are tested in this analysis, that is up to seven, we do not expect a significant effect on the results from multiple testing. There are strong ecological justifications for the coefficients that are considered significant under the model and hence we believe the results are robust. Future analyses may wish to account for the risk of multiple testing to ensure that it is not a problem.

3.3.3 Unexplained variation

The magnitude of the random effect variance can give an idea of the amount of variation in species counts that is not explained by the covariates. The results presented in Table 3.7 show the posterior means of the random effect variances. There is an order of magnitude between the smallest (robin) and largest (collared dove) variances. The largest variances were generally associated with the species that most readily form flocks around feeders. This might suggest that an additional variable should be included in the model relating to this phenomenon, although how to measure it is not obvious. Clearly larger sites are able to support more birds than smaller ones. Conversely, modelling change in the expected number of birds visiting feeders should remove some of this dependence. However, the size of the site or the number of feeding units provided, is likely to be a contributing factor to the changing fortunes of some species. Chamberlain et al. (2009) and Chamberlain et al. (2005) analysed similar data with respect to the number of feeding units and found that there was a positive association. As data on this were not readily available for these analyses, the random site effects will partially be accounting for this. We cannot be certain that some of the variability attributed to other covariates does not correspond to this covariate.

Larger random effect variances may also suggest there are additional covariates affecting changes in these species that are not currently accounted for in the model and may only be affecting these species. In this analysis, the larger variances seem to correspond mainly with species that are more inclined to form flocks in winter. Other possible reasons that are more specific to individual species may also be postulated. For example, greenfinch shows a particularly large random effect variance. Towards the latter part of the years covered by the survey, greenfinches at some garden bird feeding stations were found to be suffering from *salmonella* or *trichomonosis* (Lawson et al., 2010, 2012). Populations of this species in particular have declined as a result (Robinson et al., 2010). The large variance relating to this species may be in part down to this.

The use of a univariate random effect relating to the site grouping seems justified. Adding a time dimension to the random effects would make the correlation structure much more complicated and the additional benefit gained by this would be severely outweighed by the computational cost. Also much of the year-on-year changes between sites should be modelled by the time-specific covariates included in the model.

3.3.4 Algorithm tuning

The analyses were run initially in the full model with all covariates included to guide the choice of proposal distribution parameter for the reversible-jump covariate dependence step. Posterior means and variances for each of the regression parameters from this analysis were then set as the mean and variances for the normal proposal distributions $q(.)$. Then the reversible jump step was added to account for model uncertainty and determine covariate dependence. The variance of the proposal distributions for each of the parameters updated using the Metropolis-Hastings algorithm, that is all parameters apart from the random effect variance σ^2, is tuned at each iteration to give acceptance probabilities within the interval (0.1,0.8). Figure 3.4 shows the traceplots of these proposal variances for each of the regression parameters $\alpha, \boldsymbol{\beta}, \nu$ and $\boldsymbol{\gamma}$ for the house sparrow analysis, with the final proposals used for the regression parameters presented in Table 3.9. All variances were started at the values 0.01. The tuning only occurs when the parameter is in the model so the traceplots for density dependence and collared dove in this case are rarely tuned, with the covariate for these two parameters rarely being in the model. The mean proposal variance is clearly different in each case with variances for the parameters included in the hierarchical centring being approximately at least twice those for the time-varying covariates. After a relatively short initial period, the proposal variances seem to converge reasonably quickly. The ability to tune the proposals in this way allows the chain to converge much more quickly than would be possible when arbitrarily fixing the proposal parameters at the point of initiation. Tuning within the algorithm procedure quickens the process in the long run as it prevents the need to run multiple analyses, checking the efficiency of the results and then re-running with improved parameters.

Table 3.9: Final tuned proposal standard deviations for regression parameters at the end of the burn-in period. Variances are tuned at each iteration to induce acceptance probabilities between (0.1,0.8).

Species/Covariate	Intercept	Northing	Easting	Sub/rur	Dens. dep.	Sparr.	Col. dove	G. frost
Blackbird	0.0086	0.0091	0.0024	0.0075	0.0004	0.0007	0.0009	0.0010
Blue tit	0.0035	0.0041	0.0047	0.0079	0.0005	0.0004	0.0007	0.0008
Chaffinch	0.0016	0.0121	0.0019	0.0047	0.0027	0.0002	0.0009	0.0007
Coal tit	0.0012	0.0045	0.0031	0.0034	0.0010	0.0012	0.0020	0.0029
Collared dove	0.0158	0.0074	0.0125	0.0106	0.0021	0.0039	-	0.0013
Greenfinch	0.0074	0.0052	0.0044	0.0109	0.0006	0.0003	0.0004	0.0011
Great tit	0.0019	0.0027	0.0039	0.0022	0.0006	0.0009	0.0009	0.0009
House sparrow	0.0040	0.0127	0.0173	0.0060	0.0001	0.0032	0.0005	0.0013
Robin	0.0010	0.0020	0.0018	0.0014	0.0005	0.0005	0.0004	0.0010
Starling	0.0082	0.0062	0.0238	0.0111	0.0002	0.0010	0.0013	0.0010

3.4 Sensitivity analysis

3.4.1 Prior sensitivity

In order to determine whether the specification of the prior distributions on the model parameters has had any undue effect on the posterior estimates of the parameters, it is standard practice to conduct a prior sensitivity analysis. In the simplest case, this involves altering the prior distributions, refitting the model and noting any significant subsequent changes in parameter estimates and model probabilities. We change

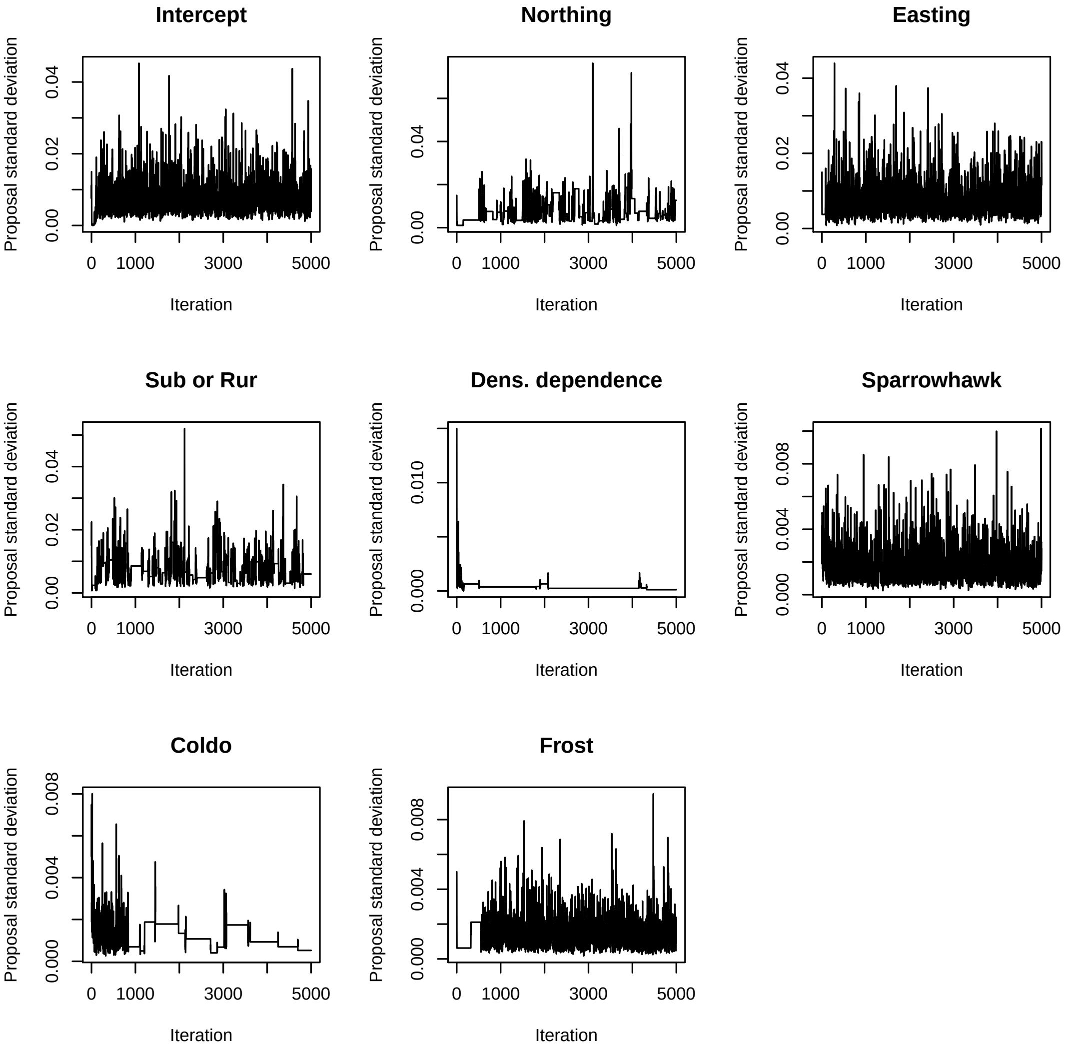


Figure 3.4: Trace plots of the proposal standard deviations for each of the regression parameters in the house sparrow analysis.

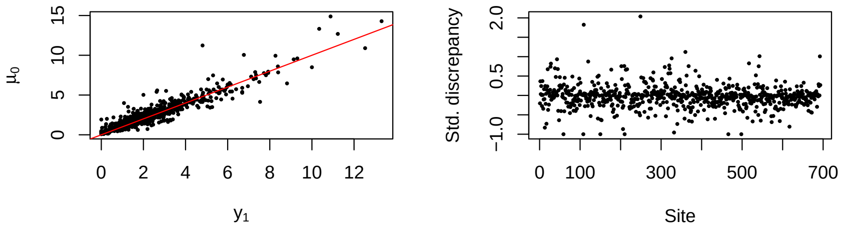
prior distributions in turn and refit the model with only one (set of) prior distribution changed from the initial analysis. This enables us to highlight which (if any) of the adjusted prior distributions is causing changes in the results. Changing more than one prior distribution at the same time could cause confounding and prevent us from determining which prior the results are sensitive to.

For illustration we only re-run analyses for one species in particular, namely house sparrow (Table 3.10). Although we cannot be certain that all species analyses will respond in the same way to changes in prior distribution, the similarity in the nature of the results between alternative prior specifications suggest that our results are robust to theses changes. In addition, we have ecological justification for our choice of priors and as such feel that the results obtained from these analyses are best used.

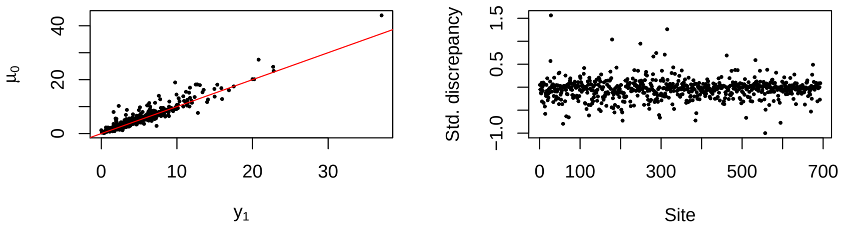
Parameter posterior means were largely invariant to changes in prior distributions. Any small changes were for parameters which were rarely in the model and therefore precision for these parameters is subsequently low. No changes were noted for the random effect variance or either of the Tweedie variance parameters. The aspect of the results that did show some susceptibility to the choice of prior distribution were the marginal posterior probabilities for the regression covariate parameters. This sensitivity to the prior variance is a well known occurrence, referred to as Lindley's paradox. In the case of the house sparrow analysis, interpretation only changed for one of the parameters: urbanisation level. It seems acceptable to assume that only parameters with Bayes' factors closer to the cut off value will change interpretation under alternative prior specifications. Interpretation of the results must always be conducted in light of the prior distributions specified on the parameters. In this case we are aware that some parameters may be sensitive to this but the choice of priors was carried out with justifiable reasons.

3.4.2 Sensitivity to outlying sites

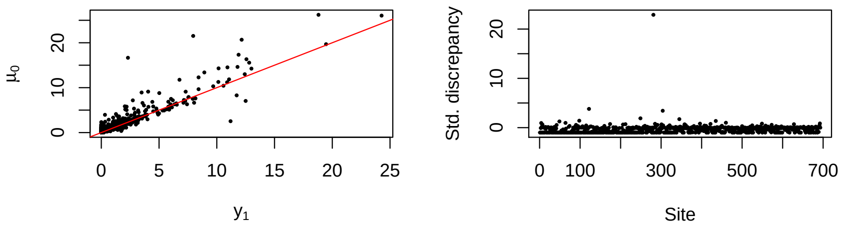
In using a vague flat prior on the $\boldsymbol{\mu}_0$, it is important to ensure that there is not a significant effect on the results being caused by uncertainty on these pseudo-parameters. From Figure 3.7, there is a very strong linear positive relationship between the posterior means of the $\boldsymbol{\mu}_0$ and the corresponding observed data from year 1 for all species. There is some scatter around this line which would be expected, especially at sites with larger counts of individual species. The second plot in this figure shows sites plotted in order



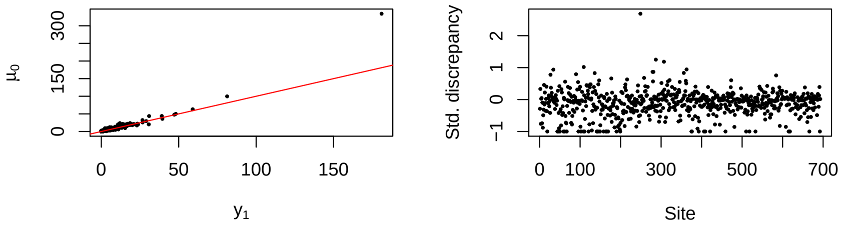
Blackbird



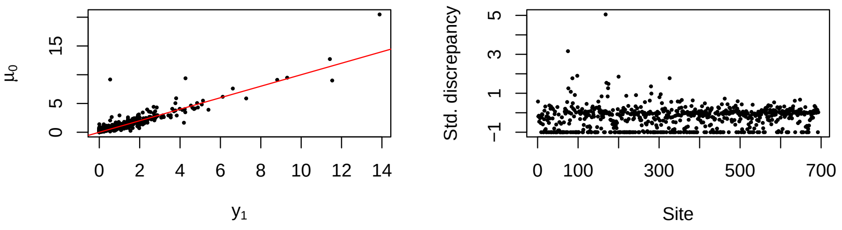
Blue tit



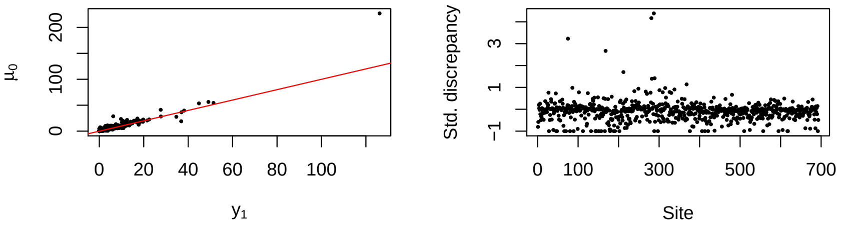
Collared dove



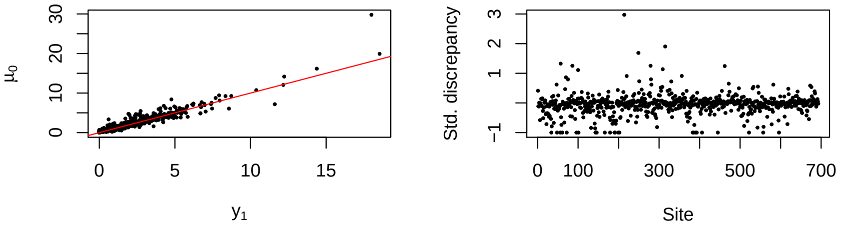
Chaffinch



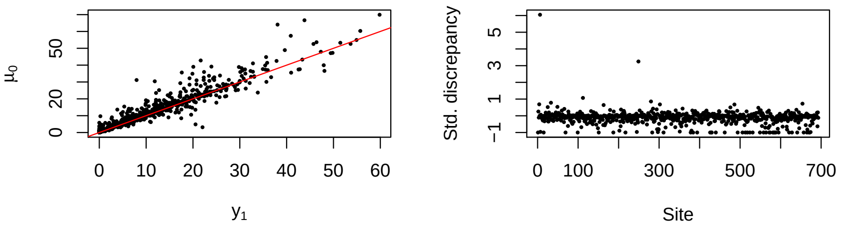
Coal tit



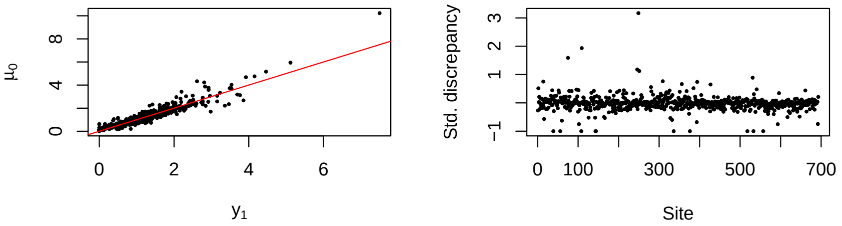
Greenfinch



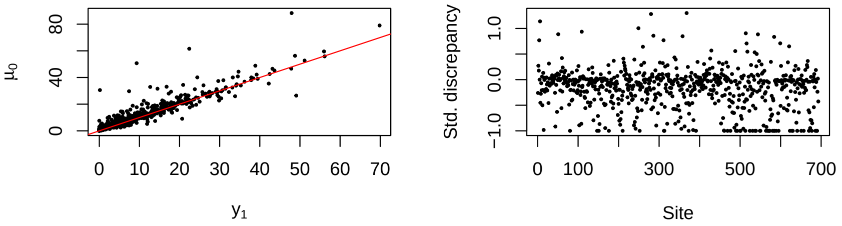
Great tit



House Sparrow



Robin



Starling

Figure 3.7: Plots of first year observed data against estimated μ_0 for each site with $y = x$ line in red (left-hand plots) and standardised discrepancy between first observed year and estimated μ_0 (right-hand plots).

Table 3.10: Prior sensitivity analysis applied to the mixed-effects house sparrow model. Variances of the prior distribution for the regression covariate parameters are increased and decreased by an order of magnitude and the upper limit on the uniform prior on ϕ is increased. Posterior means and Bayes factors are presented, with significant parameters highlighted in bold.

	$\sigma_\beta^2 = 10^{-3}$		$\sigma_\beta^2 = 10^{-1}$		$\phi \sim U[0, 50]$	
Parameter	**Posterior mean**	**BF**	**Posterior mean**	**BF**	**Posterior mean**	**BF**
α	-0.0717	-	-0.0750	-	-0.0749	-
β_1	-0.0088	0.5502	-0.0102	0.0868	-0.0110	0.3544
β_2	**-0.0240**	> 10	**-0.0254**	> 10	**-0.0254**	> 10
β_3	**-0.0137**	3.4196	-0.0139	0.2951	-0.0137	0.9797
ν	-0.0005	0.0204	-0.0002	0.0015	-0.0007	0.0040
γ_1	**-0.0384**	> 10	**-0.0387**	> 10	**-0.0382**	> 10
γ_2	0.0013	0.1042	0.0000	0.0038	0.0021	0.0178
γ_3	**0.0429**	> 10	**0.0437**	> 10	**0.0454**	> 10
ϕ	0.6845	-	0.6844	-	0.6846	-
p	1.3486	-	1.3484	-	1.3482	-
σ^2	0.0129	-	0.0131	-	0.0130	-

against a standardised measure of the discrepancy between the two values. That is,

$$\text{standardised discrepancy} = \frac{(y_{i1} - \overline{\mu}_{i0})}{\overline{\mu}_{i0}}.$$

A couple of sites do seem to show some degree of further discrepancy for each species and warrant further study. Choosing house sparrow as an example, there appear to be two sites, namely 6 and 249, which seem to fall outside of the general distribution of the discrepancy function. In general, where large discrepancies exist, they are always positive, suggesting the model is under-estimating in this case, or equivalently that the data for year one is significantly greater than the average of the following years. Looking specifically at the two sites highlighted in the house sparrow plot, the latter explanation appears to be the case. The individual observations for these two sites across all years are printed in Table 3.11 for reference. For site 6, a very large average count of house sparrow is observed in the first year compared to the following years. The value of μ_{i0} (posterior mean 3.128) for this site is weighted down and more consistent with the following years. However, it is somewhat higher than the following years and is therefore a trade-off between the two. The significantly higher value of the first year observation for this site may indicate a data entry error or just a coincidental influx of this species in the first year. For site 249, the variation in observations appears to be relatively high with some years of high counts interspersed with years of lower numbers. The first year, although more consistent with the rest of the data than site

6, is one of the years of higher counts and as such the following years weigh down the corresponding estimate for μ_{i0}. These two examples seem to indicate that the method used to estimate the prior year's observation is consistent with data, being predicted by the first year but also averaging over the proceeding years if these are different.

The very large value for one site in the collared dove analysis corresponds to a site where most of the observations are zero, giving a posterior mean of 0.0090, and hence the standardised discrepancy becomes relatively large. Overall, due to the small number of sites that this seems to affect and the relatively small deviations from the observed data, we do not expect this to be having undue effect on the results of the analysis. This appears to be the best way of dealing with the problem, without putting strong modelling assumptions on the unknown values in the prior year.

3.5 Posterior autocorrelation

Posterior autocorrelation was notably better for the regression parameters included in the hierarchical centring compared to those that were not (Figure 3.8). There still appears to be quite severely significant autocorrelation in chains for the non-hierarchically centred regression parameters, even at lag 40. Thinning, that is deleting all but the kth iteration, is frequently used in this case. However, using this method is inefficient and can reduce the precision of any resulting estimates as part of the posterior sample, which can still be useful in estimation, must be deleted. Link and Eaton (2012) discuss the use of thinning in MCMC applications and conclude it is rarely justifiable, mainly in cases where memory storage is an issue. Still, the correlation was least for the Tweedie parameters.

Due to high autocorrelation, the effective sample size (ESS) can be severely reduced and this could give rise to concern that parameter space was not being covered. To verify this was not the case, the house sparrow analysis was re-run for 80,000 iterations to ensure that the whole of parameter space was being covered. Results were compared with the shorter run of the data and no differences were found for any of the parameters.

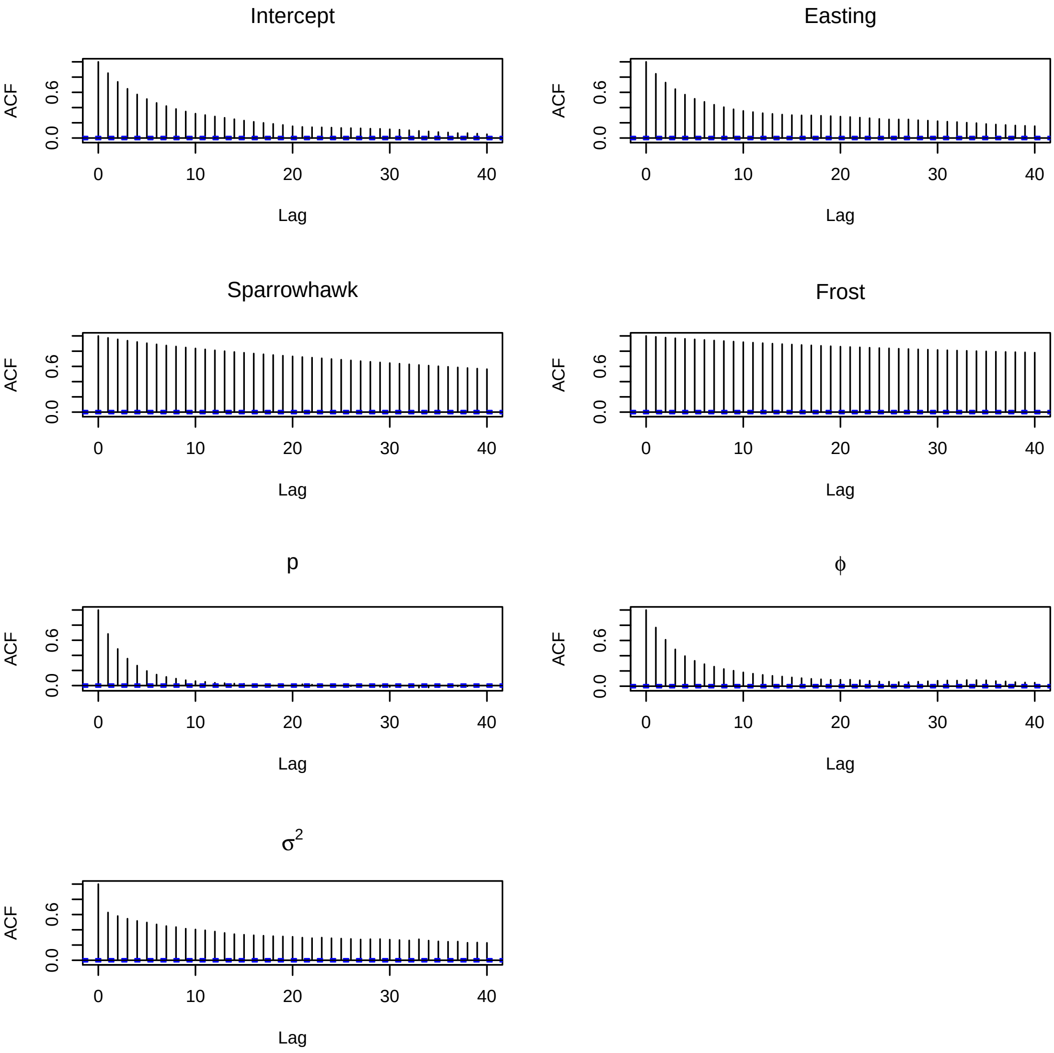


Figure 3.8: ACF plots for parameters for the house sparrow analysis. Parameters chosen are ones (almost) always in the model, with the autocorrelation only calculated for the time the parameter is in the model.

Table 3.11: Mean of weekly maxima of house sparrows from site 6 (left) and 249 (right).

Year	Mean count
1970	22.04
1971	1.00
1972	0.35
1973	0.19
1974	0.85
1975	1.46
1976	0.81

Year	Mean count
1981	20.55
1982	3.67
1983	2.56
1984	6.83
1985	7.82
1986	7.38
1987	5.87
1988	12.96
1989	4.79
1990	2.62
1991	3.43
1992	2.49
1993	14.54
1994	11.65
1995	5.52
1996	2.21
1997	3.72
1998	8.85
1999	16.80
2000	31.50
2001	21.01
2002	9.27
2003	1.38
2004	13.96
2005	18.23

3.6 Model fit

The observed and fitted densities for each species are shown in Figure 3.9. There is good agreement in most cases, although there is some suggestion that the multi-modal aspect of the collared dove and coal tit data are not well modelled.

We use Bayesian p-values to check for further evidence of poor model fit (Tables 3.12 and 3.13), using the deviance as the discrepancy statistic. Values significantly away from 0.5 are indicative of a poor fitting model. Usually a 5% rejection region in each tail is used. Model fit was predominantly consistent between the models with and without

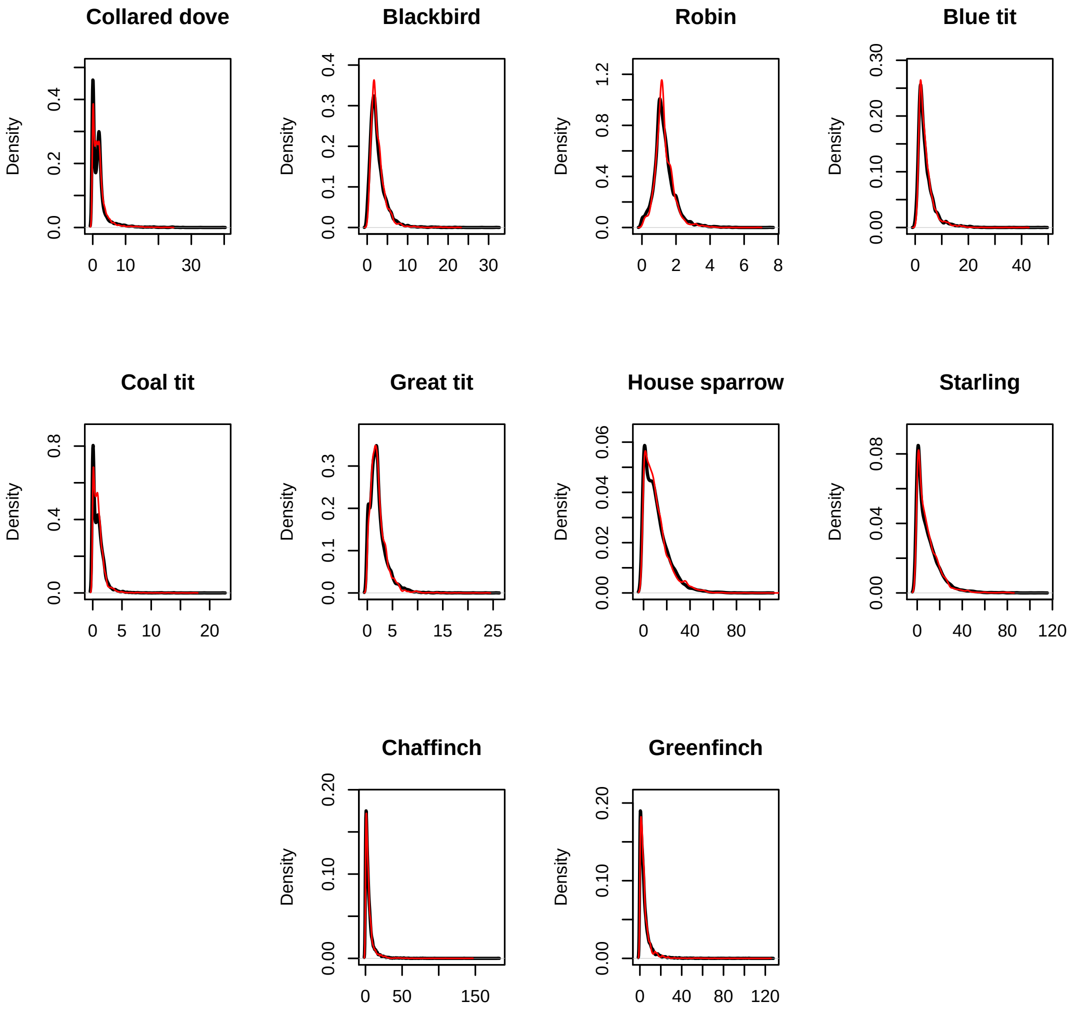


Figure 3.9: Density of the observed data (black line) against density of the mean of fitted values across post burn-in iterations (red line).

random effects but variability of fit is fairly large between species. Coal tit was the only species to show signs of poor model fit according to the Bayesian p-values for the model with random effects. Looking at the density plots in Figure 3.9 for the species, it is clear that coal tit shows a marginally bimodal distribution with a second mode away from zero that the Tweedie distributions are not flexible enough to accommodate. Although the spike at zero is captured, there is a second peak a little above zero that the model does not capture. A similar problem is evident in the collared dove plot, although the p-value for this species was not significant. Chamberlain et al. (2005) also found that model fit was poor for less common species, due to underdispersion present in the data for these species. In these analyses, a mixture model may be more appropriate for this species, particularly a delta model for example, which could capture the spike at zero and then fit better to the second peak a little away from zero. The Tweedie distributions in this case average over this second peak, which is also somewhat evident in the collared dove density plot. In the case of blackbird, the model without random effects also showed evidence of a poor fitting model. Taking account of the serial correlation in this species evidently improves the fit of the model.

Table 3.12: Bayesian p-value for models without random effects using the deviance as the discrepancy statistic.

Species	**Bayesian p-value**
Collared Dove	0.8761
Blackbird	0.9992
Robin	0.7058
Blue tit	0.2861
Coal tit	0.1424
Great tit	0.1809
House sparrow	0.6263
Starling	0.6847
Chaffinch	0.8730
Greenfinch	0.8476

Table 3.13: Bayesian p-values for the independent species model with random effects. The deviance is used as the discrepancy function in each case.

Species	**Bayesian p-value**
Collared Dove	0.8941
Blackbird	0.8164
Robin	0.7511
Blue tit	0.4399
Coal tit	0.0204
Great tit	0.1683
House sparrow	0.6263
Starling	0.4644
Chaffinch	0.7005
Greenfinch	0.7132

3.7 Summary

In this chapter we have outlined a highly flexible method for analysing changes in the average numbers of birds visiting garden bird feeding stations. Several aspects of the data made for more complex extensions of standard linear model theory to be required. The use of the Tweedie distributions allow very different shaped distributions to be well modelled, with discrete peaks at zero, long tails and bounded below by zero. In the case of more severe bimodality, the Tweedie distributions fail to fit well to the data and alternative distributions may be more appropriate in this case.

The inclusion of random effects was found to be highly advantageous in this analysis. Our analyses show that without the individual site effects, overall effects of covariates were severely underestimated and many of the effects that appear to actually be inherent in the data were missed. The use of hierarchical centring no doubt aided in reducing autocorrelation within parameters and resulted in better mixing of both between and within model moves in the reversible jump algorithm. Mixing was further improved with the use of an adaptive algorithm which tuned proposal distributions independently for each parameter and resulted in near-optimum acceptance probabilities.

Negative effects of sparrowhawk on changes in garden bird counts were found with three species, house sparrow, starling and blue tit. As previous analyses of sparrowhawks on overall breeding density of these species have failed to find any significant impact of sparrowhawks, our results may correspond to a reduction in the non-breeding density of these species that would otherwise succumb to other external factors in the absence of predation pressure.

Density dependence was found to be a limiting factor in the number of birds visiting gardens as each site has a limited amount of food and space for each species to be dependent on. Adverse weather was associated with a behavioural response of significantly greater numbers of half the species turning up in gardens during these periods. Easting and level of urbanisation were associated negatively with changes in numbers of birds visiting gardens.

Conducting a prior sensitivity analysis on one of the models showed that the Bayes factors were the quantities most susceptible to changes in prior specification. The marginal posterior mean of the parameters conditional on the parameter being in the model, however, were largely robust to changes in the prior distributions. The effect on model probabilities is well known and in this application had little effect on the interpretation of the results for the species we conducted the sensitivity analysis on. Only parameters with Bayes factors right on the boundary showed any variation in interpretation. As the choice of cut-off points is a somewhat grey area, their interpretation should be conducted in light of this. For the house sparrow analysis, only the parameter associated with the urbanisation level changed interpretation under alternative prior specifications. Although we cannot be certain that no change in interpretation would be observed in the other species, we feel that the priors that were specified on the parameters are realistic in the setting of the application. The lack of change in posterior means is also a good indication that our results are robust.

Chapter 4

An independent change-change model

4.1 Introduction

In the previous chapter we analysed the GBFS data using a log-linear model using various environmental covariates, including a measure of sparrowhawk abundance, as explanatory variables. We assumed the model was additive on the log scale with the covariates entering the model merely directly as unlagged values. How the covariates enter a model often receives little attention in log-linear models, however various plausible covariate structures could be used and may offer alternative information on the underlying drivers of population change. Having analysed the effect of sparrowhawks on the number of various species of birds visiting garden feeding sites across the UK, this chapter will now look at how year-on-year changes in sparrowhawk numbers affect the prey species abundance. That is a change-change model. Many of the concepts associated with the modelling framework used in this chapter are identical or very similar to those used in Chapter 3. For brevity, and to avoid repetition where possible, references will be made to the appropriate sections in the previous chapter.

4.2 The model

Once again the observed means of weekly maxima y_{it} are assumed to follow a Tweedie distribution with mean μ_{it}. We have the same vectors of site-specific covariates $\boldsymbol{x}_i$ with parameter vector $\boldsymbol{\beta}$ and time-varying covariates $\boldsymbol{v}_{it}$ with parameter vector $\boldsymbol{\gamma}$. This time the mean structure is defined as follows:

$$y_{it} \sim Tw(\mu_{it}, \phi, p) \tag{4.1}$$

where

$$\mu_{it} = \exp\left\{\alpha + \boldsymbol{\beta}\boldsymbol{x}_i + \boldsymbol{\gamma}\log\left(\frac{\boldsymbol{v}_{it}+1}{\boldsymbol{v}_{i1}+1}\right) + \log\left(\mu_{i1}\right) + \epsilon_i\right\}.$$

Using the hierarchical centring reparameterisation method and following some simple algebraic manipulation, the model can be rewritten as follows.

$$\log\left(\frac{\mu_{it}}{\mu_{it-1}}\right) = \boldsymbol{\gamma}\log\left(\frac{\boldsymbol{v}_{it}+1}{\boldsymbol{v}_{it-1}+1}\right) + \epsilon_i \tag{4.2}$$

$$\epsilon_i \sim N(\alpha + \boldsymbol{\beta}\boldsymbol{x}_i, \sigma^2)$$

That is, the mean of the Tweedie distribution from Equation 3.2 is rewritten in terms of change in covariate values between consecutive years. The time-invariant covariates are specified as previously as they remain constant across the period of the survey. The random effects are assumed to be normally distributed once the above algebra has been conducted to ensure consistency with the model in the previous chapter. The final model used is hence the one in Equation 4.2. Due to the findings in Chapter 3, we only use a mixed-effects model in this chapter.

The choice of a change model was suggested by Newson et al. (2010) to account for density-dependence effects. Assuming predators are indeed having an effect on a prey species at a given site, changes in predator numbers may lead to a density-dependent compensation in the prey population dynamics. As such, we would want a model in which both a zero-rate of change in predator numbers and an absence of predators

Table 4.1: Prior distributions specified on parameters in Equation 4.2.

Parameter	Prior
α	$N(0, 10^{-2})$
β_j	$N(0, 10^{-2})$
γ_j	$N(0, 10^{-2})$
μ_{i0}	$U[0, 200]$
ϕ	$U[0, 5]$
p	$U[1, 2]$
σ^2	$\Gamma^{-1}(10^{-3}, 10^{-3})$

correspond to the same rate of change in prey abundance. Modelling the change in prey abundance as purely a function of the abundance of predators will match these two occurrences to different rates of change, unless other means for accounting for density dependence are included (Newson et al., 2010). In the previous chapter, density dependence was accounted for in an alternative manner and the equivalent covariate is not included in this model formulation.

The model is once again relating log of the change in the expected average count of prey species to a function of covariates and site-specific random effects. In the same way as outlined in Section 3.2.3, we estimate the year prior to the survey being conducted at each site using a data augmentation approach. As the covariate values are now the respective change in successive years, we must reduce the size of the data by one year per site to allow for this as the covariate value associated with observation y_{it} is the change between year $t-1$ and t.

4.2.1 Priors

Similar priors are specified on the parameters to those and are presented in Table 4.1 for reference.

4.3 Model Results

The analyses were run initially in the saturated model to guide the choice of proposal distribution parameter for the reversible-jump covariate dependence step. Once again, posterior means and variances for each of the regression parameters from this analysis were set as the normal distribution mean and variances for the proposal distributions. Then the reversible jump step was added to acount for model uncertainty and determine covariate dependence. The model was run independently for each of the ten species. Convergence was much slower for this model than the models fitted in Chapter 3. A total number of 100,000 iterations were run with the first 60,000 discarded as burn-in. The additional time taken for the model to converge may be a result of the fact that there is now one less observation at each site than there was in the analyses for the previous chapter, that is an 11% reduction in the overall dimension of the data. However, due to the large volume of data, the poor mixing may more likely be due to greater correlation between parameters and/or covariates. Posterior summary statistics are presented for these analyses in Tables 4.2 and 4.3 with example posterior distributions for the starling analysis in Figure 4.1.

Easting is once again the dominant time-invariant parameter, with all significant parameter estimates being negative. The reasons for this have already been discussed in Section 3.3.2. Coal tit, which shows a significant relationship with easting in the change-change model that was not present in the alternative specification, is largely dependent on coniferous woodland. The establishment and maturation of new conifer plantations, which has been conducted on a large scale over the last 40 years, may influence coal tit distribution and we would therefore expect there to be some pattern to the species distribution linked to easting.

The rural or urban factor variable was once again always negative when significant, suggesting greater negative trends in urban gardens, but in this model was only significant for one species, that is house sparrow. The magnitude of the effect is not greatly different from that in Table 3.5 (-0.0166 in this model vs -0.0140 in Chapter 3), but the corresponding Bayes factor is(> 10 vs 1.1542). The trend in parameter estimates for the other species are similar in both model specifications although Bayes factors were generally much lower in the change-change model.

Table 4.2: Posterior means (conditional on the parameter being in the model) and Bayes factors for regression covariate parameters in parentheses. Significant covariates are highlighted in bold.

Species	**Intercept**	**North**	**East**	**Rur/sub**	**S/whawk**	**C. dove**	**Frost**
Collared Dove	-0.0232	0.0008	0.0073	-0.0069	-0.0069	-	**0.0365**
	-	(0.1)	(0.1)	(0.1)	(0.2)	-	(>10)
Blackbird	0.0036	-0.0018	**-0.0073**	-0.0051	0.0043	**0.0131**	**0.0076**
	-	(0.4)	(3.1)	(0.3)	(0.1)	(>10)	(4.7)
Robin	0.0002	0.0003	-0.0010	-0.0005	-0.0005	**0.0045**	0.0002
	-	(<0.1)	(<0.1)	(<0.1)	(<0.1)	(3.2)	(<0.1)
Blue tit	-0.0313	0.0027	-0.0026	-0.0015	**-0.0087**	0.0016	0.0087
	-	(<0.1)	(<0.1)	(<0.1)	(>10)	(<0.1)	(1.7)
Coal tit	-0.0330	0.0102	**-0.0146**	0.0016	0.0117	**0.0166**	**-0.0165**
	-	(1.9)	(3.3)	(<0.1)	(1.3)	(>10)	(8.3)
Great tit	-0.0200	0.0013	-0.0014	-0.0008	0.0005	0.0022	0.0069
	-	(<0.1)	(<0.1)	(<0.1)	(<0.1)	(<0.1)	(0.6)
House sparrow	-0.0782	**0.0183**	-0.0108	**-0.0166**	**-0.0325**	**0.0100**	**0.0556**
	-	(>10)	(0.4)	(>10)	(>10)	(3.3)	(>10)
Starling	-0.0798	0.0076	0.0021	0.0000	**-0.0187**	**0.0131**	**0.0427**
	-	(0.2)	(<0.1)	(<0.1)	(>10)	(>10)	(>10)
Chaffinch	-0.0113	0.0083	-0.0002	-0.0100	0.0020	**0.0122**	**0.0266**
	-	(0.6)	(<0.1)	(1.6)	(<0.1)	(>10)	(>10)
Greenfinch	-0.0393	0.0070	**-0.0199**	-0.0131	-0.0032	-0.0020	**0.0182**
	-	(0.2)	(>10)	(1.5)	(<0.1)	(<0.1)	(>10)

Table 4.3: Posterior means of the variance parameters.

Species	ϕ	p	σ^2
Collared Dove	0.5748	1.3420	0.0126
	0.0116	0.0065	0.0008
Blackbird	0.2086	1.2780	0.0016
	0.0049	0.0165	0.0002
Robin	0.0681	1.0674	0.0007
	0.0015	0.0076	0.0001
Blue tit	0.1661	1.4603	0.00184
	0.0052	0.0203	0.0002
Coal tit	0.3476	1.2738	0.0034
	0.0078	0.0063	0.0003
Great tit	0.2044	1.1859	0.0017
	0.0040	0.0078	0.0003
House sparrow	0.6574	1.3390	0.0105
	0.0130	0.0066	0.0007
Starling	0.6945	1.3864	0.0079
	0.0131	0.0068	0.0006
Chaffinch	0.3884	1.3712	0.0061
	0.0076	0.0087	0.0005
Greenfinch	0.5291	1.4220	0.0088
	0.0097	0.0082	0.0006

The significant parameters for the sparrowhawk covariate correspond to three species and were all negative. These three species were blue tit, house sparrow and starling, i.e. the same three species showing significant negative relationships under the previous model. These negative relationships are relatively small in size in practical terms, corresponding to reductions in the numbers of the prey species visiting gardens of -0.6%, -2.2% and -1.3% respectively, for each doubling of sparrowhawk numbers. Conversely, no significant positive relationships were found.

The number of significant relationships found between prey species and collared doves increased in comparison to the previous model, but all were again positive. This once again gives greater support to the idea that these are merely positive associations between species as here we are now directly relating change in abundance of one species with change in abundance of the other.

The parameters associated with ground frost were significant for seven of the ten species in the change model. This suggests that years with higher amounts of ground frost lead in general to a greater number of ground-feeding birds visiting feeders. If the birds are unable to access their usual food supply then they will tend to enter gardens in larger numbers where food is independent of weather conditions. There was no evidence of a significant relationship for this covariate with robin, blue tit or great tit. These are species that are less dependent on granivorous food and may be less affected by ground frost. The negative relationship between numbers of coal tits visiting gardens and change in the number of frost days was contrary to the results of Chamberlain et al. (2005), although only temperature was used in their analysis. The use of garden feeding stations by coal tits has been shown to be influenced by the size of conifer seed crops, the birds switching to feed on garden feeders more often in years with fewer cones than in mast years (McKenzie et al., 2007). Access to the conifer seeds may also be influenced by the weather conditions that are modelled here, namely that the cones are likely to open on dry days and close on damp ones. A winter with more frost days, which are typically associated with clear skies and dry conditions, may see the cones open more often throughout the winter. Consequently, coal tits would then have greater access to this natural food resource and would become less reliant on garden feeders.

Weighted means were calculated for the six covariates again according to Equation 3.5 and presented in Table 4.4. Ground frost appears to have the greatest overall effect across species, followed by collared dove abundance in this modelling framework.

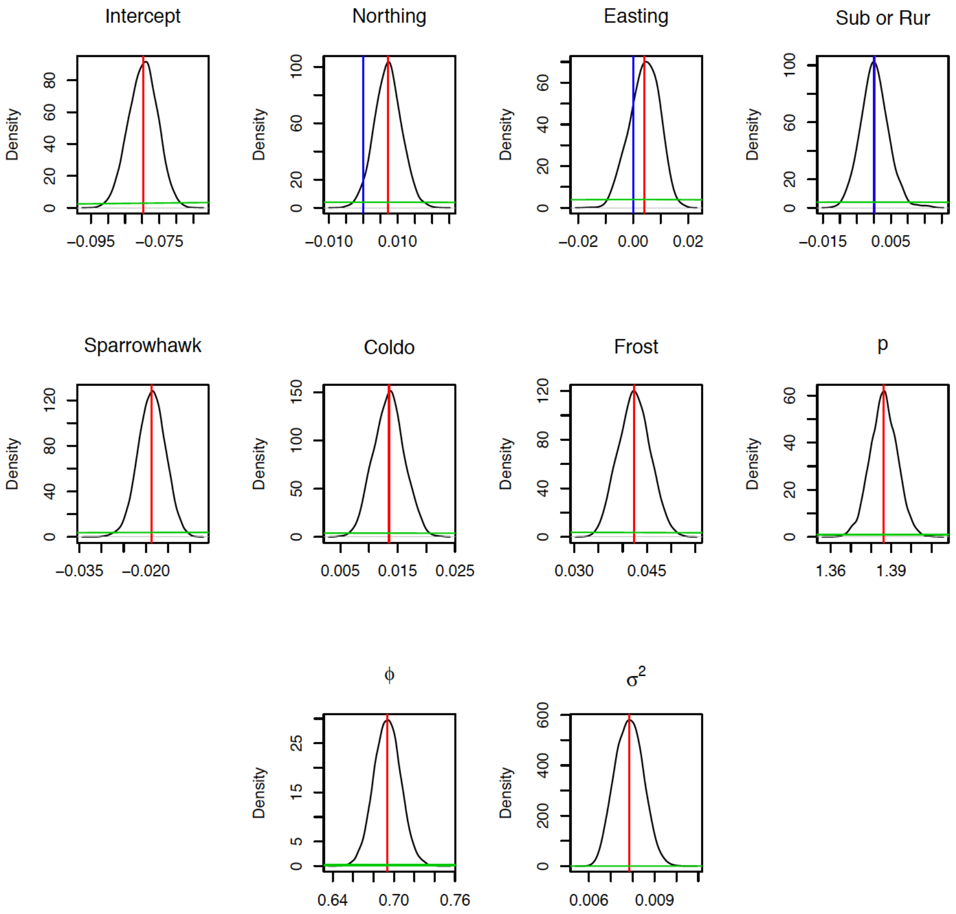


Figure 4.1: Posterior distributions for the starling analysis (black lines). Red lines are posterior means, green lines the prior distribution, blue lines (where present) at $x = 0$.

Table 4.4: Weighted mean for each covariate across all species in the mixed-effects models calculated according to Equation 3.5 with the number of species showing a significant effect for this parameter in parentheses.

Covariate	Weighted mean
Northing	0.0003 (1)
Easting	-0.0004 (3)
Sub/rur	-0.0003 (1)
Sparrowhawk	-0.0005 (3)
Collared Dove	0.0007 (6)
Ground frost	0.0018 (7)

Posterior means for the Tweedie variance parameters are very similar under the two model specifications; the slight differences can easily be explained by the smaller dimension of data that is used in this model. Where differences in random effect variance were apparent, the variance tended to be greater in the models from Chapter 3. Why the change in time-varying covariates should generally be able to account for more variation is not clear.

4.3.1 Algorithm tuning

The adaptive tuning of proposal variances to give acceptance probabilities roughly between (0.1,0.8) was once again added to the modelling algorithm during the burn-in phase. The final tuned standard deviations for the regression parameters are given in Table 4.5. As in the previous model, the standard deviations corresponding to the site-specific covariate parameters were on the whole larger than those associated with time-varying covariate parameters, although more variability was apparent in this specification.

Table 4.5: Final tuned proposal standard deviations for regression parameters at the end of the burn-in period. Variances are tuned at each iteration to induce acceptance probabilities between (0.1,0.8).

Species/Covariate	Intercept	Northing	Easting	Sub/rur	Sparr.	Col. dove	G. frost
Blackbird	0.0015	0.0015	0.0018	0.0015	0.0015	0.0028	0.0007
Blue tit	0.0021	0.0032	0.0032	0.0011	0.0010	0.0010	0.0039
Chaffinch	0.0050	0.0027	0.0020	0.0027	0.0016	0.0027	0.0070
Coal tit	0.0025	0.0026	0.0025	0.0048	0.0038	0.0019	0.0048
Collared dove	0.0064	0.0070	0.0021	0.0077	0.0016	-	0.0022
Greenfinch	0.0033	0.0068	0.0068	0.0109	0.0039	0.0021	0.0019
Great tit	0.0022	0.0027	0.0011	0.0027	0.0006	0.0009	0.0010
House sparrow	0.0027	0.0100	0.0105	0.0061	0.0006	0.0010	0.0032
Robin	0.0013	0.0008	0.0024	0.0021	0.0011	0.0005	0.0008
Starling	0.0070	0.0031	0.0048	0.0037	0.0038	0.0014	0.0009

Table 4.6: Bayesian p-values for the change model with random effects.

Species	
Collared Dove	0.8499
Blackbird	0.5240
Robin	0.2228
Blue tit	0.5097
Coal tit	0.1650
Great tit	0.2229
House sparrow	0.5812
Starling	0.8089
Chaffinch	0.7182
Greenfinch	0.8919

4.3.2 Model fit

Once again we use Bayesian p-values to check for evidence of poor model fit (Table 4.6), with the deviance used as the discrepancy function. No evidence to suggest poor fit of the model is found for any species in this analysis, even coal tit that was highlighted in the previous analysis. The fitted densities shown in Figure 4.2 also suggest similarly well-fitting models to those in Chapter 3. The bimodality of the collared dove and coal tit models appears to once again be a problem.

4.4 Relationship with predation risk

Our results so far have showed a varying effect of sparrowhawks on different species of potential prey. We now consider why some of the species may be more susceptible to sparrowhawk predation than others. As sparrowhawks are generalist predators of birds, being able to take any prey species up to a given maximum size (Cramp and Perrins, 1979), several studies have looked at how vulnerable different species are to predation by sparrowhawks relative to each other (e.g. Creswell, 1995; Gotmark and Post, 1996; Møller et al., 2012). These studies use various methods to determine the susceptibility of various species of birds to predation by sparrowhawks.

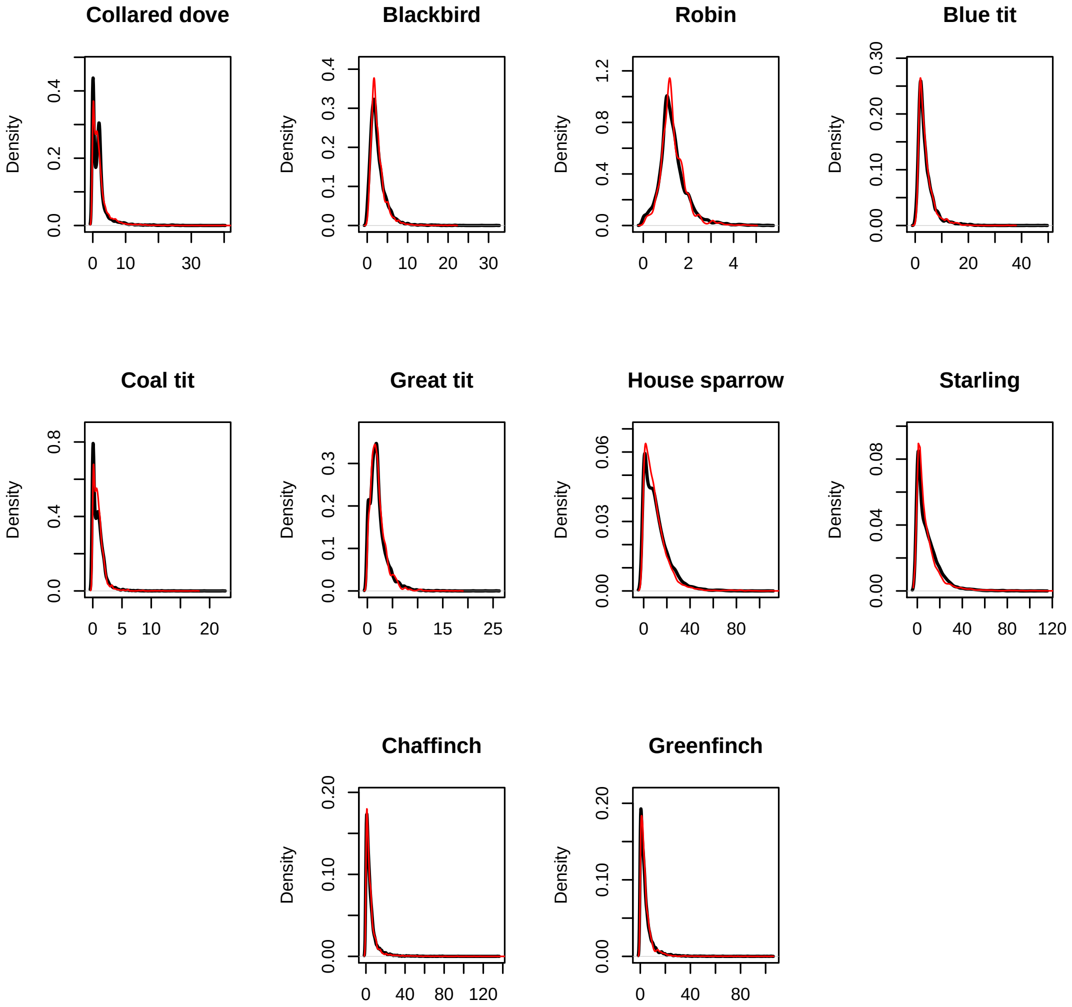

Collared dove
Blackbird
Robin
Blue tit
Coal tit
Great tit
House sparrow
Starling
Chaffinch
Greenfinch

Figure 4.2: Observed (black) and mean of post burn-in fitted (red) densities for the 10 species modelled using the change-change model approach.

In particular, we use the results of Gotmark and Post (1996) who calculated a relative measure of predation risk by accounting for the number of each species available to be predated on by sparrowhawks. This avoids the problem of certain species forming a large part of the sparrowhawk diet purely for the reason they are so abundant. Gotmark and Post (1996) provide relative predation risks for all species analysed in Chapters 3 and 4 except collared dove, a larger proportion of corresponding species than does either Creswell (1995) or Møller et al. (2012). However, the results were checked against the other two papers for the species that did overlap and very similar results were found in each case. In Gotmark and Post (1996)'s method, the species under consideration were ranked according to frequency in the surveyed sparrowhawks' diet, as were the occurrence of each species in the survey area. The rank of each species' occurrence in the diet was then subtracted from the rank of the species' abundance giving a *relative predation risk* for each species. Zero is then the point at which a species is considered to be predated upon directly in proportion to its abundance, or equivalently that the sparrowhawk is randomly selecting prey. Positive values suggest a species is predated upon more frequently than merely by chance and negative values less frequently.

Figure 4.3 plots the posterior means of the parameter associated with the sparrowhawk covariate from the two models fitted in Chapters 3 and 4 against the corresponding relative predation risk for that species. Lines are plotted for the two models separately (black and green lines respectively) and for the pooled data (red line). These are calculated using an ordinary linear model fitted to the data. As can be seen from Figure 4.3, there is a strong negative relationship between the estimated sparrowhawk effect on average garden bird counts and the associated relative predation risk for that species. This suggests that species that are appear more frequently in the diet of sparrowhawks than would be expected if it were a random process are showing declines or a reduction in population growth associated with increases in sparrowhawk abundance. This appears to be the strongest evidence obtained so far that sparrowhawks may be having population level effects on some of the species on which they feed. An alternative, and equally plausible interpretation of this could be that the reduction is a behavioural response of the birds reacting to the presence of sparrowhawks, avoiding the sites that sparrowhawks frequent.

The dotted blue lines in Figure 4.3 show the estimated effect from our models that would correspond to a relative predation risk of zero. This does not mean that there

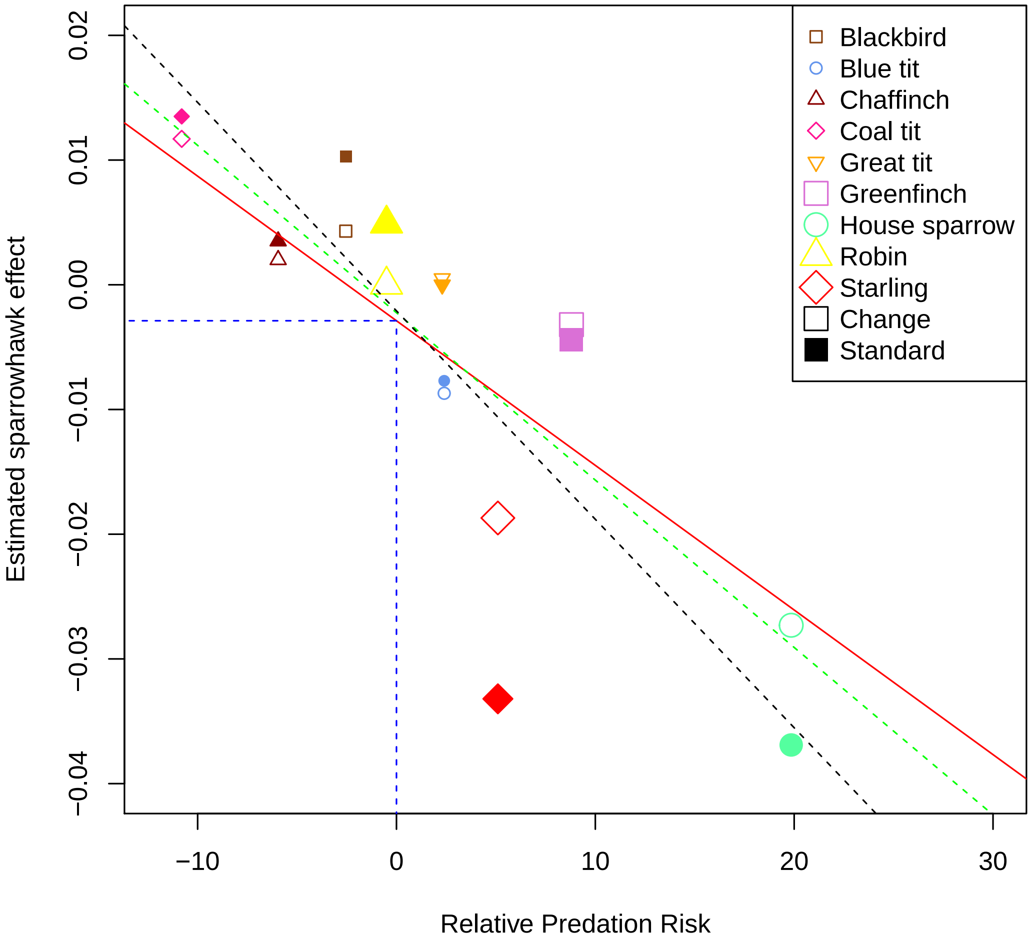


Figure 4.3: Relationship between estimated sparrowhawk effects obtained from the two mixed-effect model specifications and relative predation risk estimated by Gotmark and Post (1996). Filled symbols are posterior means from Chapter 3 and open symbols from Chapter 4. The dashed lines relate to a linear model fitted to the results from Chapter 3 (black) and Chapter 4 (green). The solid red line is a linear model fitted to the pooled results from the two chapters. The blue line corresponds to an expected value of sparrowhawk effect when predation risk is zero.

is no predation risk, rather that the prey is selected directly in proportion to its total abundance in the local environment. As such, the slightly negative effect estimated under our models is consistent with expectation.

Of the twenty possible correlations between predator and prey species in the mixed-effects models fitted in Chapters 3 and 4, eight were found to be significant, three in the change-change model. Of the five significant relationships found in the previous model, two were positive. These two relate to blackbird and coal tit. From Figure 4.3, these two species have two of the lowest relative predation risks of any of the species analysed. As such, these may be spurious correlations. Given the number of possible associations, we would expect roughly one spurious correlation purely due to chance. There are potentially additional confounding variables that might be driving these positive relationships. As suggested by Chamberlain et al. (2009), we cannot rule out the effect of improvement of garden habitats and the quality of the food provided, particularly as only site-specific random effects were included in the model. However, it seems somewhat unlikely that an improvement in garden quality would only encourage greater numbers of sparrowhawks, blackbirds and coal tits and not the other species. A more likely explanation may be that sites that were recolonised by and are generally more able to support sparrowhawks are more attractive to these two species. We cannot be certain that the same interpretation does not hold for the significant negative relationships, however the lack of any significant positive affects in the change-change model gives no support to this hypothesis.

Of the four species with the highest relative predation risk, three show significant negative sparrowhawk effects under both independent model specifications. This appears to give relatively strong evidence, although admittedly only from an observational study, that sparrowhawks are strongly associated with reduction in the numbers of certain species of birds visiting garden feeding stations across the UK. This is particularly the case for species that are selected more frequently or are more susceptible to predation by sparrowhawks. It is difficult to extrapolate these effects on the number of birds visiting winter garden feeding stations to an overall effect on breeding numbers of these three species. Chamberlain et al. (2005) found strong relationships between probability of occurrence at GBFS sites and CBC index from 1970 to 2000 in both starling and house sparrow (Spearman's ρ of 0.962 and 0.967 respectively) although not in blue tit (-0.319). When only the years 1980 to 2000 were used the blue tit this increased to 0.2999. As Newson et al. (2010) failed to find any effect of predators on the breeding density of these species, the effects found may correspond to the "doomed surplus" of prey that will not ultimately form part of the breeding population for that species (Section 1.4; Gibbons et al., 2007; Newton, 2004). In the absence of sparrowhawk pressure, these birds would otherwise have succumbed to other density-dependent factors, either through a lack of food or suitable nesting habitat. The sparrowhawks may just change the dynamics of mortality in the species they prey on. As such these effects may be consistent with the suggestion that predators merely change the seasonal pattern of mortality and/or reduce the annual peak in numbers of prey (Newton, 1998; Perrins and Geer, 1980).

4.5 Summary

In this chapter we have outlined an alternative model to that fitted in Chapter 3 which models changes in the expected annual mean count as a function of *change* in the covariates. The most appropriate model for detecting interactions between species has been discussed previously (Newson et al., 2010), with these authors suggesting that a change-change approach is the more appropriate model formulation enabling density-dependent factors to be directly accounted for.

For this application the results are largely similar between the two model formulations presented in this chapter and the preceding one. Although we do not expect that this will necessarily always be the case, accounting for density dependence in Chapter 3 may have reduced any discrepancy between the two model formulations that Newson et al. (2010) outlined in relation to a zero rate of change in prey abundance corresponding to two different levels of predator abundance. Evidently the spatially-explicit covariates are the same in both model specifications as is the specification of the random-effects. The large degree of agreement is therefore not altogether surprising. The only differences relate to the specification of the relationship between prey and the time-varying covariates. It is reasonable to suggest that the sites that can support more sparrowhawks are the ones where the rate of change has generally been greatest over the past 40 years. Similar arguments could be made for collared dove, although there were more significant relationships in the change-change model.

Model fit did not vary much between the two model formulations, although convergence to the stationary distribution was slower for the change-change model. This may be associated with a reduction in the dimension of the data that was required in this case. In other applications, covariate values may be available for the year prior to the first observation, in which case this problem could be avoided. Another option would be to impute the values for this year using a similar data augmentation approach to that used for estimating the $\boldsymbol{\mu}_0$, but would not really add any extra information without specifying a model on the covariate values. The extra uncertainty that this would add to the model seems too great to make this worthwhile in practice, especially as these will relate to site-specific, time-invariant parameters. As such, they will likely be highly confounded with the corresponding $\boldsymbol{\mu}_0$.

The efficiency of the change-abundance method outlined in Chapter 3 may be greater due to its ability to maximise the use of the data available. However, the two models are testing slightly different hypotheses about the relationships between prey species and their predators (or other environmental covariates). Therefore the correct model specification will be somewhat dependent on the application and the questions that are to be answered. As with any modelling procedure, careful consideration to the model specification should be given.

Chapter 5

Multi-species analysis

5.1 Introduction

The analyses conducted so far have modelled changes in garden bird numbers independently for each of the ten species of interest. However, in a large-spatial-scale analysis such as this, it may be of interest to determine to what extent the observed population dynamics of each species are synchronous with each other. Some species are ecologically very similar and hence we may expect that these species will show similar responses to the environment that they share. It may also be of interest to identify environmental factors that influence multi-population or multi-species dynamics (Grosbois et al., 2009).

Multi-species models have the potential to express or test alternative hypotheses within ecosystems that cannot be achieved through analyses of single species only (Mutshinda et al., 2011; Wells and O'Hara, 2013). How species respond similarly or differently to similar environmental factors may help ecologists better understand ecosystems as a whole and provide better insight into important drivers of population change. Consideration of species singly has the potential to only understand part of the ecology of that species or group of species (McCarthy, 2011). Parameters can also be shared between species giving a greater amount of data to estimate these same parameters leading to improved precision in the results. This increase in power can similarly be achieved through integrated population modelling (Besbeas et al., 2005). However, multi-species models have received generally less attention than single-species models, mainly due to the complexity required to account for spatial correlation across wide areas.

5.1.1 Types of synchrony and how to measure it

The idea of ecological synchrony can be defined in numerous ways and often has a rather vague concept of parameters varying over time and/or space in a similar way (Vik et al., 2004). Different measures of synchrony have been proposed, but each has its own interpretation and hence even when applied to the same data set, may give conflicting results (Buonaccorsi et al., 2001). Most of these methods, however, have only been conducted for two populations to check for pairwise synchrony. In this section we outline different measures of synchrony summarised by Buonaccorsi et al. (2001) and Lahoz-Monfort (2012).

For a given time series of observations, summary statistics, etc., there are numerous ways of measuring synchrony between successive observations. These include:

1. Correlations between time series values using Pearson's or Spearman's correlations can give a simple measure of how related two series of data or point estimates are (e.g. Bjørnstad et al., 1999; Shanker and Sukumar, 1999; Swallow, 2011). Synchrony of this type can also be measured using cross-correlation, which enables lagged synchrony to be tested (e.g. Bjørnstad and Bascompte, 2001; Ranta et al., 1995). This type of synchrony can occur when the effect of a particular external factor takes different lengths of time to reach different populations, either due to the geographical distance or the ecology of the species concerned.

2. Correlation in the residuals after a model has been fitted to each series. Commonly auto-regressive models are used as the model in this case. Then, once the autoregressive model has been fitted, synchrony in the residuals can be assessed (e.g. Sutcliffe et al., 1996).

3. The time series could be converted into a different series relating to the direction of the series at each time point (i.e. positive change or negative change). Measures that detect similarities in the direction of trends in series can then be used. Typically correlation measures are used to compare the direction of the statistic across time.

4. Coincidental peaks have been used to detect synchrony, frequently synchrony in plant crop production (e.g. Swallow, 2011) or outbreak years in lepidoptera (e.g. Klemola et al., 2006).

Extensions to these methods may be required if synchrony across more than two series is to be measured. Either pairwise comparisons can be conducted as above, or more frequently an average measure over the corresponding pairwise measures is calculated. However, this is a relatively simplistic approach to determining synchrony. Increasingly sophisticated models allowing synchrony across multiple series have been proposed, mainly using random effects to give a more model-based approach to estimating covariances across series. The methods of Lahoz-Monfort et al. (2011) and Grosbois et al. (2009), stemming from work by Loison et al. (2002), follow this type of approach.

5.1.2 Modelling synchrony in parameters

Where modelling approaches have been developed for multi-species synchrony in demographic parameters, this has largely been for seabirds, and often on a small scale (e.g. Lahoz-Monfort, 2012). When it comes to garden birds, the level of synchrony between species may be much greater over a large area. The nature of the feeding sites that are monitored by the GBFS lends itself to the detection of synchrony, as they are relatively small settings where all species are subject to similar exogenous factors. The ecology of many of the songbirds monitored under this scheme will be largely similar and the species will also have similar traits, as the results from the previous chapters suggest.

Lahoz-Monfort et al. (2011) introduced a multi-species model based on work by Grosbois et al. (2009) for testing synchrony in survival in multiple species. In principal, the main idea of the method involves partitioning unexplained variation into two separate random effects. Here, separate site random effects can be included in the model, one explicitly modelling unexplained variation that is constant across species (which we refer to as ϵ_i as in previous chapters), whilst the other accounts for unexplained, species-specific variation (δ_{si}). These random effects have associated variances σ_ϵ^2 and σ_s^2 respectively and are independent of each other. A separate σ_s^2 is estimated for each species included in the model.

From the variance of these two random effects, an intra-class correlation coefficient

ICC_s can be calculated for each species, defined as follows

$$\mathrm{ICC}_s = \frac{\sigma_\epsilon^2}{\sigma_\epsilon^2 + \sigma_s^2},$$

where σ_ϵ^2 is the variance of the site-specific random effects and σ_s^2 the variance of the species-specific random effect for species s. This ratio gives an indication of how much of the variance not explained by the covariates is common, or synchronous, to all species. Values of $\mathbb{E}(\mathrm{ICC}_s)$ close to 1 indicate that species s is largely synchronous with the other species and that any unexplained variance is mostly attributable to unmeasured differences in the individual sites. Values close to zero suggest that the species is largely asynchronous with the others and that the extra variation in that species is unmodelled heterogeneity due to the species' different reactions to local environmental conditions.

Of additional interest is the contribution of any covariates included in the model to the dynamics of the detected synchrony. By fitting two different models, one with and one without covariates, the subsequent change in the random effect variances observed when covariates are added to the model can be calculated. This can further be used as a means for obtaining an estimate for how the covariates act as synchronising or desynchronising agents for each of the species involved. Following the methods of Loison et al. (2002) and Lahoz-Monfort et al. (2011), the fraction of the variance accounted for by the covariates can also be calculated as follows, where $\sigma^2(\mathrm{res})$ is the variance from the model with covariates and $\sigma^2(\mathrm{total})$ the model with intercept only:

$$\mathrm{C}_\epsilon = 1 - \frac{\sigma_\epsilon^2(\mathrm{res})}{\sigma_\epsilon^2(\mathrm{total})}.$$

This coefficient measures the contribution of the environmental covariates to the inter-specific synchronous component of the between site variances. Similarly,

$$\mathrm{C}_s = 1 - \frac{\sigma_s^2(\mathrm{res})}{\sigma_s^2(\mathrm{total})}$$

measures the contribution of the environmental covariates to the inter-specific *asynchronous* component of the between site variances. The expected value of these coefficients measure how much the covariates contribute as a whole to the relevant components of the random effect variances. As such they can provide insight into whether the variation that is explained by those covariates is largely synchronous or asynchronous across the species in the model. One disadvantage of this approach, however, is that when more than one covariate is included in the model it is not possible to discern which of the covariates is synchronous and which asynchronous and over which species. In addition, when removing the covariates, both the species-specific intercepts and the dynamics of the two random effects could potentially change. In this case, the level of synchrony inherent in the species could be mis-identified.

The methods outlined in this chapter provide a more flexible and unified way of discerning synchrony in species' responses to certain covariates that only requires a single model to be fitted. The method can also highlight which covariate(s) is (are) synchronous instead of being limited to making sweeping statements about the covariates as a whole.

5.2 The model

We adapt the model developed in Chapter 3 to the multi-species framework outlined by Lahoz-Monfort et al. (2011). The choice to use the model from Chapter 3 over the change-change model of Chapter 4 was taken due to the maximal use of the data under this model. In the case of the latter, the first year of data cannot be used as it is used up in the calculation of the change between years 1 and 2. The framework outlined in the following sections, however, could easily be altered to the change-change approach or an alternative linear predictor as required.

In a multi-species framework, the response variable is y_{sit}, the observed mean of weekly maxima of species s at site i in year t. The model hence becomes

$$y_{sit} \sim Tw\left(\mu_{sit}, \phi, p\right) \tag{5.1}$$

where

$$\log\left(\frac{\mu_{sit}}{\mu_{sit-1}}\right) = \alpha_s + \boldsymbol{x}_i^\top \boldsymbol{\beta}_s + \boldsymbol{v}_{sit}^\top \boldsymbol{\gamma}_s + \widetilde{y}_{sit-1}^\top \boldsymbol{\nu}_s + \epsilon_i + \delta_{si}, \tag{5.2}$$

where

$$\epsilon_i \sim N(0, \sigma_\epsilon^2)$$

and

$$\delta_{si} \sim N(0, \sigma_s^2).$$

That is, we are now modelling the expected mean of weekly maxima of species s at site i in year t as a function of the expected value in year $t-1$, environmental covariates (which may or may not be species-specific) and two independent random effects. In contrast to the previous analyses, the variance not explained by the covariates is now partitioned into two. One of the random effects, ϵ_i, is invariant to species and therefore represents the unexplained variance that is synchronous to all species in the analysis. The δ_{si} random effects are also species-specific in addition to being site-specific and account for extra variation that is specific to species s. As seen from the previous analyses, there is clearly additional variation specific to sites that is not explained by the covariates included in the model. We would expect some of these species, which are subject to similar exogenous environmental factors, to share some of that unexplained variation.

Lahoz-Monfort et al. (2011) maintain the s subscripts on all of the regression covariate parameters (i.e. $\boldsymbol{\beta}$ and $\boldsymbol{\gamma}$ in Equation 5.2) for all species. This means that the model outlined in equations 5.1 and 5.2 is then largely similar to the independent models fitted in Chapter 3, albeit with the variation unexplained by the covariates being partitioned into two. As discussed below, in our modelling approach we allow the data to inform which of these regression parameters should be shared across species and over which species they should be shared. The Tweedie variance parameters are also constrained to be the same across all species. We would expect this to have some effect on the means for each site-year-species combination as it will restrict the mean-variance relationship to be the same for all species, and consequently the regression parameters for each species may subsequently change. Although this effect will be relatively small for species with very similar shaped distributions, larger discrepancies will inevitably arise for species whose mean-variance relationships are significantly different.

Whilst many species with similar ecological requirements will react similarly to the same environmental phenomenon, others will inevitably respond differently. Testing which species respond similarly and to which exogenous factors may be of particular interest for managing conservation practices. For example, if two possible management strategies were proposed there may be concern over detrimental effects on other species. Monitoring how multiple species respond to the same covariates could give an idea of which strategy would be most beneficial overall. Similarly, the effect of invasive species on ecological populations is a current area of interest (e.g. Blackburn et al., 2004; Clavero and García-Berthou, 2005). The adverse effect of any management practice put into place to remove the invasive species on native populations could be monitored using this type of modelling approach. As mentioned above, sharing parameters across species can also lead to greater precision. We therefore extend the methods of Lahoz-Monfort et al. (2011) to account for model uncertainty and allow any combination of species to share regression parameters for any of the covariates of interest. We also test for the effect that assuming species-invariant ϕ and p has, if any, on the regression parameter estimates and corresponding posterior model probabilities.

5.3 Species synchrony in response to covariates

The method of Lahoz-Monfort et al. (2011) outlined above tests for synchrony among species by allowing a portion of the variation not explained by the covariates to be shared across species. In their method, the authors assume that all covariates in the model have a separate regression parameter for each species in the analysis. In estimating separate parameters for each species, there is little potential for considering how species respond similarly to the same measured covariates, other than ad hoc, post-analysis comparisons of parameter estimates. Any synchronous variance explained by the species-specific covariate parameters will also not contribute to the ICC measure of synchrony, potentially reducing the estimate of synchrony for that species. It may also be interesting to group species together in terms of their response to certain ecological phenomena as this can potentially provide greater understanding of the interactions between the species and the environment they inhabit.

The question then arises of how to decide whether or not each regression parameter should be shared between species or estimated separately for each species. In the case of two species and one covariate, this is relatively straight-forward. We could fit two models separately, one with the regression parameter being shared and one with separate parameters for the two species. Model selection criteria (such as DIC) could then be used to quantitatively discriminate between the two models. However, if there is more than one covariate and/or more than two species, the number of possible models increase quickly and it would soon become infeasible to compare models in this way. With more than two species an additional problem arises in that different subsets of the species may be better treated in different ways. For example, given species A, B, C and D, species B and D may respond similarly to a specific covariate, whilst species A and C might both respond differently to B and D and each other. That is $\boldsymbol{\theta} = \{\theta\{A\}, \theta\{B, D\}, \theta\{C\}\}$, where $\theta\{B, D\}$ is the parameter shared across species B and D.

In order to quantitatively discriminate between different models with different subsets of parameters shared across multiple species, we once again consider posterior model probabilities. The reversible jump algorithm used previously in this thesis can provide an easier method for discriminating between these competing models. We develop a method here for utilising the reversible jump algorithm to group species together according to whether or not they respond similarly to each covariate. In particular, we use the general outline for the reversible jump algorithm outlined in Section 2.3.3 and extend it specifically to allow any combinations of species to share parameters for each of the covariates. A similar type of reversible jump algorithm was used by King and Brooks (2002) and King et al. (2010) to discriminate between mark-recapture models with different time dependency groupings.

5.3.1 Reversible jump algorithm for detecting multi-species synchrony

In this section we outline the reversible jump algorithm for detecting species synchrony in response to the environmental covariates. The model is assumed to be that outlined in Equation 5.2. We denote $\theta_j s_1, s_2$ to be the parameter θ_j shared between species 1 and species 2 and n_s to be the number of different species included in the model.

STEP 1. Update model parameters

Suppose that at iteration t the Markov chain is in model m. Update all regression parameters in $\boldsymbol{\theta}_m$ and any additional model parameters using the random walk Metropolis algorithm and $\boldsymbol{\sigma}^2$ parameters via the inverse-gamma Gibbs algorithm, all conditional on model m.

STEP 2. At iteration t, select one of the parameters

Select one of the regression parameters at random, $\boldsymbol{\theta}_j$.

STEP 3. At iteration t, propose to split or merge this parameter

Choose with probability $\frac{1}{2}$ to split a current group or merge two groups of species together which currently share this parameter.

A) If we choose to split a parameter group:

  STEP 4. Choose one of the groups to split

  Suppose in model m there are n^* groups with unique values for this parameter, each containing at least two species. We randomly choose one of these groups denoted $\theta_j\{\boldsymbol{S}_h\}$. If $|n^*| = n_s$, we automatically reject this move and move to iteration $t+1$.

  STEP 5. Choose one of the groups to split

  Of the n^* groups, choose one of these with probability $\frac{1}{n^*}$, denoted $\boldsymbol{S}_h$.

  STEP 6. Split the set into two disjoint groups

  Split the group of species $\boldsymbol{S}_h$ into two disjoint groups $\boldsymbol{S}_{h_1}$ and $\boldsymbol{S}_{h_1}$ (which could be scalars or vectors).

  STEP 7. Propose new parameter values for the two new groups

  Generate a deviate u from a specified zero-mean symmetrcal proposal distribution $q(.)$ (the normal distribution is used here) and set:

$$\boldsymbol{\theta}_j\{S_{h_1}\}' = \boldsymbol{\theta}_j\{S_{h_1}\} + u$$
$$\boldsymbol{\theta}_j\{S_{h_2}\}' = \boldsymbol{\theta}_j\{S_{h_2}\} - u$$

STEP 8. Calculate the acceptance probability

Calculate acceptance probability in $\min(1, A)$, where,

$$A = \frac{\pi(\boldsymbol{\theta}'_m, m'|\boldsymbol{y})p(m|m')}{\pi(\boldsymbol{\theta}_m, m|\boldsymbol{y})p(m'|m)q(u)} \left| \frac{\partial\left(\boldsymbol{\theta}_j\{S_{h_1}\}', \boldsymbol{\theta}_j\{S_{h_2}\}'\right)}{\partial(\boldsymbol{\theta}_j\{S_h\}, u)} \right|,$$

The jacobian is calcualted as follows:

$$\left| \frac{\partial\left(\boldsymbol{\theta}_j\{S_{h_1}\}', \boldsymbol{\theta}_j\{S_{h_2}\}'\right)}{\partial(\boldsymbol{\theta}_j\{S_h\}, u)} \right| = \begin{vmatrix} \frac{\partial\boldsymbol{\theta}_j\{S_{h_1}\}'}{\partial\boldsymbol{\theta}_j\{S_h\}} & \frac{\partial\boldsymbol{\theta}_j\{S_{h_2}\}'}{\partial\boldsymbol{\theta}_j\{S_h\}} \\ \frac{\partial\boldsymbol{\theta}_j\{S_{h_1}\}'}{\partial u} & \frac{\partial\boldsymbol{\theta}_j\{S_{h_2}\}'}{\partial u} \end{vmatrix} = 2,$$

$P(m'|m) = 1/n^* \times 1/\left(2^{|\boldsymbol{S}_h|-1} - 1\right)$ and $P(m|m') = 1/\binom{n^*+1}{2}$.

B) If we choose to merge two parameter groups:

STEP 4. Choose two of the groups to merge

Suppose there are currently n^* groups with unique values for this parameter, we randomly choose two of these groups denoted $\theta_j\{\boldsymbol{S}_{h_1}\}$ and $\theta_j\{\boldsymbol{S}_{h_2}\}$. If $|n^*| = 1$, we automatically reject this move and move to iteration $t+1$.

STEP 5. Propose single parameter value for all species in the two groups

$$\begin{aligned} \boldsymbol{\theta}_j\{S_h\}' &= \left(\boldsymbol{\theta}_j\{S_{h_1}\} + \boldsymbol{\theta}_j\{S_{h_2}\}\right)/2 \\ u &= \left(\boldsymbol{\theta}_j\{S_{h_1}\} - \boldsymbol{\theta}_j\{S_{h_2}\}\right)/2 \end{aligned}$$

and accept with probability $\min(1, A^{-1})$.

STEP 9. Increase t by one and repeat

Increase iteration number to $t+1$ and repeat steps 1-8 as required.

5.3.2 Checking for species interactions

One additional advantage of using multi-species models is the ability to test for interactions *between* the different response/prey species as well as interactions within species to certain covariates. In the preceding section we have outlined a method for testing the synchrony of species' response to environmental covariates but allowing the model to be even more flexible and incorporate additional interactions between species could also highlight potentially interesting ecosystem-level relationships.

Table 5.1: Prior distributions specified on parameters in model 5.1

Parameter	Prior
α_s	$N(0, 10^{-2})$
$\beta_j s$	$N(0, 10^{-2})$
$\gamma_j s$	$N(0, 10^{-2})$
ν_s	$HN(0, 10^{-2})$
κ_s	$N(0, 10^{-2})$
μ_{si0}	$U[0, 200]$
ϕ	$U[0, 5]$
p	$U[1, 2]$
σ^2	$\Gamma^{-1}(10^{-3}, 10^{-3})$

For this model, we choose a subset of the ten prey species which for ecological reasons are considered *a priori* likely to show interactions. We add additional covariates to the model in a similar framework to the density-dependence covariate that is already present. This time, we allow the expected value of species s at site i in year t to depend on the number of the other species in the model observed in the previous year (independently of each other). That is,

$$\log\left(\frac{\mu_{sit}}{\mu_{sit-1}}\right) = \alpha_s + \boldsymbol{x}_i^\top \boldsymbol{\beta}_s + \boldsymbol{v}_{sit}^\top \boldsymbol{\gamma}_s + \sum_{l=1}^{n_s} \widetilde{y}_{lit-1}^\top \nu_{ls} + \epsilon_i + \delta_{si} \tag{5.3}$$

where $\widetilde{y}_{sit-1}$ is the annual mean of species s at site i in year $t-1$. $\boldsymbol{\nu}$ is a $(n_s \times n_s)$ matrix, with entries $\nu_{k,l}$ being the effect of species k on species l. $\nu k, k$ corresponds to the density-dependence parameter ν in species k as included in previous models. The reversible jump algorithm can then be implemented as before to obtain posterior model probabilities for the model with and without each of the inter- and intra-secific interactions. Whilst density-dependence is assumed to be a negative effect, we allow the interactions to be either positive or negative. Prior distributions specified on all parameters in the models fitted in this chapter can be found in Table 5.1. Most are the same as those specified in previous chapters but are included here again for reference.

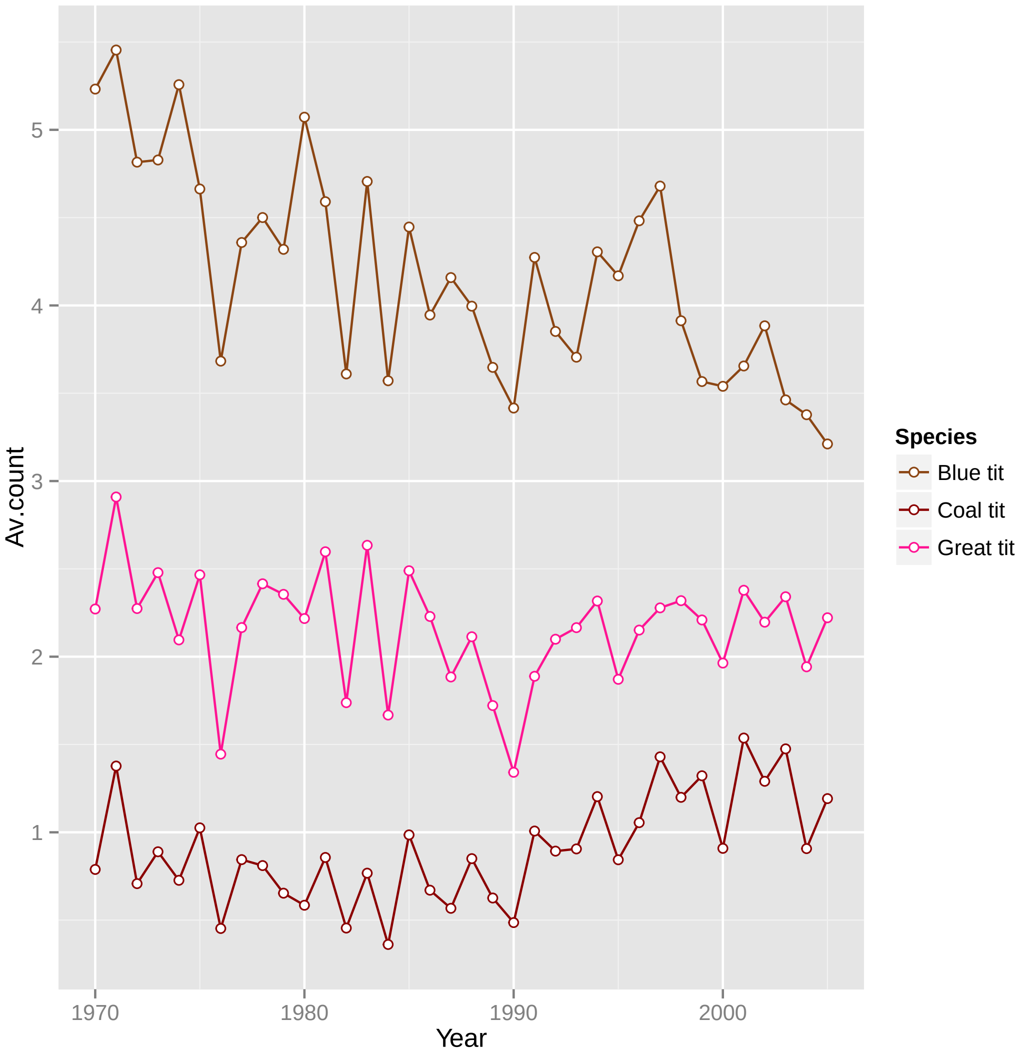


Figure 5.1: Averaged annual trends across all sites for the three tit species between 1970/71 and 2005/06. Note the coincidental peaks and troughs across all three species.

5.4 Results

For illustration purposes, we concentrate on three of the ten prey species analysed in the previous chapters. In order to maximise the likelihood of finding some degree of synchrony, we choose the three species blue tit, great tit and coal tit, as they are closely-related members of the same family and would therefore be expected to share similar traits in relationship to many ecological factors. From Figures 1.3 and 5.1, we can see the annual trends shown by these three species are very similar across time, with peaks and troughs appearing to occur in similar years. The shape of the empirical distributions are also very similar, albeit with shifts in the means of each species (Figure 1.6). Even from this generalised perspective, there visually appears to be similarities between these species. As they seem to show similar trends and are subject to similar environmental factors, some degree of synchrony would be expected across these three species. However, the results presented in Tables 3.5 and 3.7 suggest that they show differing relationships with some of the covariates included in these models. As such, they provide an ideal group for testing for both synchrony and asynchrony of various types between them by fitting different multi-species models with varying complexity and flexibility.

For all analyses presented in this chapter, 100,000 iterations were run with the first 50,000 discarded as burn-in, giving a posterior sample of size 50,000 for each model fitted. From visual checking of trace plots this appeared to be a conservative choice of burn-in.

We gradually increase the complexity and flexibility of the model to see how certain restrictions can affect the parameters and whether the added computational demand required for each level of the modelling framework is worthwhile. In addition to the results presented for the three tit species presented in this chapter, additional results from other combinations of species and models can be found in the Appendix.

Table 5.2: Blue tit, great tit and coal tit multi-species model. This model includes species-specific intercepts but no environmental covariates. Posterior means and 95% symmetrical credible intervals are given for each model parameter. Intra-class correlation coefficients measure the ratio of species-invariant to species-specific variation.

Parameter	Covariate	Posterior mean	95%CI
$\alpha\{bt\}$	Intercept	-0.0371	(-0.0425,-0.0322)
$\alpha\{gt\}$	Intercept	-0.0272	(-0.0335,-0.0224)
$\alpha\{ct\}$	Intercept	-0.0393	(-0.0498,-0.0290)
$\nu\{bt\}$	Dens dep	**-0.0169**	(-0.0202,-0.0139)
$\nu\{gt\}$	Dens dep	**-0.0231**	(-0.0271,-0.0194)
$\nu\{ct\}$	Dens dep	**-0.0364**	(-0.0436,-0.0298)
ϕ	-	0.2464	(0.2415,0.2514)
p	-	1.2134	(1.2066,1.2207)
σ^2_ϵ	-	0.0038	(0.0033,0.0045)
σ^2_{bt}	-	0.0004	(0.0003,0.0006)
σ^2_{gt}	-	0.0003	(0.0002,0.0005)
σ^2_{ct}	-	0.0077	(0.0062,0.0094)
ICC_{bt}	-	0.905	(0.863,0.939)
ICC_{gt}	-	0.928	(0.885,0.960)
ICC_{ct}	-	0.333	(0.275,0.399)

Table 5.3: Blue tit, great tit and coal tit multi-species model. Intercept and density dependence are species-specific, with additional environmental covariate parameters being species-invariant. Posterior means and 95% symmetric credible intervals (conditional on the parameter being in the model) are given with marginal posterior probabilities relating to the proportion of iterations the parameter is in the model where appropriate. Significant covariates are highlighted in bold.

Parameter	Covariate	Posterior mean	MPP	95%CI
$\alpha\{bt\}$	Intercept	-0.0360	-	(-0.0404,-0.0311)
$\alpha\{gt\}$	Intercept	-0.0276	-	(-0.0325,-0.0221)
$\alpha\{ct\}$	Intercept	-0.0399	-	(-0.0498,-0.0303)
β_1	Northing	0.0016	0.5970	(-0.0041,0.0075)
β_2	Easting	**-0.0044**	0.7784	(-0.0103,0.0014)
β_3	Sub/rur	**-0.0153**	1.0000	(-0.0213,-0.0094)
$\nu\{bt\}$	Dens dep	**-0.0213**	1.0000	(-0.0245,-0.0180)
$\nu\{gt\}$	Dens dep	**-0.0262**	1.0000	(-0.0296,-0.0227)
$\nu\{ct\}$	Dens dep	**-0.0381**	1.0000	(-0.0456,-0.0313)
γ_1	Sparrowhawk	NA	0.0000	NA
γ_2	Collared dove	NA	0.0000	NA
γ_3	Ground frost	NA	0.0000	NA
ϕ	-	0.2472	-	(0.2420,0.2526)
p	-	1.2146	-	(1.2075,1.2217)
σ^2_ϵ	-	0.0038	-	(0.0032,0.0045)
σ^2_{bt}	-	0.0004	-	(0.0002,0.0006)
σ^2_{gt}	-	0.0003	-	(0.0002,0.0005)
σ^2_{ct}	-	0.0067	-	(0.0049,0.0088)
ICC_{bt}	-	0.911		(0.864,0.953)
ICC_{gt}	-	0.919		(0.876,0.953)
ICC_{ct}	-	0.365		(0.291,0.448)

5.4.1 Species-invariant covariate parameters

The first model fitted was a multi-species model with no covariates and species-specific intercepts (Table 5.2). This is a highly simplistic model and of little interest on its own, however it will prove useful for later comparisons with other more complex models. Secondly, we add covariates to the model but with species-invariant regression parameters (except the intercept). The results from this analysis can be found in Table 5.3. In this case, the model is averaging the effect of the covariates across species. When opposing parameter estimates were found in individual in the independent models, the multi-species model is failing to find any overall effect for these covariates. For example, choosing the sparrowhawk covariate, blue tit, great tit and coal tit showed significant negative, non-significant and significant positive relationships respectively in the independent models. Overall, across the three species, it is therefore not surprising that no significant effect is found in this model when assuming the same regression coefficients for all species.

Clearly this model is still a highly simplistic model where potential discrepancies between combinations of species in response to a particular covariate are not accounted for. Some of the regression covariate parameters that were estimated as being quite different in the independent models, and should hence be species-specific, are averaged over. Presumably in this case, the species-specific variance for that species will become inflated to counteract this. This was particularly a problem for the collared dove and sparrowhawk covariates as between model mixing was poor. Once these covariates were removed from the model, in this case during the burn-in period, no non-zero values for these parameters were accepted, that is the covariate never re-entered the model. Various adjustments to the proposal distribution parameters were made, however no improvements in these between model moves were observed. Intuitively, in this scenario, if a parameter value is proposed and may be consistent with the data generating process for one species, it may be a completely unrealistic parameter value for one or more of the other species. Once the covariate has been removed from the model, the species random effects will take account of unexplained variation that this covariate may explain and hence may make it difficult for the parameter to re-enter the model. A similar problem to this is discussed in relation to hierarchical centring by Oedekoven et al. (2014) and is discussed in Section 2.4.1.

The ICC coefficients were also calculated for this model. For blue tit and great tit the posterior means were very close to one (0.91 in both cases) suggesting that most of the unexplained variation for these species is synchronous with the other species. Coal tit, however, had much more species-specific unexplained variation indicated by an ICC closer to zero (posterior mean of 0.37). This suggests that for this species there may be additional environmental factors affecting the numbers visiting garden feeding stations.

This model is only really appropriate if we are interested in inferring the overall effect of a particular covariate on the ecosystem or species group as a whole. In most scenarios, this will be too general and has the potential to miss many of the effects that are present or over-exaggerate the extent of some when they are present.

Table 5.4: Blue tit, great tit and coal tit multi-species model. All regression covariate parameters are always species-specific and updated independently for each species. Posterior means and symmetric 95% credible intervals are given. Covariate dependence is conducted using the reversible jump algorithm for the density-dependence parameter only.

Parameter	Covariate	Posterior mean	95%CI
$\alpha\{bt\}$	Intercept	-0.0334	(-0.0397,-0.0274)
$\alpha\{gt\}$	Intercept	-0.0274	(-0.0320,-0.0207)
$\alpha\{ct\}$	Intercept	-0.0439	(-0.0558,-0.0325)
$\beta_1\{bt\}$	Northing	-0.0077	(-0.0135,-0.0012)
$\beta_1\{gt\}$	Northing	-0.0060	(-0.0117,0.0002)
$\beta_1\{ct\}$	Northing	0.0136	(0.0017,0.0261)
$\beta_2\{bt\}$	Easting	-0.0115	(-0.0185,-0.0042)
$\beta_2\{gt\}$	Easting	-0.0070	(-0.0152,0.0004)
$\beta_2\{ct\}$	Easting	-0.0309	(-0.0431,-0.0185)
$\beta_3\{bt\}$	Sub/rur	-0.0170	(-0.0226,-0.0108)
$\beta_3\{gt\}$	Sub/rur	-0.0191	(-0.0261,-0.0121)
$\beta_3\{ct\}$	Sub/rur	-0.0109	(-0.0215,-0.0002)
$\nu\{bt\}$	Dens dep	**-0.0262**	(-0.0304,-0.0221)
$\nu\{gt\}$	Dens dep	**-0.0305**	(-0.0344,-0.0266)
$\nu\{ct\}$	Dens dep	**-0.0511**	(-0.0600,-0.0266)
$\gamma_1\{bt\}$	Sparrowhawk	-0.0053	(-0.0096,-0.0008)
$\gamma_1\{gt\}$	Sparrowhawk	-0.0019	(-0.0006,0.0034)
$\gamma_1\{ct\}$	Sparrowhawk	0.0263	(0.0183,0.0344)
$\gamma_2\{bt\}$	Collared dove	-0.0010	(-0.0047,0.002)
$\gamma_2\{gt\}$	Collared dove	0.0005	(-0.0042,0.0052)
$\gamma_2\{ct\}$	Collared dove	0.0122	(0.0037,0.0211)
$\gamma_3\{bt\}$	Ground frost	0.0166	(0.0118,0.0218)
$\gamma_3\{gt\}$	Ground frost	0.0098	(0.0038,0.0167)
$\gamma_3\{ct\}$	Ground frost	0.0058	(-0.0062,0.0177)
ϕ	-	0.2434	(0.2384,0.2487)
p	-	1.2114	(1.2046,1.2184)
σ^2_ϵ	-	0.0043	(0.0035,0.0053)
σ^2_{bt}	-	0.0004	(0.0002,0.0006)
σ^2_{gt}	-	0.0004	(0.0002,0.0007)
σ^2_{ct}	-	0.0086	(0.0066,0.0108)
ICC_{bt}	-	0.909	(0.860,0.951)
ICC_{gt}	-	0.912	(0.846,0.956)
ICC_{ct}	-	0.337	(0.264,0.423)
C_δ	-	-0.167	(-0.456,0.084)
C_{bt}	-	0.018	(-0.797,0.537)
C_{gt}	-	-0.362	(-1.733,0.447)
C_{ct}	-	-0.101	(-0.485,0.201)

Table 5.5: Blue tit, great tit and coal tit multi-species model. Intercept and density-dependence parameters are species-specific, with the reversible jump algorithm used to test for synchrony across the three species for all other regression covariate parameters. Posterior means and 95% symmetric credible intervals are presented. Covariate dependence is also conducted on the density-dependence parameters.

Parameter	Covariate	Posterior mean	95%CI
$\alpha\{bt\}$	Intercept	-0.0343	(-0.0410,-0.0269)
$\alpha\{gt\}$	Intercept	-0.0273	(-0.0335,-0.0202)
$\alpha\{ct\}$	Intercept	-0.0419	(-0.0524,-0.0320)
$\beta_1\{bt\}$	Northing	-0.0075	(-0.0142,-0.0003)
$\beta_1\{gt\}$	Northing	-0.0078	(-0.0140,-0.0009)
$\beta_1\{ct\}$	Northing	0.0022	(-0.0122,0.0207)
$\beta_2\{bt\}$	Easting	-0.0096	(-0.0161,-0.0028)
$\beta_2\{gt\}$	Easting	-0.0096	(-0.0161,-0.0028)
$\beta_2\{ct\}$	Easting	-0.0358	(-0.0506,-0.0220)
$\beta_3\{bt\}$	Sub/rur	-0.0160	(-0.0227,-0.0090)
$\beta_3\{gt\}$	Sub/rur	-0.0158	(-0.0229,-0.0079)
$\beta_3\{ct\}$	Sub/rur	-0.0128	(-0.0215,-0.0011)
$\nu\{bt\}$	Dens dep	**-0.0249**	(-0.0282,-0.0213)
$\nu\{gt\}$	Dens dep	**-0.0287**	(-0.0325,-0.0249)
$\nu\{ct\}$	Dens dep	**-0.0443**	(-0.0493,-0.0368)
$\gamma_1\{bt\}$	Sparrowhawk	-0.0020	(-0.0067,0.0025)
$\gamma_1\{gt\}$	Sparrowhawk	-0.0015	(-0.0066,0.0035)
$\gamma_1\{ct\}$	Sparrowhawk	0.0209	(0.0131,0.0283)
$\gamma_2\{bt\}$	Collared dove	-0.0022	(-0.0054,0.0014)
$\gamma_2\{gt\}$	Collared dove	- 0.0022	(-0.0054,0.0014)
$\gamma_2\{ct\}$	Collared dove	0.0136	(0.0057,0.0211)
$\gamma_3\{bt\}$	Ground frost	0.0167	(0.0120,0.0221)
$\gamma_3\{gt\}$	Ground frost	0.0138	(0.0091,0.0192)
$\gamma_3\{ct\}$	Ground frost	0.0140	(0.0091,0.0197)
ϕ	-	0.2437	(0.2385,0.2489)
p	-	1.2112	(1.2044,1.2183)
σ^2_ϵ	-	0.0046	(0.0040,0.0053)
σ^2_{bt}	-	0.0004	(0.0002,0.0007)
σ^2_{gt}	-	0.0003	(0.0002,0.0005)
σ^2_{ct}	-	0.0066	(0.0051,0.0085)
ICC$_{bt}$	-	0.919	(0.873,0.937)
ICC$_{gt}$	-	0.935	(0.895,0.950)
ICC$_{ct}$	-	0.414	(0.341,0.445)

Table 5.6: Marginal posterior probabilities for the sharing of the time-invariant covariate parameters $\boldsymbol{\beta}$ from the model in Table 5.5, corresponding to the time-invariant covariates. $\beta_1\{bt, gt\}$, for example, corresponds to the model where the easting coefficient is shared between blue tit and great tit.

Northing		Easting		Sub/rur	
Model	MPP	Model	MPP	Model	MPP
$\beta_1\{bt, gt\}, \beta_1\{ct\}$	0.493	$\beta_2\{bt, gt\}, \beta_2\{ct\}$	0.988	$\beta_3\{gt, ct\}, \beta_3\{bt\}$	0.566
$\beta_1\{gt, ct\}, \beta_1\{bt\}$	0.397	$\beta_2\{bt\}\beta_2\{gt\}, \beta_2\{ct\}$	0.012	$\beta_3\{bt, gt\}, \beta_3\{ct\}$	0.388
$\beta_1\{bt, ct\}, \beta_1\{gt\}$	0.103			$\beta_3\{bt, ct\}, \beta_3\{gt\}$	0.044
$\beta_1\{bt\}, \beta_1\{gt\}, \beta_1\{ct\}$	0.007			$\beta_3\{bt\}, \beta_3\{gt\}, \beta_3\{ct\}$	0.003

Table 5.7: Marginal posterior probabilities for from the model in Table 5.5, corresponding to the time-varying covariates $\boldsymbol{\gamma}$. $\gamma_1\{bt, gt\}$, for example, corresponds to the model where the sparrowhawk coefficient is shared between blue tit and great tit.

Sparrowhawk		Collared Dove		Ground frost	
Model	MPP	Model	MPP	Model	MPP
$\gamma_1\{bt, gt\}, \gamma_1\{ct\}$	0.892	$\gamma_2\{bt, gt\}, \gamma_2\{ct\}$	0.989	$\gamma_3\{gt, ct\}, \gamma_3\{bt\}$	0.902
$\gamma_1\{bt\}, \gamma_1\{gt\}, \gamma_1\{ct\}$	0.108	$\gamma_2\{bt\}, \gamma_2\{gt\}, \gamma_2\{ct\}$	0.011	$\gamma_3\{bt, ct\}, \gamma_3\{gt\}$	0.097
				$\gamma_3\{bt\}, \gamma_3\{gt\}, \gamma_3\{ct\}$	0.001

5.4.2 Species-specific covariate parameters

Next, we remove the assumption of constant regression covariate parameters across all species, allowing them to vary depending on the species. Firstly, parameters are estimated independently for each species (Table 5.4), then we use the reversible jump algorithm outlined in Section 5.3 to quantitatively discriminate between which groups of species have similar responses to each of six of the regression covariates (Tables 5.5-5.7). The marginal posterior probabilities for the parameters associated with density dependence were equal to one for all species in both the model with and without the reversible jump algorithm for shared covariates.

In the case of the former model, the model is largely similar to the independent models from Chapter 3. The differences here are that the unexplained variation is being split into two and the Tweedie parameters are shared across all three species. The relatively good agreement between the regression parameter estimates in this framework and the independent models are representative of this. The Tweedie variance parameters are assumed to be constant across species and as mentioned for the parameters in Section 5.4.1 the estimate is roughly the average of the individual estimates from

Chapter 3. We also calculate the C coefficients representing the contribution of the covariates to the two variance components. Interestingly here, negative estimates are obtained for three of the four coefficients. The credible intervals for these coefficients do all contain zero. Lahoz-Monfort et al. (2011) and Lahoz-Monfort et al. (2013) only quote the coefficeints evaluated at the posterior means of the random effect variances and fail to account for the fact that they themselves have a distribution in a Bayesian framework. This suggests that adding covariates changes the dynamics of the model beyond the level of the means. The estimates of the intercepts and the Tweedie parameters are slightly different under both models, and hencethis highlights the problem of using the comparatively simplistic approach to detecting synchrony in response to covariates. Fixing the parameters at the posterior means from Table 5.2 and rerunning the model gave more consistent estimates. The 95% credible interval for the coal tit coefficient does span zero, however the others, although not vastly far from zero, do not contain zero. This may indicate one of the problems with the framework outlined by Lahoz-Monfort et al. (2011) in that when a more flexible class of distributions such as Tweedie was used, merely adding and removing covariates may not be an ideal way of measuring covariate contributions. When adding covariates to the model, the dynamics of the model changed as did the estimates for ϕ, p and the species-specific intercepts. With such a flexible family of distributions as the Tweedie family, adding or removing covariates appears to change the dynamics of the whole model.

Tables 5.6 and 5.7 show the posterior model probabilities corresponding to each of the regression parameters and give an indication of whether or not the given parameter should be shared across multiple species. In the case of the time-invariant covariates, there is strong posterior support for a synchronous effect for all three parameters across blue tit and great tit, with coal tit showing distinct relationships with these covariates. This is also observed in the independent models with parameters being fairly similar for the first two species and different for the third in each case. When considering the time-varying covariates, the model with highest posterior probability was the one with shared parameters for great tit and coal tit in relation to sparrowhawk and ground frost but shared across blue tit and great tit in relation to collared dove. This once again agrees well with the independent models.

The ICC coefficients are largely similar to the previous analyses, suggesting that even with the covariates added, there is still additional variation for coal tit which is not attributable to any of the covariates included in this model.

Table 5.8: Blue tit, great tit and coal tit multi-species model. All regression covariate parameters are species-specific with the reversible jump algorithm used to test for synchrony across species. Interactions between the response species are also included in the model but none of the interaction parameters had posterior support so are omitted for brevity.

Parameter	Covariate	Posterior mean	95%CI
$\alpha\{bt\}$	Intercept	-0.0362	(-0.0427,-0.0300)
$\alpha\{gt\}$	Intercept	-0.0278	(-0.0342,-0.0209)
$\alpha\{ct\}$	Intercept	-0.0422	(-0.0541,-0.0307)
$\beta_1\{bt\}$	Northing	-0.0052	(-0.0124,0.0011)
$\beta_1\{gt\}$	Northing	-0.0053	(-0.0124,0.0011)
$\beta_1\{ct\}$	Northing	0.0080	(-0.0041,0.0194)
$\beta_2\{bt\}$	Easting	-0.0073	(-0.0132,-0.0017)
$\beta_2\{gt\}$	Easting	-0.0073	(-0.0132,-0.0017)
$\beta_2\{ct\}$	Easting	-0.0332	(-0.0442,-0.0223)
$\beta_3\{bt\}$	Sub/rur	-0.0123	(-0.0198,-0.0063)
$\beta_3\{gt\}$	Sub/rur	-0.0126	(-0.0197,-0.0069)
$\beta_3\{ct\}$	Sub/rur	-0.0097	(-0.0197,0.0031)
$\nu\{bt\}$	Dens dep	**-0.0221**	(-0.0259,-0.0183)
$\nu\{gt\}$	Dens dep	**-0.0255**	(-0.0297,-0.0215)
$\nu\{ct\}$	Dens dep	**-0.0460**	(-0.0536,-0.0390)
$\gamma_1\{bt\}$	Sparrowhawk	-0.0032	(-0.0073,0.0008)
$\gamma_1\{gt\}$	Sparrowhawk	-0.0030	(-0.0073,0.0011)
$\gamma_1\{ct\}$	Sparrowhawk	0.0220	(0.0137,0.0305)
$\gamma_2\{bt\}$	Collared dove	-0.0015	(-0.0049,0.0017)
$\gamma_2\{gt\}$	Collared dove	-0.0015	(-0.0049,0.0017)
$\gamma_2\{ct\}$	Collared dove	0.0135	(0.0052,0.0215)
$\gamma_3\{bt\}$	Ground frost	0.0149	(0.0097,0.0198)
$\gamma_3\{gt\}$	Ground frost	0.0093	(0.0040,0.0141)
$\gamma_3\{ct\}$	Ground frost	0.0093	(0.0040,0.0141)
ϕ	-	0.2443	(0.2394,0.2495)
p	-	1.2120	(1.2050,1.2189)
σ^2_ϵ	-	0.0041	(0.0034,0.0048)
σ^2_{bt}	-	0.0003	(0.0001,0.0005)
σ^2_{gt}	-	0.0003	(0.0002,0.0005)
σ^2_{ct}	-	0.0075	(0.0058,0.0097)
ICC_{bt}	-	0.929	(0.892,0.966)
ICC_{gt}	-	0.928	(0.886,0.962)
ICC_{ct}	-	0.353	(0.280,0.428)

Table 5.9: Density-dependence and interaction coeffcients marginal posterior probabilities for the model from Table 5.8, corresponding to the proportion of iterations where the parameter is included in the model.

	Blue tit	Great tit	Coal tit
Blue tit	1.0000	0.0000	0.0000
Great tit	0.0000	1.0000	0.0000
Coal tit	0.0000	0.0000	1.0000

Table 5.10: Marginal posterior probabilities for the sharing of the time-invariant covariate parameters $\boldsymbol{\beta}$ from the model in Table 5.9, corresponding to the time-invariant covariates. $\beta_1\{bt, gt\}$, for example, corresponds to the model where the easting coefficient is shared between blue tit and great tit.

Northing		Easting		Sub/rur	
Model	MPP	Model	MPP	Model	MPP
$\beta_1\{bt, gt\}, \beta_1\{ct\}$	0.995	$\beta_2\{bt, gt\}, \beta_2\{ct\}$	0.962	$\beta_3\{gt, ct\}, \beta_3\{bt\}$	0.543
$\beta_1\{bt\}, \beta_1\{gt\}, \beta_1\{ct\}$	0.005	$\beta_2\{bt, ct\}, \beta_2\{gt\}$	0.027	$\beta_3\{bt, gt\}, \beta_3\{ct\}$	0.453
		$\beta_2\{bt\}, \beta_2\{gt\}, \beta_2\{ct\}$	0.011	$\beta_3\{bt\}, \beta_3\{gt\}, \beta_3\{ct\}$	0.004

Table 5.11: Marginal posterior probabilities for from the model in Table 5.9, corresponding to the time-varying covariates $\boldsymbol{\gamma}$. $\gamma_1\{bt, gt\}$, for example, corresponds to the model where the sparrowhawk coefficient is shared between blue tit and great tit.

Sparrowhawk		Collared Dove		Ground frost	
Model	MPP	Model	MPP	Model	MPP
$\gamma_1\{bt, gt\}, \gamma_1\{ct\}$	0.956	$\gamma_2\{bt, gt\}, \gamma_2\{ct\}$	0.996	$\gamma_3\{gt, ct\}, \gamma_3\{bt\}$	0.998
$\gamma_1\{bt\}, \gamma_1\{gt\}, \gamma_1\{ct\}$	0.044	$\gamma_2\{bt\}, \gamma_2\{gt\}, \gamma_2\{ct\}$	0.004	$\gamma_3\{bt\}, \gamma_3\{gt\}, \gamma_3\{ct\}$	0.002

5.4.3 Multi-species interactions

The next model fitted added multi-species interactions as discussed in Section 5.2. Similar to density dependence in previous analyses, we use the reversible jump algorithm to test all two-way interactions between the three species. Density dependence remains in the model as an intra-specific interaction. Parameters associated with the inter-species interactions are allowed to be positive or negative.

Results from this more flexible analysis are presented in Tables 5.8-5.11. Posterior means were similar to the previous analysis, as were the posterior model probabilities for shared regression parameters. Density dependence was significant for all three species with posterior probabilities of 1 and credible intervals well away from zero. There was no evidence for inter-specific interactions, however, with this combination of species. Due to the interaction covariates never being in the linear predictor, the model is equivalent in this case to that in the previous section; however with different species this would not necesarrily be the case (see the Appendix). Marginal posterior probabilities were zero for all pairwise interactions. A lot of time was spent trying to adjust the proposal densities of the reversible jump algorithm for these parameters to ensure that different models were visited, however it seems that once density dependence (i.e. intra-specific interactions) have been accounted for, there is little additional variation that can be explained by interactions with any other species. This is probably due to the fact that the numbers of these species visiting each site are likely to be highly correlated and hence it is unlikely that other species will be able to explain any additional variation not accounted for by the number of conspecifics. As these species were chosen specifically because they have similar ecological requirements, the model seems unable to discern between interactions with other species and interactions within that species. As interactions with conspecifics are likely to be stronger in general than those between different species it is positive that the model is prioritising these interactions over inter-specific ones. Interpretation of these probabilities should therefore be made conditional on this.

Haftorn (1993) studied inter-specific relationships between tit species in Norway and found that the following relationship existed in the dominance structure for the three species analysed here:

$$\text{Great tit} > \text{blue tit} > \text{coal tit}$$

In modelling these species, our model fails to find any dominance structure other than that within species. An additional model was fitted with alternative species groups and can be found in the Appendix. For these species, namely house sparrow, greenfinch and chaffinch, interactions were found between some of these species (Table A.16). This shows that it is possible to find interactions between species, but the model more readily finds interactions when the species trends are different as intra-specific interactions are then sufficiently distinct. This highlights the care needed when interpreting these interactions.

The posterior model probabilities relating to the environmental covariate parameters showed some differences under this model formulation. For northing and easting, the shared blue tit-great tit parameter once again dominated, but the suburban or rural parameter showed much more posterior uncertainty with all three pairwise combinations having greater than 20% posterior mass. For the time-varying covariates, further differences were observed. For sparrowhawk, most of the posterior support was for the model where blue tit and great tit shared a parameter in contrast to the previous model where great tit and coal tit shared a parameter. From the independent models, the sparrowhawk parameter estimate for great tit was roughly half way between the one for blue tit and the one for coal tit. In the multi-species model this coefficient is shared across the blue tit and great tit and rouhgly the average of the two coefficients from the independent model. It is perhaps a little surprising that there is little support for the model with distinct parameters for all three species.

The posterior model probabilities associated with the collared dove covariate were very consistent with the previous model without interactions. Ground frost continued to show positive support for a shared great tit-coal tit parameter, although the highest probability was now associated with the model with shared blue tit and great tit parameter. The differences between the estimates for this parameter under the independent models were relatively small compared to other parameters so uncertainty in the posterior probabilities is not altogether surprising.

Allowing the covariate parameters to be either species-specific or not had a small effect on the ICC values. Unsurprisingly, all three values increased when compared to some of the more simplistic model formulations, suggesting that when inter-specific differences are taken into consideration, the species-specific random effects reduce in magnitude.

Table 5.12: Blue tit, great tit and coal tit multi-species model. All covariate parameters are species-specific as are the Tweedie regression parameters. Synchrony across the species is tested for each of these parameters. None of the interaction parameters had posterior support so are again omitted for brevity.

Parameter	Covariate	Posterior mean	95%CI
α_{bt}	Intercept	-0.0352	(-0.0414,-0.0284)
α_{gt}	Intercept	-0.0269	(-0.0326,-0.0202)
α_{ct}	Intercept	-0.0477	(-0.0575,-0.0378)
$\beta_1\{bt\}$	Northing	-0.0102	(-0.0177,-0.0039)
$\beta_1\{gt\}$	Northing	-0.0102	(-0.0176,-0.0039)
$\beta_1\{ct\}$	Northing	0.0076	(-0.0026,0.0180)
$\beta_2\{bt\}$	Easting	-0.0080	(-0.0143,-0.0009)
$\beta_2\{gt\}$	Easting	-0.0080	(-0.0142,-0.0009)
$\beta_2\{ct\}$	Easting	-0.0275	(-0.0375,-0.0172)
$\beta_3\{bt\}$	Sub/rur	-0.0155	(-0.0209,-0.0101)
$\beta_3\{gt\}$	Sub/rur	-0.0169	(-0.0228,-0.0114)
$\beta_3\{ct\}$	Sub/rur	-0.0133	(-0.0200,-0.0038)
ν_{bt}	Dens dep	**-0.0260**	(-0.0298,-0.0221)
ν_{gt}	Dens dep	**-0.0298**	(-0.0339,-0.0260)
ν_{ct}	Dens dep	**-0.0333**	(-0.0404,-0.0464)
$\gamma_1\{bt\}$	Sparrowhawk	-0.0032	(-0.0073,0.0010)
$\gamma_1\{gt\}$	Sparrowhawk	-0.0030	(-0.0070,0.0012)
$\gamma_1\{ct\}$	Sparrowhawk	0.0170	(0.0088,0.0255)
$\gamma_2\{bt\}$	Collared dove	-0.0005	(-0.0042,0.0033)
$\gamma_2\{gt\}$	Collared dove	-0.0004	(-0.0042,0.0034)
$\gamma_2\{ct\}$	Collared dove	0.0160	(0.0082,0.0238)
$\gamma_3\{bt\}$	Ground frost	0.0185	(0.0133,0.0238)
$\gamma_3\{gt\}$	Ground frost	0.0126	(0.0074,0.0183)
$\gamma_3\{ct\}$	Ground frost	0.0134	(0.0073,0.0197)
$\phi\{bt\}$	-	0.1654	(0.1567,0.1749)
$\phi\{gt\}$	-	0.1985	(0.1912,0.2060)
$\phi\{ct\}$	-	0.3439	(0.3298,0.3584)
$p\{bt\}$	-	1.4469	(1.4106,1.4814)
$p\{gt\}$	-	1.1797	(1.1656,1.1938)
$p\{ct\}$	-	1.2714	(1.2595,1.2831)
σ^2_ϵ	-	0.0043	(0.0036,0.0051)
σ^2_{bt}	-	0.0005	(0.0003,0.0007)
σ^2_{gt}	-	0.0004	(0.0002,0.0007)
σ^2_{ct}	-	0.0049	(0.0032,0.0059)
ICC_{bt}	-	0.903	(0.852,0.947)
ICC_{gt}	-	0.912	(0.857,0.957)
ICC_{ct}	-	0.494	(0.411,0.591)

Table 5.13: $\boldsymbol{\beta}_s$ marginal posterior probabilities testing for synchrony in response to environmental covariates from the model in Table 5.12, corresponding to northing easting, and suburban/rural respectively.

Northing		Easting		Sub/rur	
Model	MPP	Model	MPP	Model	MPP
$\beta_1\{bt, gt\}, \beta_1\{ct\}$	0.931	$\beta_2\{bt, gt\}, \beta_2\{ct\}$	0.979	$\beta_3\{bt, ct\}, \beta_3\{gt\}$	0.892
$\beta_1\{bt, ct\}, \beta_1\{gt\}$	0.041	$\beta_2\{bt\}, \beta_2\{gt\}, \beta_2\{ct\}$	0.021	$\beta_3\{gt, ct\}, \beta_3\{bt\}$	0.107
$\beta_1\{bt\}, \beta_1\{gt\}, \beta_1\{ct\}$	0.028			$\beta_3\{bt\}, \beta_3\{gt\}, \beta_3\{ct\}$	0.001

Table 5.14: $\boldsymbol{\gamma}_s$ marginal posterior probabilities testing for synchrony in response to environmental covariates from the model in Table 5.12, corresponding to sparrowhawk collared dove and ground frost respectively.

Sparrowhawk		Collared dove		Ground frost	
Model	MPP	Model	MPP	Model	MPP
$\gamma_1\{bt, gt\}, \gamma_1\{ct\}$	0.968	$\gamma_2\{bt, gt\}, \gamma_2\{ct\}$	0.997	$\gamma_3\{gt, ct\}, \gamma_3\{bt\}$	0.994
$\gamma_1\{bt\}, \gamma_1\{gt\}, \gamma_1\{ct\}$	0.032	$\gamma_2\{bt\}, \gamma_2\{gt\}, \gamma_2\{ct\}$	0.003	$\gamma_3\{bt, ct\}, \gamma_3\{gt\}$	0.006

Table 5.15: Marginal posterior probabilities relating to the sharing of the two Tweedie variance parameters across tit species from the model in Table 5.12.

ϕ		p	
Model	MPP	Model	MPP
$\phi\{bt\}, \phi\{gt\}, \phi\{ct\}$	1.0000	$p\{bt\}, p\{gt\}, p\{ct\}$	1.0000

5.4.4 Extending model space to incorporate species-specific distributions

So far, we have assumed that the Tweedie distributions for the species in the multi-species model share the same values of ϕ and p. That is, given a species-specific mean, the mean-variance relationship is constant across species. Whilst this may be a realistic assumption in some situations, relaxing this assumption may be a more realsitic assumption for others. Model selection is also able to provide evidence of whether the values are the same or not. Restricting the two Tweedie variance parameters to be constant across species may have similar effects on the other parameters as mentioned in the previous sections. The reversible jump framework outlined in Section 5.3 can easily be applied to group together species whose Tweedie parameters ϕ and p are similar and separate out those that are different. In using this methodology and relaxing the assumption that the Tweedie parameters must be the same for each species, the models become once more similar to the single-species models, with the added interactions and random effects. The overall effect on the results will depend largely on how similar the distributions are for the species being modelled. The decision over whether making the Tweedie parameters constant across species will also depend somewhat on whether the data-generating process is considered to be a single process with each species allowed to have a different mean or whether the processes are allowed to act independently of each other.

The results from this analysis are presented in Tables 5.12-5.15. Again posterior distributions were similar for the model parameters with small differences observed in the posterior model probabilities. All coefficients aside from the one associated with the suburban or rural covariate were largely consistent with the previous models. For the latter coefficient, there was differences in which species were grouped together when the species-specific shapes of the distributions are accounted for. Evidently there is some sensitivity with regards to this parameter, possibly due to the smaller range of values that the covariate can take. The time invariant covariates were similar for sparrowhawk and collared dove but quite different for ground frost. This may stem from the differences observed in the northing parameter as the two covariates will inevitably be correlated.

Allowing a different mean-variance relationship also had a positive effect on the proportion of remaining synchrony in unexplained variation for coal tit. Clearly the differing shape of the distribution for this species, when accounted for, allows a greater amount of species-specific differences in variation to be directly accounted for.

Table 5.16: Proportion of overlap of 95% credible intervals from the independent analyses from Chapter 3 (Table 3.6) for each pairwise combination of species. The negative values indicate distinct intervals for each of that pairwise species comparison. Bold values relate to the species pair with the highest posterior model probability for that covariate from Tables 5.13-5.15.

Species	North	East	Sub/rur	S.hawk	C. dove	Grd. frost	p	ϕ
BT/GT	**0.86**	**0.54**	**0.70**	**-0.01**	**0.62**	0.41	-0.67	-0.29
BT/CT	0.02	0.08	0.27	-0.31	0.09	0.44	-0.56	-0.75
GT/CT	0.07	0.03	0.17	-0.18	0.15	**0.53**	-0.55	-0.74
HS/GF	0.20	0.61	0.88	-0.38	**0.20**	-0.34	-0.42	-0.60
HS/CF	0.13	0.30	0.71	-0.54	0.05	-0.04	**0.03**	-0.78
GF/CF	**0.83**	**0.53**	**0.81**	**0.43**	-0.18	**-0.08**	-0.25	-0.63

Table 5.16 shows the proportion of the 95% credible intervals from the independent analyses friom Chapter 3 that overlap for each of the three pairwise species comparisions for the two analyses. That is:

$$\frac{||\text{overlap in 95\% CI}||}{||\text{total span of intervals}||}$$

In the case of disjoint intervals, the length of the overlap is replaced with the gap between the two intervals. The results indicate that in almost all cases the joint multi-species model groups together species that have the highest overlap of credible intervals. The only exceptions to this are covariates that were non-significant in the independent analyses. In this case the credible intervals will not necessarily be a good representation of the distribution. Posterior means of the parameters were much closer in these cases.

5.5 Conclusion

The multi-species approach outlined here, as stated in Section 5.1, allows additional hypotheses on synchrony across whole ecosystems to be tested. These hypotheses may have a wide range of applications and consequences. Multi-species models as a whole have generally been underused and their development has been slow. There is a large gap in the literature with regards to multi-species approaches that are able to incorporate multi-species interactions at the population level, whether in relation to abundance or demographic parameters. The methods of Lahoz-Monfort et al. (2011) go a long way to providing a solution to this gap, allowing multi-species synchrony to be tested and estimated. However, there are some limitations to their approach that we have addressed with our approach.

The extensions developed in this chapter to incorporate model uncertainty using the reversible jump algorithm allows further test for synchrony across species, not just in relation to unexplained variation accounted for by random effects, but additionally through shared regression covariate parameters. The ability to share parameters across species can lead to greater precision in these estimates when more data are used to estimate fewer parameters. In addition, all possible areas of synchrony can be explicitly accounted for and uncertainty in these estimates measured.

The ICCs give an idea of how synchronous unexplained variation is for each species; however it fails to take into consideration any synchronous aspect to the variation that may already have been explained by the covariates. Furthermore, we feel that this framework has the added benefit of being able to guide users to the specification of better models. The intra-class correlation coefficients give a measure of the ratio of unexplained variation attributed to all species in the model to that which is specific to a given species only. The results from analyses of this kind may therefore aid suggestion of possible additional covariates that are missing from the model in its current form. This is something that Lahoz-Monfort et al. (2011) do not discuss to a large degree. For the three species analysed in this chapter, the majority of unexplained variation (at least for blue tit and great tit), was considered synchronous across the species. In this case, this would perhaps suggest that a generic covariate acting on all species is likely to be missing from the model. For this application, a possible suggestion may be the size of the site being monitored and/or the amount of food provided at that site. In addition, for coal tit, there seems to be an additional species-specific covariate missing. McKenzie et al. (2007) analysed the importance of Sitka spruce *Picea sitchensis* and found that coal tits tend to use garden feeders to a greater extent when the spruce crop is comparatively poor. A covariate measuring either the distance to the nearest coniferous habitat or the success of the cone crop in that year may improve model performance. As a species the coal tit has taken to gardens much more readily over the past sixteen years (1995-2011), with increases of 76% in rural settlements and 63% in urban and suburban settlements (Baillie et al., 2014). Equivalent figures for blue tit are much lower at 11% and 2%, whilst for great tit are slightly lower at 67% and 41% respectively. As such, the differing changes modelled through the species-specific random effects for coal tit are consistent with this difference.

Although the results presented in this chapter concentrate on the same three species and may not be directly applicable to all species combinations and all ecosystems, it seems feasible to suggest that they do indeed represent common types of interactions and dependencies that may be present. Garden feeding sites are likely to be more homogeneous perhaps than wider and more natural environments as supplementary food provided at these sites is largely independent of external factors that may affect the availability of natural food sources or general demographic parameters. Consequently, interactions and similar responses to certain factors may be overestimated.

Calculating the C coefficients can give some general guidance on whether the set of covariates included in the model as a whole leads to some of the synchrony observed when the covariates are included. However, this requires two separate analyses to be run and compared, one with the covariates included and one without, rather than a single model incorporating the multiple forms of synchrony. A possible simpler alternative to the approach one outlined in this chapter would be to fit a model with and without each of the covariates and see where the variation no longer explained by that covariate is attributed. Aside from the additional computation time required to run all the analyses, this approach would also rely on the assumption that all the unexplained variation previously attributed to that covariate went to either of the two random effects. There is a strong possibility, however, that some of this variation would be accounted for by one of the other covariates or the species-specific intercepts. In addition, for a large number of covariates, the number of separate models that would need to be fitted would become infeasible quite quickly.

Accounting for species synchrony in response to covariates through removing them from the model and observing the subsequent change in the random effect variances gives an indication of the magnitude of the contribution of covariates to the synchrony of the species. Estimating the degree of synchrony, and across which species-covariate combinations that synchrony extends, allows much more specific conclusions to be drawn.

When using such a flexible family of distributions as the Tweedie distributions, merely adding and removing the covariates from the model seems to completely change the dynamics of the model fitted. Therefore using the methodology outlined here gives a much more robust method for detecting synchrony in response to measured covariates. Synchrony in unexplained variation is still detected, but synchrony in response to individual covariates can also now be estimated and accounted for. This framework requires only a single model to be fitted, admittedly with the added complexity of the reversible jump step, whereas the model of Lahoz-Monfort et al. (2011) would require two and the independent models of the previous chapters three. In the case of the latter, it becomes much more difficult to reliably estimate the degree of synchrony.

In addition to accounting for covariate-level synchrony between species to exogenous factors, we also add species interactions directly by incorporating not just intra-specific density dependence, but also a measure of interactions with other species included in the model. This seems to add variable amounts to the model. For species with similar population trajectories, most interactions seem to be intra-specific. Once this has been accounted for, there was no evidence for further inter-specific interactions. When species with different population trajectories are included in the model, or when density dependence is not found to have a significant effect, there seems to be a greater probability of finding an inter-specific interaction between these species. These observations may result from high collinearity between the covariates used in this instance; accounting for intra-specific interactions (which from an ecological perspective would generally be expected to be greater than inter-specific ones) may leave little further variation to be explained by a very similar covariate. The additional results provided in the Appendix for different combinations of species show that interactions can be found for some species combinations.

The flexibility of the Tweedie distributions, and the additional parameters that enable this, require yet further decisions to be made with regards to the complexity of the model. Specifying species-specific intercepts, covariate parameters (to varying degrees) and random effects means that the means of the Tweedie distributions are explicitly different for each species-site-year combination. Due to the fixed mean-variance relationship of the Tweedie distributions, the variances are consequently also different. However, the relationship between the mean and variance is constant across species if ϕ and p are assumed to be invariant to species. An added level of complexity and flexibility can be included in the modelling framework if required, by allowing species subscripts to be added to these two parameters (or equivalent variance parameters if other multi-parameter distributions are used). This seems to be as much of a philosophical question to the ecological approach than anything else. For the three species considered in this chapter, the effect of choice of one approach over the other on regression parameter estimates was unsurprisingly limited when the shapes of the distributions of each species in the model were similar. Conversely, differences were observed when the across-species empirical distributions were more varied, as the model was subsequently averaging over all species. This generally led to further averaging over species in relation to the regression covariates, and generally a reduction in the magnitude of covariate effects estimated.

Chapter 6

A spatio-temporal analysis

6.1 Introduction

So far in this thesis, we have analysed the GBFS data accounting for spatial correlation only through the inclusion of a measure of northing and easting as covariates in the model and site-specific random effects. However, the fitting of spatial models that directly account for and explain the spatial correlation inherent in this type of data is becoming more feasible and widely used. Accounting directly for the spatial structure may potentially offer a more realistic method for modelling changes in the abundance of the garden bird species.

In addition, the ability to model multiple species in a joint model, as discussed extensively in the previous chapter, can also add more information than would be possible through the use of single species models. We have already modelled the 10 prey species as a function of both sparrowhawk and collared dove abundance but a more flexible model that can infer something about dependency between the latent spatial processes between multiple species has the potential to more realistically account for that dependency.

To adequately model the spatial-temporal dynamics in the sparrowhawk-prey relationship, we fit a joint multi-species model that can account for the inter- and intra-specific correlation inherent in the data. Until relatively recently, a model of this complexity would have been completely infeasible as the only approach for estimating the parameters would have been MCMC framework. The computational cost of estimating all the model parameters would be much too great to be considered feasibly. Using the INLA methodological approach outlined in section 2.6, this joint spatio-temporal approach becomes computationally feasible.

In this chapter, we outline a method for modelling spatio-temporal data of multiple species simultaneously. The method uses replications of the latent field applied to each response variable.

6.2 A brief introduction to the SPDE approach

In this section we provide a brief introduction to the stochastic partial differential equation (SPDE) approach to modelling the latent spatio-temporal process. A full discussion of the type of model fitted can be found in Cameletti et al. (2013). Suppose we have a continually indexed spatial process (or random field) that changes in time. We denote this process at location $\boldsymbol{s}$ and time t

$$Y(\boldsymbol{s},t) \equiv \{y(\boldsymbol{s},t) : (\boldsymbol{s},t) \in \mathcal{D} \subseteq \mathbb{R}^2 \times \mathbb{R}\}. \tag{6.1}$$

where $\mathcal{D}$ is the spatio-temporal domain. We assume this random field is a Gaussian field (GF) specified by its mean and spatio-temporal covariance function $\text{Cov}(y(\boldsymbol{s},t), y(\boldsymbol{s}',t')) = \sigma^2\mathcal{C}((\boldsymbol{s},t),(\boldsymbol{s}',t'))$ for all $(\boldsymbol{s},t)$ and $(\boldsymbol{s}',t')$in $\mathcal{D}$. The model is formulated as a second-order stationary process such that its covariance function $\mathcal{C}(.,.)$ depends only on the location and time through the distance vector $\boldsymbol{h} = (\boldsymbol{s} - \boldsymbol{s}')$ and time lag $l = (t - t')$.

The spatio-temporal model of the type fitted in this chapter can be written as follows:

$$y(\boldsymbol{s},t) = \boldsymbol{b}(\boldsymbol{s},t)\boldsymbol{\beta} + \boldsymbol{x}\{\boldsymbol{s},t\} + \epsilon(\boldsymbol{s},t) \tag{6.2}$$

where $\boldsymbol{b}(\boldsymbol{s},t)$ is a vector of covariates with coefficients $\boldsymbol{\beta}$, $\epsilon(\boldsymbol{s},t)$ measurement error and $\boldsymbol{x}\{\boldsymbol{s},t\}$ is a first-order autoregressive dynamic model for the latent process given by

$$\boldsymbol{x}\{\boldsymbol{s},t\} = \xi\boldsymbol{x}\{\boldsymbol{s},t-1\} + \omega(\boldsymbol{s},t). \tag{6.3}$$

This is defined for $t = 2, ..., T$ and $|\xi| < 1$.

The covariance function of the zero-mean Gaussian $\omega(\boldsymbol{s}, t)$ is defined as

$$\text{Cov}(\omega(\boldsymbol{s}, t), \omega(\boldsymbol{s}', t')) = \begin{cases} 0 & \text{if } t \neq t' \\ \sigma_\omega^2 \mathcal{C}(h), & \text{if } t = t'. \end{cases} \tag{6.4}$$

The spatial correlation function $\mathcal{C}(h)$, for $h = \|\boldsymbol{s} - \boldsymbol{s}'\|$, is defined as the Matérn function

$$\mathcal{C}(h) = \frac{1}{\Gamma(\nu)2^{\nu-1}}(\kappa h)^\nu K_\nu(\kappa h), \tag{6.5}$$

where K_ν denotes the modified Bessel function of the second kind and order ν. $\kappa > 0$ is a scale parameter relating to the range ρ, distance at which the spatial correlation becomes small. ρ is defined as $\rho = \frac{\sqrt{8\nu}}{\kappa}$ such that ρ is close to 0.1 for each ν (Lindgren et al., 2011).

We are interested in the posterior marginals of the latent field and the hyperparameters, given by:

$$\pi(x_i|\boldsymbol{y}) = \int \pi(x_i|\boldsymbol{\theta}, \boldsymbol{y})\pi(\boldsymbol{\theta}|\boldsymbol{y})d\boldsymbol{\theta}$$
$$\pi(\theta_j|\boldsymbol{y}) = \int \pi(\boldsymbol{\theta}|\boldsymbol{y})d\boldsymbol{\theta}_{-j}, \tag{6.6}$$

where $\boldsymbol{\theta}_{-j}$ is the vector $\boldsymbol{\theta}$ without element j.

The INLA algorithm outlined in Section 2.6 can be used to calculate deterministic approximations to these distributions.

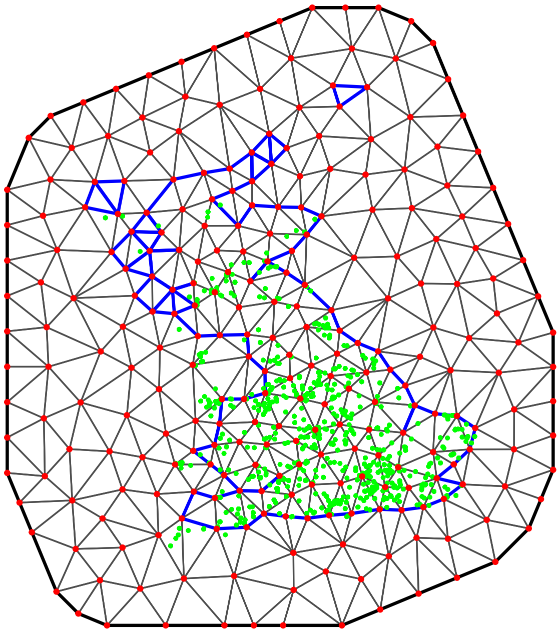


Figure 6.1: Mesh triangulation of the spatial domain. Green dots correspond to the geographical locations of the observation sites whilst the red dots are the nodes of the triangulation. The thick blue line shows the spatial polygon describing a coarse representation of the border of the UK. The boundary is extended to the thick black line to reduce boundary effects.

6.3 The model

To fit the spatio-temporal model we must first define a 'mesh' over the spatial region, that is the UK. The mesh is a discrete triangulation of the continuous spatial region. In general, the resolution of the mesh will determine the accuracy of the results. However, the computational efficiency will reduce as the mesh becomes finer. As such, a compromise between the two must be made. The mesh used in the analyses in this chapter is shown in Figure 6.1. As the resolution of the mesh increases, the approximations will be more accurate, however consequently the computational cost will increase. Fitting the model with different mesh resolutions and comparing the results will provide some indication on the level of resolution required to give good approximations. If the results are 'similar enough' with a coarser mesh, then it can be considered acceptable.

We concentrate on one species of prey, namely the house sparrow and model interactions between the latent processes driving the spatial distribution of this species and that of two other species. The spatial distributions of collared dove and sparrowhawk are also modelled simultaneously to test for how, if at all, the spatial structure of the house sparrow evolves with, or inversely to, that of these other two species. We denote $p_i\{A\}$ the probability of occurrence of species A at location i and $\mu_i\{A\}$ the expected abundance of species A at location i conditional on it being present. Let y_i be the observed mean count of a given species at location i, then we define z_i to be a binary variable with $z_i = 1$ denoting the presence of a species at site i and $z_i = 0$ is the species is not observed. If the species is present, or alternatively $z_i = 1$, we denote d_i conditional on z_i, to be the observed (positive) average count of that species. Formally:

$$z_i = \begin{cases} 1, & \text{if } y_i > 0 \\ 0, & \text{otherwise} \end{cases}$$

and subsequently

$$d_i = \begin{cases} \text{NA}, & \text{if } y_i = 0 \\ y_i, & \text{otherwise.} \end{cases}$$

The first model is formulated as follows, where subscripts denote the model component and species in parentheses (SH=sparrowhawk; CD=collared dove; HS=house sparrow):

$$
\begin{aligned}
&\text{logit}(p_i\{SH\}) = \alpha_z\{SH\} + \mathbf{x}\{\mathbf{s}_i, t\}\\
&\log(\mu_i\{SH\}) = \alpha_y\{SH\} + \beta_y\{SH\}\mathbf{x}\{\mathbf{s}_i, t\}\\
&\\
&\text{logit}(p_i\{CD\}) = \alpha_z\{CD\} + \mathbf{m}\{\mathbf{s}_i, t\}\\
&\log(\mu_i\{CD\}) = \alpha_y\{CD\} + \beta_y\{CD\}\mathbf{m}\{\mathbf{s}_i, t\}\\
&\\
&\text{logit}(p_i\{HS\}) = \alpha_z\{HS\} + \gamma_z\{HS\}\mathbf{x}\{\mathbf{s}_i, t\} + \delta_z\{HS\}\mathbf{m}\{\mathbf{s}_i, t\}\\
&\log(\mu_i\{HS\}) = \alpha_y\{HS\} + \gamma_y\{HS\}\mathbf{x}\{\mathbf{s}_i, t\} + \delta_y\{HS\}\mathbf{m}\{\mathbf{s}_i, t\}.
\end{aligned}
\tag{6.7}
$$

This model formulation estimates separate spatio-temporal GFs for each of the explanatory variable species ($\mathbf{x}\{\mathbf{s}_i, t\}$ and $\mathbf{m}\{\mathbf{s}_i, t\}$), and then these GFs are 'copied' through to the other sub-models and the house sparrow formula to estimate the relatedness between each species pair. That is a shared spatio-temporal random effect term fitted across the two model components simulatenously. In the first component of the sparrowhawk and collared dove sub-models, the spatio-temporal random effects have coefficient one. In the subsequent sub-models, the relevant random effects are scaled according to the β, γ and δ coefficients, giving a measure of how related these two processes are to each other.

The model for the sparrowhawk is defined as a delta gamma model, with the probability of sparrowhawk occurrence modelled using a binary regression model. On the link scale the spatial distribution of occurrence probability for this species is modelled as a function of a fixed intercept $\alpha_z\{SH\}$ and a random effect $\mathbf{x}\{\mathbf{s}_i, t\}$ defined as a GF. The expected count of sparrowhawks, conditional on them being present, is then modelled as a function of a different fixed intercept $\alpha_y\{SH\}$ and a scaled shared random effect $\mathbf{x}\{\mathbf{s}_i, t\}$ which is the same as that fitted to the probability of occurrence spatial distribution. The parameter $\beta_y\{SH\}$ then scales the random effect and is an estimate of the relatedness of the two spatio-temporal processes. A similar model is fitted to the collared dove data.

We project the spatial model through time according to first-order autoregressive model, with a parameter ξ which estimates the relationship between average counts in successive years. That is $\boldsymbol{x}\{\boldsymbol{s}_i, t\} = \xi\boldsymbol{x}\{\boldsymbol{s}_i, t-1\} + w\{\boldsymbol{s}_i, t\}$ where $w\{\boldsymbol{s}_i, t\}$ has a zero-mean Gaussian distribution. An analogous formulation is used for $\boldsymbol{m}\{\boldsymbol{s}_i, t\}$. The model thus enables us to account for both spatial and temporal correlation within and between each of the species of interest.

Secondly, we fit a similar model to that outlined in Equation 6.7, however the GF is first fitted to the abundance data and then copied through to the probability of occurrence in each case. That is:

$$\begin{aligned}
\log(\mu_{i\{SH\}}) &= \alpha_y\{SH\} + \mathbf{x}\{\mathbf{s}_i, t\} \\
\text{logit}(p_{i\{SH\}}) &= \alpha_z\{SH\} + \beta_z\{SH\}\mathbf{x}\{\mathbf{s}_i, t\} \\
\\
\log(\mu_{i\{CD\}}) &= \alpha_y\{CD\} + \mathbf{m}\{\mathbf{s}_i, t\} \\
\text{logit}(p_{i\{CD\}}) &= \alpha_z\{CD\} + \beta_z\{CD\}\mathbf{m}\{\mathbf{s}_i, t\} \\
\\
\text{logit}(p_{i\{HS\}}) &= \alpha_z\{HS\} + \gamma_z\{HS\}\mathbf{x}\{\mathbf{s}_i, t\} + \delta_z\{HS\}\mathbf{m}\{\mathbf{s}_i, t\} \\
\log(\mu_{i\{HS\}}) &= \alpha_y\{HS\} + \gamma_y\{HS\}\mathbf{x}\{\mathbf{s}_i, t\} + \delta_y\{HS\}\mathbf{m}\{\mathbf{s}_i, t\}.
\end{aligned} \tag{6.8}$$

The difference between these two model formulations is how the distributions of sparrowhawks and collared doves are modelled. In Equation 6.7, we initially model the distribution of the probability of occurrence for each of these two species and 'copy' this through to the density of that species and into the house sparrow sub-model. In the second case, we initially model the spatio-temporal distribution of the *density* of sparrowhawks and collared doves (conditional on them being present) and then copy these distributions throughout the other sub-models. The two different modelling approaches may offer alternative insights into how the populations of these different species are evolving in relation to each other. If significant relationships between sparrowhawks and hosue sparrows are found in the first model, then this may suggest that merely the presence of sparrowhawks at a given site is enough to effect local populations of their prey, whilst the second model will indicate if a higher density of sparrowhawks can have a larger effect. As the sparrowhawks are related to both the presence and abundance of house sparrows in separate submodels, it may be possible to find differing effects on each of these processes. In the former case, this would indicate that sparrowhawks can potentially wipe out a local population of house sparrows or prevent it from frequenting a given location. In the latter, it would suggest that local populations of house sparrows are reduced in number but not necessarily completely wiped out.

Table 6.1: Prior distributions for the model parameters, where $N(a, b)$ is defined for mean a and precision b.

Parameter	Prior
α	$\propto 1$
β	$N(1, 10)$
γ	$N(1, 10)$
δ	$N(1, 10)$
ξ	$N(0, 0.15)$
θ_1	$N(0, 1)$
θ_2	$N(0, 1)$

6.3.1 Priors

The priors used are the default priors in the `r-INLA` package, given in Table 6.1, where $\theta_1 = \log(\tau)$ and $\theta_2 = \log(\kappa)$.

Table 6.2: Posterior means and 95% credible intervals for the model parameters from Equation 6.7.

Parameter	Posterior mean	95%CI
$\alpha_z\{SH\}$	-1.41	(-2.19,-0.67)
$\alpha_y\{SH\}$	-1.06	(-1.36,-0.71)
$\alpha_z\{CD\}$	0.86	(0.08,1.60)
$\alpha_y\{CD\}$	1.10	(0.85,1.37)
$\alpha_z\{HS\}$	3.23	(2.54,3.95)
$\alpha_y\{HS\}$	2.49	(2.11,2.86)
$\beta_y\{SH\}$	0.37	(0.28,0.46)
$\beta_y\{CD\}$	0.31	(0.26,0.37)
$\gamma_z\{HS\}$	-0.13	(-0.30,0.04)
$\gamma_y\{HS\}$	-0.17	(-0.23,-0.10)
$\delta_z\{HS\}$	0.79	(0.62,0.97)
$\delta_y\{HS\}$	0.42	(0.34,0.51)
$\xi\{SH\}$	0.97	(0.96,0.98)
$\xi\{CD\}$	0.97	(0.96,0.98)

Table 6.3: Posterior means and 95% credible intervals for the model parameters from Equation 6.8.

Parameter	Posterior mean	95%CI
$\alpha_z\{SH\}$	-1.79	(-2.00,-1.58)
$\alpha_y\{SH\}$	-0.43	(-0.72,-0.13)
$\alpha_z\{CD\}$	0.38	(0.11,0.60)
$\alpha_y\{CD\}$	1.51	(1.10,1.92)
$\alpha_z\{HS\}$	2.29	(2.04,2.53)
$\alpha_y\{HS\}$	2.61	(2.23,2.99)
$\beta_z\{SH\}$	1.26	(1.01,1.57)
$\beta_z\{CD\}$	1.66	(1.37,1.97)
$\gamma_z\{HS\}$	-0.47	(-0.60,-0.35)
$\gamma_y\{HS\}$	-0.31	(-0.56,-0.07)
$\delta_z\{HS\}$	0.90	(0.74,1.06)
$\delta_y\{HS\}$	1.43	(1.15,1.72)
$\xi\{SH\}$	0.96	(0.94,0.98)
$\xi\{CD\}$	0.98	(0.96,0.99)

6.4 Results

The first of the two models fitted initially accounts for the spatio-temporal distribution of the probability of occurrence of sparrowhawks and collared dove and then uses these to explain the distribution of house sparrow, that is the model outlined in Equation 6.7. The second models the abundance of sparrowhawks and collared doves and uses these results to model the house sparrow distribution according to Equation 6.8. Results are presented in Tables 6.2 and 6.3. A finer mesh was tried to ensure good approximations to the spatio-temporal field were achieved, and the results were very similar. Hence the finer mesh which took considerably longer to converge, was considered unnecessary.

The results show that there is strong temporal correlation between the latent spatial processes in successive years in both sparrowhawk and collared dove, with posterior means for ξ being 0.97 in both cases. This suggests that the probability of presence of either species in year $t+1$ at a given spatial location is highly dependent on the same probability in year t. These results also hold for the spatial distribution of the density of these two species, that is posterior means of 0.96 for sparrowhawks and 0.98 for collared dove. Both species also show significant positive correlation under both model formulations between the probability of occurrence and the subsequent density of that species at a given location, with $\beta_y\{SH\}$, $\beta_z\{SH\}$, $\beta_y\{CD\}$ and $\beta_z\{CD\}$ being positive and significant (posterior means of 0.37, 0.31, 1.26 and 1.66 respectively). This suggests that locations that have a higher probability of occurrence also tend to have a higher abundance of that species if it is present. Mathematically it means there is correlation between the latent processes driving each of the spatial fields.

The estimates for the correlation between collared dove and house sparrow are also significant and positive($\delta_z\{HS\}$=0.79 and 0.90, $\delta_y\{HS\}$=0.42 and 1.43), suggesting that the spatio-temporal processes driving the latent structure for these species has developed similarly. As these species will have similar ecological requirements, it is not altogether surprising that they show similar trajectories in presence and abundance. The results from previous chapters have also suggested significant positive relationships between the numbers of these species observed at GBFS sites, with significant positive correlation between changes in house sparrow counts and collared doves when collared dove was fitted as a fixed effect (Chapters 3-5).

In the first model, copying the latent field for sparrowhawk presence through the other model components, gives an posterior mean for $\gamma_z\{HS\}$ of -0.13 with 95% CI of (-

0.30,0.04). This suggests that there is no significant relationship between the presence of sparrowhawks and the presence of house sparrows. Ecologically, this suggests that there is no evidence to suggest that the presence of sparrowhawks alone is sufficient to cause significant changes in the probability of house sparrows occupying a site or equivalently that sparrowhawks cannot completely deplete the local populations. The estimate of the effect of the presence of sparrowhawks on abundance of house sparrows, however, is significant and negative (-0.17, 95% CI (-0.23,-0.10)). This suggests there is an inverse relationship between the processes driving the probability of sparrowhawk presence and the abundance of house sparrows or that fewer house sparrows are observed in areas frequented by sparrowhawks.

The results from the second model in Table 6.3 are very similar in interpretation to those from Table 6.2. The main difference is that there is now a significant negative effect of sparrowhawk abundance on both the probability of house sparrow occurrence at a given site and on the abundance of house sparrows when they are present. This suggests that the presence of sparrowhawks only effects the abundance of house sparrows at a given site, whilst having no significant effect on the probability of occurrence. Conversely, the abundance of sparrowhawks has a significant effect on both probability of occurrence and the subsequent abundance of house sparrows.

This result has potentially important ramifications on how to include sparrowhawks in a model. Some analyses have only used presence or absence of predators to detect effects on prey species (e.g. Bell et al., 2010; Chamberlain et al., 2009). In that case there is a risk of underestimating the overall effect of predators on their prey as presence alone here was not significantly correlated with changes in abundance of the prey species.

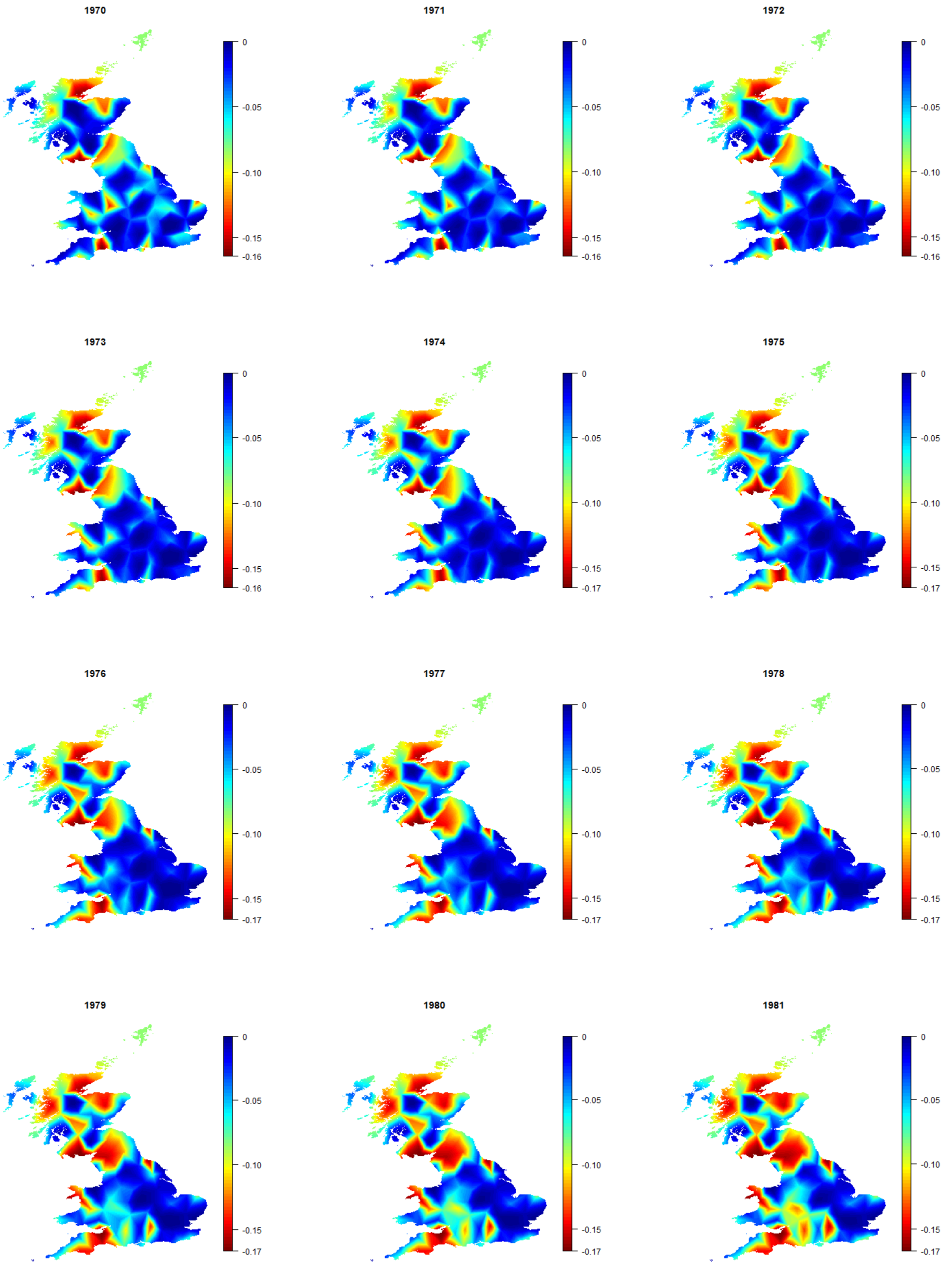


Figure 6.2: $\gamma_y\{HS\}\mathbf{x}\{\mathbf{s}_i, t\}$ for t =1970-81 from model 6.7. That is, the estimated effect of the probability of sparrowhawk presence on the abundance of house sparrows. In the early years the estimated effect of sparrowhawks is relatively low due to small numbers of sparrowhawks being observed.

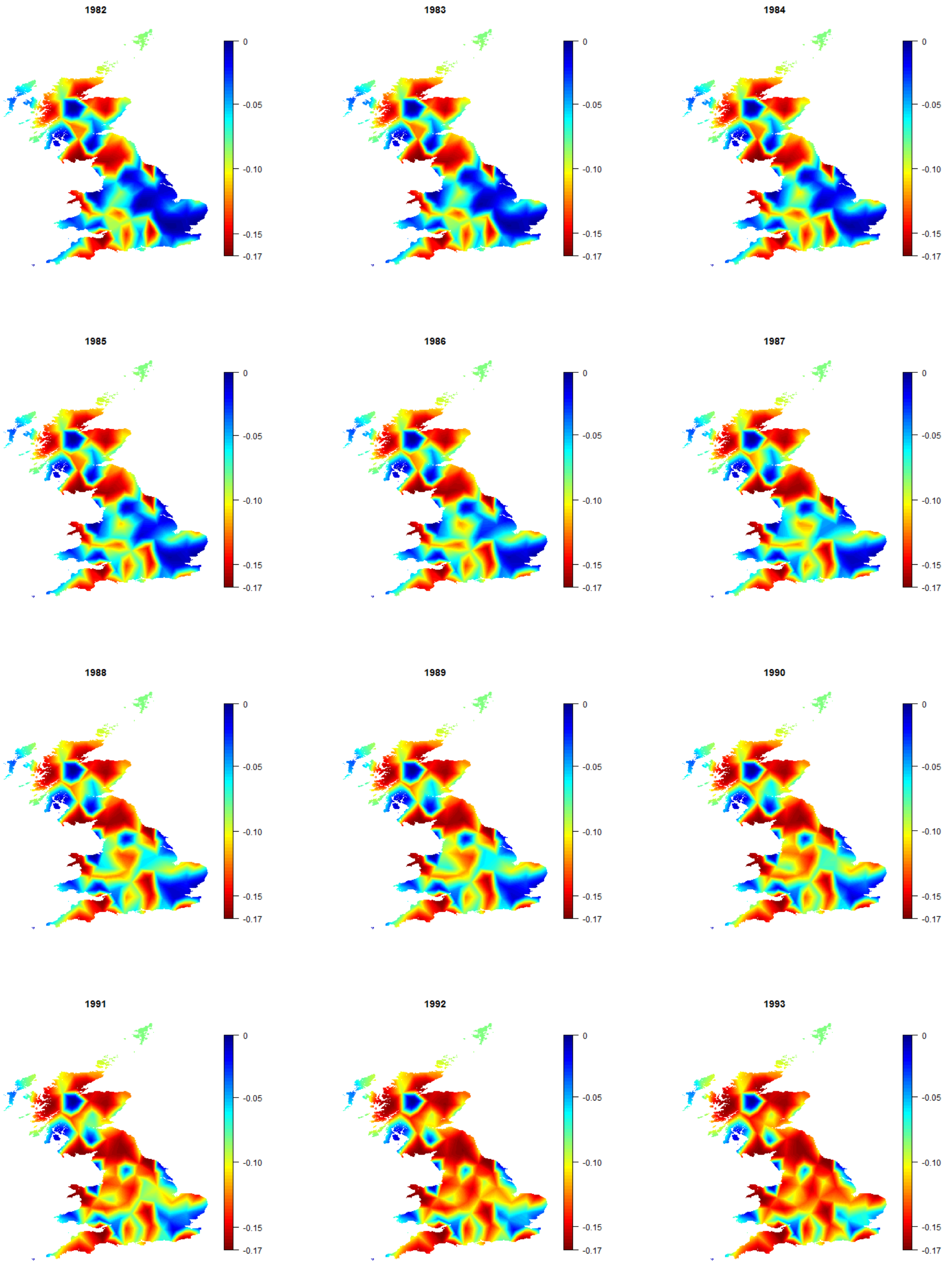


Figure 6.2: (cont.) $\gamma_y\{HS\}\mathbf{x}\{\mathbf{s}_i, t\}$ for t =1982-93 from model 6.7. That is, the estimated effect of the probability of sparrowhawk presence on the abundance of house sparrows. As the years progress the effect of sparrowhawks increases due to an increase in numbers of individuals observed and the overall distribution of sparrowhawks moving south and east.

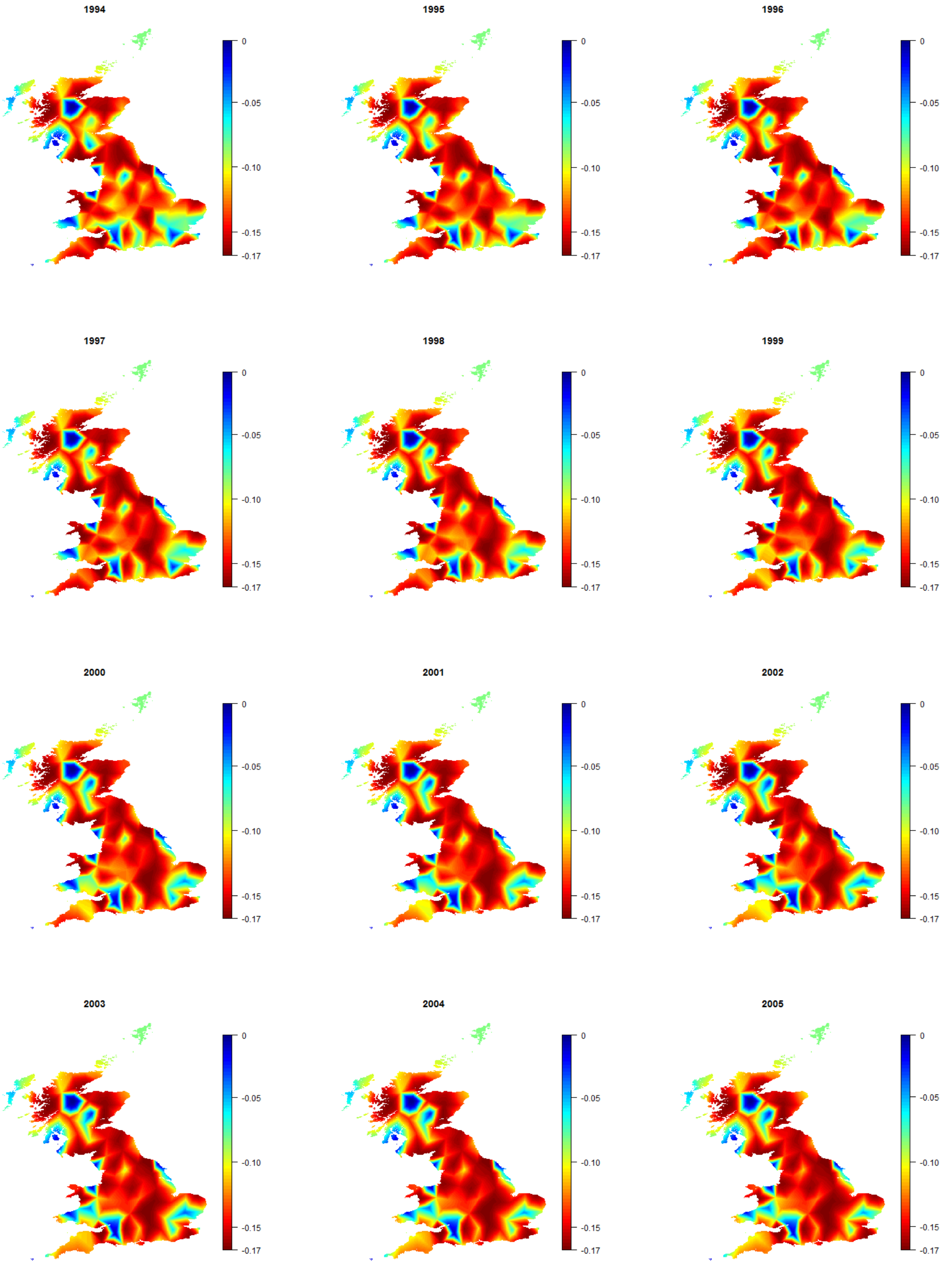


Figure 6.2: (cont.) $\gamma_y\{HS\}\mathbf{x}\{\mathbf{s}_i, t\}$ for t =1994-2005 from model 6.7. That is, the estimated effect of the probability of sparrowhawk presence on the abundance of house sparrows. In the early years the estimated effect of sparrowhawks is relatively low due to small numbers of sparrowhawks being observed. By 2005, the effect of sparrowhawks is evident across the majority of the UK.

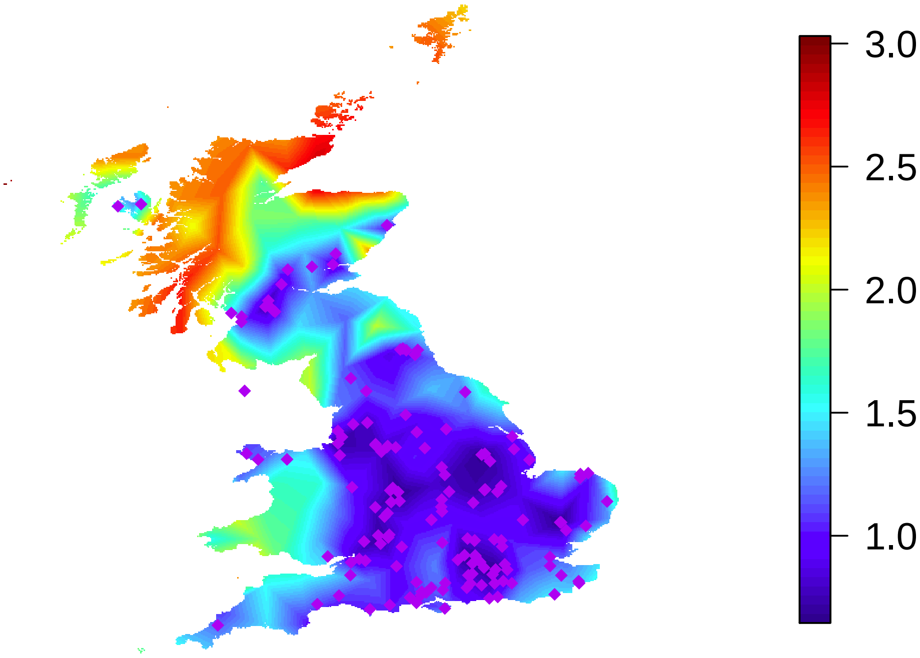


Figure 6.3: Standard deviation for the latent field for the year 1998. Purple points show the locations of the sites monitored during that year.

Figure 6.2 shows the product of $\gamma_y\{HS\}$ and $\mathbf{x}\{\mathbf{s}_i, t\}$ from model 6.7, that is the predicted effect of sparrowhawk presence on the abundance of house sparrows for each year between 1970 and 2005. There is a clear increase in the abundance of sparrowhawks from the north and west to the south and east over the course of the 36 years and hence the effect of sparrowhawks on house sparrow abudance increases in magnitude and distribution across the UK.

The spatial certainty associated with the estimation process clearly reflects areas where survey effort is particularly high. Figure 6.3 shows the uncertainty across space associated with the model from Equation 6.8 in year 1998. Evidently the north of Scotland has a high level of uncertainty as there are few sites here at any point during the survey. Conversely, central and southern England show much lower levels of uncertainty. Due to the dependency between successive years, some areas will show higher precision even if there are few sites monitored nearby in that year if previous years had a high concentration of sites in that area.

6.4.1 Prior sensitivity

To check for sensitivity of the results to changes in prior specification we ran the model again using penalized complexity priors for each of the AR(1) parameters as detailed in Fuglstad et al. (2015); Simpson et al. (2014). These priors are weakly informative priors constructed based on the range and the marginal variance of the Matérn GRFs. The only notable change as a consequence of this was $\gamma_z\{HS\}$ becoming weakly negatively significant (95% credible interval $(-0.337, -0.009)$), indicating that this parameter is somewhat sensitive to prior choice. The interpretation of this is that the probability of presence of sparrowhawks now also has a negative effect on the probability of presence of house sparrows.

6.4.2 Limitations of the method

Despite being significantly quicker than would be to fit this model using MCMC methods, the methodology outlined in this chapter still requires a very large computational cost. This is particularly problematic due to the mixture model aspect of the delta model. In this method, each species has two likelihood components, one for the presence/absence and another for the positive values conditional on being present, with dependency assumed between these two likelihood components. As such, the model fitting process is much more complex and intensive than would be an application where zero-inflation was not a problem, so that a standard distribution alone could be used. The inability to include fixed effects, such as climate variables, in the model prevents us from testing for additional factors that could, and from the analyses in Chapters 3-5 almost certainly are, also affecting the numbers of house sparrow visiting garden feeding sites. Without including additional environmental factors we risk overestimating the magnitude of any sparrowhawk effect as some of the variation that is attributed to the random effect copied from the sparrowhawk variable could be explained by the fixed effects. Although consistent with our other results, the negative sparrowhawk effect detected could be overestimated if we fail to account for additional environmental factors.

6.5 Conclusion

In conclusion, this modelling process has enabled us to understand some of the processes underlying the dynamics of house sparrow distribution, particularly in relation to the processes underlying the other species considered. Although it was not possible to directly attribute changes in sparrowhawk populations to changes in house sparrow distribution and abundance, this has shown that the spatio-temporal process of changes in house sparrow abundance at garden feeding sites has developed inversely to that of sparrowhawks. Whether this is due to concurrent and confounding variables that are independently driving the two latent processes, it is not possible to say but it is consistent with either a behavioural response of birds avoiding favoured locations for sparrowhawks within those regions or overall numbers being reduced. It is perhaps more likely that the observed negative effect is due to numbers taken by sparrowhawks than to sparrows leaving the region, especially as now, they would have nowhere to go that is sparrowhawk-free.

Ideally we would wish to include fixed effects in the model additional to the underlying spatial random effects. However, the complexity of the model, in particular the mixture likelihood for each of the species, made this infeasible even on large servers with multiple core processors. As such, the results from this analysis must be interpreted carefully. A simplification of the model to include fewer distinct spatio-temporal random effects would allow fixed effects to be included more easily, but would reduce the ability of the model to account for the spatio-temporal effects shared across species.

Part of the reason that the model is computationally so demanding is the mixture likelihood used to deal with the large numbers of zeros. If this were not a problem, a simpler likelihood for each species could be used and hence there would be fewer parameters and dependencies to estimate in the model. This would reduce the complexity of the model and make fitting easier and quicker. Thus, it may then be more feasible to add additional environmental effects into the model. In addition, a model similar to that presented in Chapter 5, with both shared random effects and species-specific random effects, would also provide an interesting comparison between the two modelling approaches to multi-species data.

Overall, this modelling framework does allow very complex spatio-temporal models to be fitted in a more efficient and quicker way than would be possible with MCMC methods. The results are once again consistent with previous chapters, but can propagate uncertainty from the different underlying model processes through the model to ensure estimates of uncertainty are more accurate. In particular, this method no longer assumes that the numbers of sparrowhawks and collared doves are known. We initially fit a model to these species and then use the predicted numbers as the input into the final house sparrow model. Evidently this means the inputs to the house sparrow model are dependent on the accuracy of the models fitted. As such this is a more realistic model if observation error is present, accounting for uncertainty in the ‘covariates’ and the response variable.

Chapter 7

Ecological conclusions

In this chapter we will outline the general ecological conclusions we can make from the work conducted in the previous chapters and the thesis as a whole. The thesis set out to determine if there is any evidence to suggest that the increase in abundance and distribution of sparrowhawks observed over the past 40 years has had a discernible effect on the populations of any of the species it predates. As discussed previously in Chapter 1, most previous analyses of data covering the past 40 years have failed to find consistent effects of sparrowhawks on their prey species (e.g. Chamberlain et al., 2009; Newson et al., 2010; Thomson et al., 1998).

Throughout our analyses we have accounted for additional covariates that would be expected to have an effect on the species considered. Some previous analyses have faced criticism for failing to account for known environmental covariates, which risks over estimating the relationship between changes in prey species and sparrowhawks. If sparrowhawk abundance is confounded with other covariates, then more variation can be attributed to this covariate than should be. Although it is not possible to be completely certain that all relevant covariates have been taken into consideration in an observational study such as this, we have attempted to account for as many plausible additional factors as possible.

The overall results considered across analyses suggest there is some evidence to suggest that sparrowhawks have had a statistically significant, although practically relatively small, effect on the numbers of some species of their prey visiting garden bird feeders across the UK. In particular we have found that the number of house sparrows, starlings and blue tits visiting garden feeding stations across the UK over the past 36 years have decreased in relation to sparrowhawk abundance at these same sites. Difficulty then arises in the interpretation of this. In particular as to whether this relates to a true reduction in the populations of these species or whether it is merely a behavioural response of the birds avoiding sites that sparrowhawks frequent or at which they have become more abundant. Unfortunately it is not possible from these data alone to determine which of these situations is actually happening. It equally may be a mixture of the two.

The prevalence of negative easting effects on a large number of species, particularly those associated with farmland habitats, supports the general hypothesis that farmland birds are currently under the greatest pressure. In addition, populations in urban and suburban habitats are also generally faring worse than those in rural populations. Research into why urban populations are doing particularly badly has already been carried out (e.g. Mennechez and Clergeau, 2006; Peach et al., 2008; Shawn et al., 2011; Vincent, 2005). Further research into why this may be the case could be of benefit.

Annual differences in numbers of birds visiting garden feeders were most severely affected by the climate variable, that is the number of days of ground frost. This effect was positive, suggesting that birds were attracted to garden feeders more frequently and in greater numbers when the weather was colder. This suggests a behavioural response, namely a greater dependence on provisioned food when natural resources are lower or more difficult to come by. This really emphasises the importance of feeding birds in the garden when the weather is severe.

The results from our joint multi-species model presented in Chapter 5 show that there is a large amount of synchrony amongst species in relation to both their response to environmental covariates and in unexplained variation. Concentrating specifically on the three tit species, there was evidence to suggest the majority of variation across these three species was synchronous although coal tit was less synchronous that the other two. In this instance, most of the variation unexplained by the covariates was common to the three species and would perhaps suggest that a global variable may be missing from this model. The addition of some measure of the size or amount of food provided at the site may well offer better model fit, or at least reduce the size of the unexplained variation. The greater size of the asynchronous coal tit variance component suggested that they are also responding independently to additional factors not included in our model that appear to be having a lesser effect on the other two species.

The results from Chapter 6 suggest that, in the case of the house sparrow, there may be an effect of sparrowhawks on both the probability of occurrence at a given location as well as the subsequent abundance of house sparrows if they are present. Our results suggest that the presence alone of sparrowhawks at a site is not enough to cause local extinction, however at sites where sparrowhawks are particularly prevalent, the probability of that site being occupied by house sparrows is significantly reduced. For stronger conclusions to be made about the nature of the interactions between species, the incorporation of additional fixed effects in the model would be advantageous. The two-component likelihoods that were required in this instance to account for the zero-inflation inherent in the data meant that the computational cost of fitting the three-species interaction model with fixed effects was too great. Simplifying the model, perhaps if the Tweedie distributions were available in the `R-INLA` package, would possibly allow fixed effects to be included. However, the Tweedie distributions do have their own computational costs so this may not help with model fitting.

All things considered, we are dealing with species that have coexisted for a long period of time, both before and after sparrowhawk recolonisation. There is no evidence to suggest that sparrowhawks were having significant negative effects on songbirds in the period prior to their population collapse due to pesticides (Newton et al., 1997). Predators and prey species have coexisted for millennia so it would generally be expected that the species should be able to reach equilibrium. Even if the prey species are suppressed in number by the presence of sparrowhawks, we would expect some form of equilibrium to be reached. Clearly if the prey populations are reduced too much, then the sparrowhawks themselves will be unable to maintain their population levels, which at the current time seems to be the case. Although, it is possible that if the population of prey species is currently at its maximum sustainable yield, the addition of extra predators could then cause the prey population to collapse (McCleery and Perrins, 1991). In the case of blue tits, the overall populations of this species have remained largely stable, so the estimated negative effects of sparrowhawks on this species are clearly being counteracted by other factors. In the case of starling and house sparrow, the effect of sparrowhawk is not nearly strong enough to fully explain the severe declines observed in these species. Additional factors, such as intensification of farming methods, are clearly having an additional and more severe effect in this case. It seems reasonable to suggest that the effect of natural predators on the populations of prey species have evolved such that the species can coexist together. Under the absence of additional exogenous factors, the reproductive or survival rate in prey populations should be able to adjust to the level of predation (McCleery and Perrins, 1991; Newton et al., 1997). Only when other factors are much greater would predation be expected to be great enough to cause serious problems for their prey species.

Chapter 8

Discussion and further work

This thesis has proposed a suite of different methods for analysing relationships between multiple species in an ecological context, ranging from models of a single response species up to ecosystem level models. Each of the methods has both advantages and disadvantages from both a statistical and ecological perspective. In this chapter we will discuss the overall statistical conclusions that can be drawn from the analyses conducted in the previous chapters and discuss future possible directions in which these methods could be extended.

8.1 Model specification

The main consideration given to the model specification initially was how to deal with a data set that was of a high dimension with complex spatial and temporal correlation. The repeated measures related to weeks within years within sites. Although this can be dealt with through the use of mixed-effects models with random effects accounting for the serial correlation within sites and within years, the gain of using standard discrete distributions, such as Poisson, over the more complex Tweedie distributions begins to disappear as more complex correlation structures are required. In addition, a non-trivial problem of missing data for weeks when the survey is not conducted at a particular site becomes apparent, again reducing the benefit of the simpler distributions. When data of this type are under consideration, taking an average over the weeks in each year removes some of this problem. Obvious care must be taken when there are a large number of missing observations, especially when there are patterns to the years or sites. Sites with very small runs of data should be seriously scrutinised to discern whether they can provide anything meaningful to the analysis and if not discarded.

The problem of zero-inflation is also one which is common to ecological problems and the reason for this zero-inflation should be carefully considered prior to model specification to ensure the most appropriate approach is taken (Martin et al., 2005; Min and Agresti, 2005; Warton, 2005). In this data set, most of the zeros seemed to be associated with sites with low numbers of birds visiting. There were generally few sites for most species where that species was never observed. The two species where this was most obvious, namely coal tit and collared dove, were the two that showed poorest model fit in general. We therefore emphasise the importance of consideration of zero-inflation and the most appropriate method for dealing with it. This will be largely specific to the application being studied, but simplistic and ad hoc approaches may not always correctly capture the underlying dynamics (Lecomte et al., 2013).

From Chapters 3 and 4 we have shown that in this case and for these data, the results are highly consistent when either the change-abundance model or change-change model is used. This would not necessarily be the case for all applications and for all model formulations. It is recommended that careful consideration should be given to the model structure to ensure that it not only makes statistical sense, but also is as realistic a representation of the ecological processes as possible. Using two different model formulations, specifically in this case allowing the form by which the covariates enter the model to change, can potentially strengthen any conclusions gained from the model if the two sets of results complement each other. They may also provide additional conclusions that cannot be tested through a single model.

The extension of the modelling framework to jointly model multiple prey species allows for additional interactions between the species to be measured. The ability to detect how species respond similarly or differently to various exogenous factors can provide important information on possible areas of conservation management, whilst also accounting for varying levels of interactions and similarities between species. Varying the level of complexity and flexibility of this model added to the computational demand of the analysis but also allowed a more realistic representation of the ecological processes. The most flexible model, although allowing each of the relevant parameters to be shared or distinct across any combination of species, produced results that were very consistent with the independent single-species models. This may bring into question whether the additional cost of fitting this model is worthwhile. The main advantages of the joint multi-species model were allowing interactions between response species to be tested and providing quantitative evidence for the similarities of the estimated regression coefficients across species. The model also has the added advantage of partitioning the unexplained variation into that which is synchronous with the other species and that which is species-specific. Subsequently, possible missing covariates can also be suggested based on the nature of the unexplained variance for each species considered. We feel that this is a worthwhile addition to the modelling framework.

The SPDE approach used in Chapter 6 highlighted the inverse relationship between the spatio-temporal processes driving the concurrent changes in house sparrow and sparrowhawk occurrence distribution. This modelling framework provided very interesting results and allowed a very flexible model to be fitted to all the data. However, the difficulty of including additional information through fixed effects in the model somewhat reduced the impact of these results.

Considering the data as a whole, there are clearly geographical regions that are under monitored, notably the north of Scotland, however these relate to areas of the country where population density is low and hence garden feeding of birds is also low. As such it is unlikely that survey effort in these areas could easily be increased. Uncertainty in the modelling of these areas can be taken into consideration when interpreting the results. As the survey was set up to monitor the effect of garden feeding on birds there is little that could be gained on this front if there is a general lack of feeding stations in these areas.

8.2 The Tweedie distributions: advantages and recommendations

Firstly, it is important to note that the Tweedie distributions are an incredibly flexible family of distributions that we believe are an underused resource in statistics. In this thesis, we have used only a small subset of the range of distributions that can be fitted using this framework. Even within this small subset, the range and shapes of distributions it is possible to fit are very large.

The flexibility, however, does not come without cost. The computational demand in estimating the likelihood for a Tweedie distribution is relatively high. The functions in the `fishMod` package (Foster, 2014) are currently significantly quicker than those in the `tweedie` package (Dunn, 2014), however but are only defined on a limited range for p. Most applications that would suit the Tweedie distributions, however, seem to fall into this range. Certainly if a standard distribution such as the normal, Poisson or gamma is appropriate, then using these distributions is likely the best option for model fitting as interpretation of Tweedie parameters is more complex than their well-known special cases. If a standard distribution is appropriate, then the functions used to calculate likelihoods for these distributions will also generally be much less computationally expensive.

8.3 Further work

One drawback of the analyses conducted in this thesis is that they have concentrated solely on abundance of the species of interest throughout the winter months concentrated around garden bird feeders. Whilst there is strong correlation between GBFS data and equivalent breeding indices for most species, we cannot easily extend the interpretation of the results from these analyses to effects on breeding density. In particular the non-sedentary species, such as chaffinch and greenfinch, whose numbers are augmented with migrants from continental Europe over the winter, may show completely different dynamics at other times of the year. Any sparrowhawk effect found here is only on non-breeding birds. Ecologists are often more interested in effects on overall breeding densities and previous analyses of such data have failed to find significant sparrowhawk effects (e.g. Newson et al., 2010). Therefore the ability to test these results with similar data but of breeding counts rather than non-breeding densities would be of a great advantage.

It is unlikely that other data sets would be able to give such an opportunity to cover the full time period necessary, that is the periods of absence, recolonisation and sustained abundance of sparrowhawks across the UK. An alternative modelling framework that may be of interest would be an integrated population model (Abadi et al., 2010). If sufficient data were available relating to breeding numbers of birds and at similar locations to those monitored under the GBFS, then a model incorporating all the data and modelling all the processes in the life histories of the prey species could be modelled. An integrated approach such as this would allow the conclusions drawn here to be potentially extended to sparrowhawk effects, or a lack thereof, on breeding numbers of birds. This would then potentially support either a seasonal change in mortality, if sparrowhawk effects were only found on non-breeding numbers, or an overall population level response if effects were also found on breeding numbers or summer survival. Unfortunately it seems unlikely that such data are available. Harrison et al. (2015) supply the predicted abundance of common species by 1km square throughout the UK, based on fitting models to BBS data. However, these only start in 1994 and as such do not span the full period of sparrowhawk population changes or the period covered by the GBFS data set. An integrated analysis of data from the corresponding years would be an interesting area to look into. Nicoll and Norris (2010), in a meta-analysis of predation studies, found that the probability of detecting a predation effect was dependent on the quality and quantity of data used to detect it. The GBFS provides the quantity of data but a more experimental approach would undoubtedly give more robust conclusions than a purely observational study such as this.

As with most citizen science surveys, the data is reliant on the hard work of volunteers and as such tends to be concentrated in areas of high population density. Although there is generally reasonable coverage in areas of high population density, we can see from Figure 1.5 that many of these sites are concentrated around the south and east of the UK, with a relatively small number in Scotland. Incorporating a greater number of sites in Scotland would ensure that the results outlined in the thesis were consistent, whilst also reducing uncertainty levels in these regions (see Figure 6.3).

Extension of the spatio-temporal approach to consider other possible drivers of the inverse relationship between predator and prey species would be advantageous. As computer capabilities become ever-greater, it may became feasible to fit a more complex model with the added fixed effects to ensure that the inverse relationship found between house sparrows and sparrowhawks is not accounted for by other covariates.

In this thesis, we have only considered a single predator of songbirds, that is the sparrowhawk. There are obviously other species of predator that may be having additional and potentially greater effects on the populations of songbirds, both natural and human-introduced. Sparrowhawks have received most of the attention as a potential causal factor in the declines of songbirds due to the temporal correlation in the increases in the former and decreases in the latter. An additional predator that has received a lot less research interest is the domestic cat. Baker et al. (2005) and

Bonnington et al. (2013) have studied the effect of domestic cats on birds and found that it has the potential to be significant. Baker et al. (2005) found that for house sparrows predation by cats was high relative to annual productivity and hence may have created local reductions in the populations of this species. Further research on the level of these analyses would be ideal, however it may be unrealistic to expect the data to be available on the number of domestic cats at a similar spatial scale.

Overall, the continued and long-term monitoring of species such as this gives huge potential for analysing and understanding the dynamics and drivers of population change. It is unlikely that at the time of its inception the importance of the data collected from the GBFS could have been fully comprehended, however the analyses conducted in this thesis would not have been possible without them. The types of data that can be collected is becoming ever greater with the advancement of new technologies and the methods developed to analyse these data are becoming more sophisticated. However, the need for long-term data collected by armies of volunteers is as important as ever in a constantly changing environment, as the results of this thesis prove.

Appendix

Further results

Additional species-model combinations to those fitted in Chapter 5. Below are the results from these models.

Table A.1: House sparrow, starling and blue tit multi-species model. Intercept only model (no covariates).

Parameter	Covariate	Posterior mean	MPP	95%CI
α_{hs}	Intercept	-0.0497	NA	(-0.0602,-0.0398)
α_{st}	Intercept	-0.0591	NA	(-0.0701,-0.0472)
α_{bt}	Intercept	-0.0234	NA	(-0.0275,-0.0177)
ϕ	-	0.5851	NA	(0.5709,0.6002)
p	-	1.3820	NA	(1.3734,1.3908)
σ^2_ϵ	-	0.0007	NA	(0.0004,0.0010)
σ^2_{hs}	-	0.0136	NA	(0.0116,0.0158)
σ^2_{st}	-	0.0147	NA	(0.0125,0.0172)
σ^2_{bt}	-	0.0004	NA	(0.0002,0.0007)
ICC_{hs}	-	0.0490		
ICC_{st}	-	0.0455		
ICC_{bt}	-	0.6364		
C_ϵ	-	-0.2857		
C_{hs}	-	-0.0816		
C_{st}	-	-0.1838		
C_{bt}	-	-0.5000		

Table A.2: Starling and coal tit multi-species model. Intercept and density dependence species-specific.

Parameter	Covariate	Posterior mean	MPP	95%CI
α_{st}	Intercept	-0.0592	NA	(-0.0710,-0.0478)
α_{ct}	Intercept	-0.0744	NA	(-0.0783,-0.0356)
β_1	Northing	-0.0033	0.7580	(-0.0137,0.0136)
β_2	Easting	-0.0136	0.9329	(-0.0227,0.0017)
β_3	Sub/rur	0.0023	0.6189	(-0.0131,0.0132)
ν_{st}	Dens dep	NA	0.0000	NA
ν_{ct}	Dens dep	NA	0.0000	NA
γ_1	Sparrowhawk	-0.0173	1.0000	(-0.0230,-0.0118)
γ_2	Collared dove	NA	0.0000	NA
γ_3	Ground frost	0.0367	1.0000	(0.0301,0.0436)
ϕ	-	0.5955	NA	(0.5815,0.6106)
p	-	1.3971	NA	(1.3886,1.4056)
σ^2_ϵ	-	0.0162	NA	(0.0136,0.0191)
σ^2_{st}	-	0.0037	NA	(0.0026,0.0049)
σ^2_{ct}	-	0.0013	NA	(0.0007,0.0023)
ICC$_{st}$	-	0.0743		
ICC$_{ct}$	-	0.2600		

Table A.3: Blackbird, blue tit, chaffinch, coal tit, greenfinch, great tit, house sparrow, robin and starling multi-species model. Intercept and density dependence species-specific.

Parameter	Covariate	Posterior mean	MPP	95%CI
α_{bb}	Intercept	-0.0083	NA	(-0.0133,-0.0032)
α_{bt}	Intercept	-0.0325	NA	(-0.0387,-0.0264)
α_{ch}	Intercept	-0.0034	NA	(-0.0110,0.0042)
α_{ct}	Intercept	-0.0502	NA	(-0.0609,-0.0391)
α_{gf}	Intercept	-0.0307	NA	(-0.0403,-0.0215)
α_{gt}	Intercept	-0.0295	NA	(-0.0348,-0.0221)
α_{hs}	Intercept	-0.0475	NA	(-0.0582,-0.0374)
α_{rb}	Intercept	-0.0255	NA	(-0.0307,-0.0183)
α_{st}	Intercept	-0.0560	NA	(-0.0672,-0.0449)
β_1	Northing	0.0027	0.5925	(0.0132,0.0119)
β_2	Easting	-0.0056	0.8060	(-0.0115,0.0028)
β_3	Sub/rur	-0.0093	1.0000	(-0.0136,-0.0052)
ν_{bb}	Dens dep	NA	0.0000	NA
ν_{bt}	Dens dep	-0.0065	0.5441	(-0.0103,-0.0031)
ν_{ch}	Dens dep	-0.0156	1.0000	(-0.0198,-0.0108)
ν_{ct}	Dens dep	NA	0.0000	NA
ν_{gf}	Dens dep	-0.0120	1.0000	(-0.0171,-0.0073)
ν_{gt}	Dens dep	-0.0077	1.0000	(-0.0119,-0.0037)
ν_{hs}	Dens dep	NA	0.0000	NA
ν_{rb}	Dens dep	-0.0138	1.0000	(-0.0183,-0.0090)
ν_{st}	Dens dep	NA	0.0000	NA
γ_1	Sparrowhawk	NA	0.0000	NA
γ_2	Collared dove	NA	0.0000	NA
γ_3	Ground frost	NA	0.0000	NA

Cont.

Parameter	Covariate	Posterior mean	MPP	95%CI
ϕ	-	0.6834	NA	(0.6779,0.6877)
p	-	1.3567	NA	(1.3552,1.3581)
σ^2_ϵ	-	0.0015	NA	(0.0012,0.0018)
σ^2_{bb}	-	0.0005	NA	(0.0003,0.0007)
σ^2_{bt}	-	0.0006	NA	(0.0004,0.0008)
σ^2_{ch}	-	0.0037	NA	(0.0029,0.0048)
σ^2_{ct}	-	0.0027	NA	(0.0021,0.0036)
σ^2_{gf}	-	0.0091	NA	(0.0076,0.0109)
σ^2_{gt}	-	0.0003	NA	(0.0002,0.0005)
σ^2_{hs}	-	0.0129	NA	(0.0111,0.0152)
σ^2_{rb}	-	0.0002	NA	(0.0001,0.0003)
σ^2_{st}	-	0.0142	NA	(0.0122,0.0167)
ICC_{bb}	-	0.7500		
ICC_{bt}	-	0.7143		
ICC_{ch}	-	0.2885		
ICC_{ct}	-	0.3571		
ICC_{gf}	-	0.1415		
ICC_{gt}	-	0.8333		
ICC_{hs}	-	0.1042		
ICC_{rb}	-	0.8824		
ICC_{st}	-	0.0955		

Table A.4: House sparrow, starling and blue tit multi-species model. Intercept and density dependence species-specific.

Parameter	Covariate	Posterior mean	MPP	95%CI
α_{hs}	Intercept	-0.0511	NA	(-0.0617,-0.0407)
α_{st}	Intercept	-0.0580	NA	(-0.0684,-0.0476)
α_{bt}	Intercept	-0.0234	NA	(-0.0300,-0.0163)
β_1	Northing	-0.0143	1.0000	(-0.0120,-0.0087)
β_2	Easting	-0.0167	1.0000	(-0.0225,-0.0107)
β_3	Sub/rur	-0.0070	0.8134	(-0.0132,0.0076)
ν_{hs}	Dens dep	NA	0.0000	NA
ν_{st}	Dens dep	NA	0.0000	NA
ν_{bt}	Dens dep	-0.0081	0.7141	(-0.0366,-0.0225)
γ_1	Sparrowhawk	-0.0321	1.0000	(-0.0357,-0.0283)
γ_2	Collared dove	NA	0.0000	NA
γ_3	Ground frost	0.0337	1.0000	(0.0294,0.0382)
ϕ	-	0.5715	NA	(0.5584,0.5847)
p	-	1.3691	NA	(1.3606,1.3782)
σ^2_ϵ	-	0.0019	NA	(0.0014,0.0026)
σ^2_{hs}	-	0.0127	NA	(0.0108,0.0150)
σ^2_{st}	-	0.0118	NA	(0.0099,0.0143)
σ^2_{bt}	-	0.0012	NA	(0.0008,0.0018)
ICC_{hs}	-	0.1301		
ICC_{st}	-	0.1387		
ICC_{bt}	-	0.6129		

Table A.5: Blackbird, chaffinch, greenfinch, house sparrow, robin and starling multi-species model. Intercept and density dependence species-specific.

Parameter	Covariate	Posterior mean	MPP	95%CI
α_{bb}	Intercept	-0.0054	NA	(-0.0128,0.0026)
α_{cf}	Intercept	-0.0054	NA	(-0.0152,0.0033)
α_{gf}	Intercept	-0.0340	NA	(-0.0464,-0.0205)
α_{hs}	Intercept	-0.0526	NA	(-0.0653,-0.0404)
α_{rb}	Intercept	-0.0183	NA	(-0.0266,-0.0113)
α_{st}	Intercept	-0.0641	NA	(-0.0775,-0.0507)
β_1	Northing	-0.0153	1.0000	(-0.0208,-0.0103)
β_2	Easting	-0.0189	1.0000	(-0.0242,-0.0138)
β_3	Sub/rur	-0.0033	0.5581	(-0.0145,0.0162)
ν_{bb}	Dens dep	NA	0.0000	NA
ν_{cf}	Dens dep	NA	0.0000	NA
ν_{gf}	Dens dep	NA	0.0000	NA
ν_{hs}	Dens dep	NA	0.0000	NA
ν_{rb}	Dens dep	-0.0166	1.0000	(-0.0212,-0.0116)
ν_{st}	Dens dep	NA	0.0000	NA
γ_1	Sparrowhawk	NA	0.0000	NA
γ_2	Collared dove	NA	0.0000	NA
γ_3	Ground frost	0.0403	1.0000	(0.0369,0.0441)
ϕ	-	0.4482	NA	(0.4409,0.4553)
p	-	1.4061	NA	(1.3990,1.4134)
σ^2_ϵ	-	0.0026	NA	(0.0022,0.0032)
σ^2_{bb}	-	0.0002	NA	(0.0001,0.0004)
σ^2_{cf}	-	0.0049	NA	(0.0040,0.0059)
σ^2_{gf}	-	0.0118	NA	(0.0099,0.0143)
σ^2_{hs}	-	0.0157	NA	(0.0135,0.0184)
σ^2_{rb}	-	0.0002	NA	(0.0001,0.0003)
σ^2_{st}	-	0.0154	NA	(0.0131,0.0182)
ICC$_{bb}$	-	0.9286		
ICC$_{cf}$	-	0.3467		
ICC$_{gf}$	-	0.1806		
ICC$_{hs}$	-	0.1421		
ICC$_{rb}$	-	0.9286		
ICC$_{st}$	-	0.1444		

Table A.6: House sparrow and starling multi-species model. Intercept and time-varying coefficients species-specific. RJ on $\boldsymbol{\beta}$ and $\boldsymbol{\nu}$.

Parameter	Covariate	Posterior mean	MPP	95%CI
α_{hs}	Intercept	-0.0528	NA	(0.0633,-0.0426)
α_{st}	Intercept	-0.0548	NA	(-0.0673,-0.0445)
β_1	Northing	-0.0148	0.8961	(-0.0254,0.0018)
β_2	Easting	-0.0161	0.9469	(-0.0262,-0.0032)
β_3	Sub/rur	-0.0019	0.4860	(-0.0139,0.0149)
ν_{hs}	Dens dep	NA	0.0000	NA
ν_{st}	Dens dep	NA	0.0000	NA
γ_{1hs}	Sparrowhawk	-0.0461	-	(-0.0550,-0.0401)
γ_{1st}	Sparrowhawk	-0.0444	-	(-0.0506,-0.0366)
γ_{2hs}	Collared dove	0.0038	-	(-0.0020,0.0075)
γ_{2st}	Collared dove	0.0053	-	(0.0012,0.0113)
γ_{3hs}	Ground frost	0.0442	-	(0.0378,0.0501)
γ_{3st}	Ground frost	0.0442	-	(0.0378,0.0501)
ϕ	-	0.7307	NA	(0.7131,0.7497)
p	-	1.3852	NA	(1.3761,1.3938)
σ^2_ϵ	-	0.0081	NA	(0.0065,0.0100)
σ^2_{hs}	-	0.0066	NA	(0.0049,0.0089)
σ^2_{st}	-	0.0058	NA	(0.0043,0.0078)
ICC$_{hs}$	-	0.5510		
ICC$_{st}$	-	0.5827		

Table A.7: Blackbird and house sparrow multi-species model. Intercept, density dependence and sparrowhawk effect species-specific.

Parameter	Covariate	Posterior mean	MPP	95%CI
α_{bb}	Intercept	0.0007	NA	(-0.0042,0.0062)
α_{hs}	Intercept	-0.0538	NA	(-0.0648,-0.0430)
β_1	Northing	-0.0097	0.9938	(-0.0159,-0.0044)
β_2	Easting	-0.0130	1.0000	(-0.0185,-0.0071)
β_3	Sub/rur	-0.0017	0.5735	(-0.0154,0.0142)
ν_{bb}	Dens dep	NA	0.0000	NA
ν_{hs}	Dens dep	NA	0.0000	NA
γ_{1bb}	Sparrowhawk	0.0051	-	(0.0004,0.0099)
γ_{1hs}	Sparrowhawk	-0.0581	-	(-0.0630,-0.0522)
γ_2	Collared dove	NA	0.0000	NA
γ_3	Ground frost	0.0256	1.0000	(0.0208,0.0309)
ϕ	-	0.4615	NA	(0.4490,0.4748)
p	-	1.3700	NA	(1.3573,1.3818)
σ^2_ϵ	-	0.0011	NA	(0.0007,0.0016)
σ^2_{bb}	-	0.0007	NA	(0.0004,0.0013)
σ^2_{hs}	-	0.0167	NA	(0.0143,0.0193)
ICC$_{bb}$	-	0.6111		
ICC$_{hs}$	-	0.0618		

Table A.8: Robin, great tit and blue tit multi-species model. Intercept, density dependence and sparrowhawk effect species-specific.

Parameter	Covariate	Posterior mean	MPP	95%CI
α_{rb}	Intercept	-0.0069	NA	(-0.0144,-0.0019)
α_{gt}	Intercept	-0.0192	NA	(-0.0261,-0.0141)
α_{bt}	Intercept	-0.0265	NA	(-0.0350,-0.0199)
β_1	Northing	0.0001	0.5092	(-0.0165,0.0156)
β_2	Easting	-0.0035	0.5560	(-0.0128,0.0131)
β_3	Sub/rur	-0.0153	1.0000	(-0.0206,-0.0101)
ν_{rb}	Dens dep	-0.0365	1.0000	(-0.0408,-0.0319)
ν_{gt}	Dens dep	-0.0240	1.0000	(-0.0274,-0.0206)
ν_{bt}	Dens dep	-0.0193	1.0000	(-0.0220,-0.0169)
γ_{1rb}	Sparrowhawk	0.0061	-	(0.0024,0.0101)
γ_{1gt}	Sparrowhawk	-0.0052	-	(-0.0087,-0.0015)
γ_{1bt}	Sparrowhawk	-0.0138	-	(-0.0170,-0.0096)
γ_2	Collared dove	NA	0.0000	NA
γ_3	Ground frost	NA	0.0000	NA
ϕ	-	0.1632	NA	(0.1597,0.1668)
p	-	1.2420	NA	(1.2280,1.2567)
σ^2_ϵ	-	0.0031	NA	(0.0027,0.0036)
σ^2_{rb}	-	0.0006	NA	(0.0004,0.0013)
σ^2_{gt}	-	0.0006	NA	(0.0004,0.0013)
σ^2_{bt}	-	0.0006	NA	(0.0004,0.0009)
ICC_{rb}	-	0.8378		
ICC_{gt}	-	0.8378		
ICC_{bt}	-	0.8378		

Table A.9: House sparrow, starling and blue tit multi-species model. Intercept and density dependence species-specific. Other parameters reversible jump to test for pairwise synchrony.

Parameter	Covariate	Posterior mean	MPP	95%CI
α_{hs}	Intercept	-0.0566	NA	(-0.0677,-0.0458)
α_{st}	Intercept	-0.0507	NA	(-0.0617,-0.0393)
α_{bt}	Intercept	-0.0245	NA	(-0.0293,-0.0190)
β_{1hs}	Northing	-0.0103	NA	(-0.0264,-0.0008)
β_{1st}	Northing	-0.0102	NA	(-0.0172,-0.0046)
β_{1bt}	Northing	-0.0153	NA	(-0.0156,-0.0047)
β_{2hs}	Easting	-0.0051	NA	(-0.0154,0.0066)
β_{2st}	Easting	-0.0114	NA	(-0.0315,-0.0039)
β_{2bt}	Easting	-0.0072	NA	(-0.0122,-0.0013)
β_{3hs}	Sub/rur	0.0008	NA	(-0.0094,0.0125)
β_{3st}	Sub/rur	-0.0056	NA	(-0.0168,-0.0004)
β_{3bt}	Sub/rur	-0.0052	NA	(-0.0100,-0.000)
ν_{hs}	Dens dep	NA	0.0000	NA
ν_{st}	Dens dep	NA	0.0000	NA
ν_{bt}	Dens dep	NA	0.0000	NA
γ_{1hs}	Sparrowhawk	-0.0411	NA	(-0.0494,-0.0329)
γ_{1st}	Sparrowhawk	-0.0516	NA	(-0.0585,-0.0431)
γ_{1bt}	Sparrowhawk	-0.0074	NA	(-0.0122,-0.0024)
γ_{2hs}	Collared dove	0.0051	NA	(0.0007,0.0100)
γ_{2st}	Collared dove	0.0009	NA	(-0.0028,0.0060)
γ_{2bt}	Collared dove	-0.0005	NA	(-0.0064,0.0032)
γ_{3hs}	Ground frost	0.0462	NA	(0.0400,0.0516)
γ_{3st}	Ground frost	0.0460	NA	(0.0396,0.0510)
γ_{3bt}	Ground frost	0.0086	NA	(0.0025,0.0148)
ϕ	-	0.5645	NA	(0.5512,0.5787)
p	-	1.3679	NA	(1.3587,1.3767)
σ^2_ϵ	-	0.0009	NA	(0.0006,0.0014)
σ^2_{hs}	-	0.0161	NA	(0.0139,0.0188)
σ^2_{st}	-	0.0159	NA	(0.0137,0.0185)
σ^2_{bt}	-	0.0006	NA	(0.0003,0.0011)
ICC_{hs}	-	0.0529		
ICC_{st}	-	0.0536		
ICC_{bt}	-	0.6000		

Table A.10: $\boldsymbol{\beta}_s$ marginal posterior probabilities for each pair of species from the model in Table A.9, corresponding to northing easting, and suburban/rural resectively.

Parameters	MPP	Parameters	MPP	Parameters	MPP
$\beta_{1hs}, \beta_{1st}, \beta_{1bt}$	0.0530	$\beta_{2hs}, \beta_{2st}, \beta_{2bt}$	0.1395	$\beta_{3hs}, \beta_{3st}, \beta_{3bt}$	0.0927
$\beta_{1hs:bt}, \beta_{1st}$	0.9150	$\beta_{2hs:bt}, \beta_{2st}$	0.5319	$\beta_{3hs:bt}, \beta_{3st}$	0.8677
$\beta_{1st:bt}, \beta_{1hs}$	0.0209	$\beta_{2st:bt}, \beta_{2hs}$	0.3250	$\beta_{3st:bt}, \beta_{3hs}$	0.0385
$\beta_{1hs:st}, \beta_{1bt}$	0.0111	$\beta_{2hs:st}, \gamma_{2bt}$	0.0036	$\beta_{3hs:st}, \gamma_{3bt}$	0.0011

Table A.11: $\boldsymbol{\gamma}_s$ marginal posterior probabilities for each pair of species from the model in Table A.9, corresponding to sparrowhawkm collared dove and ground frost respectively.

Parameters	MPP	Parameters	MPP	Parameters	MPP
$\gamma_{1hs}, \gamma_{1st}, \gamma_{1bt}$	0.7408	$\gamma_{2hs}, \gamma_{2st}, \gamma_{2bt}$	0.1657	$\gamma_{3hs}, \gamma_{3st}, \gamma_{3bt}$	0.1324
$\gamma_{1hs:st}, \gamma_{1bt}$	0.2592	$\gamma_{2hs:st}, \gamma_{2bt}$	0.1627	$\gamma_{3hs:st}, \gamma_{3bt}$	0.8676
		$\gamma_{2st:bt}, \gamma_{2hs}$	0.0025		
		$\gamma_{2hs:bt}, \gamma_{2st}$	0.6690		

Table A.12: House sparrow, starling and blue tit multi-species model. All parameters species-specific. Other parameters reversible jump to test for pairwise synchrony.

Parameter	Covariate	Posterior mean	95%CI
α_{hs}	Intercept	-0.0540	(-0.0643,-0.0436)
α_{st}	Intercept	-0.0645	(-0.0749,-0.0540)
α_{bt}	Intercept	-0.0289	(-0.0337,-0.0235)
β_{1hs}	Northing	-0.0090	(-0.0205,0.0015)
β_{1st}	Northing	-0.0072	(-0.0176,-0.0004)
β_{1bt}	Northing	-0.0040	(-0.0091,0.0014)
β_{2hs}	Easting	-0.0257	(-0.0367,-0.0148)
β_{2st}	Easting	-0.0035	(-0.0087,0.0018)
β_{2bt}	Easting	-0.0032	(-0.0077,0.0018)
β_{3hs}	Sub/rur	-0.0020	(-0.0077,0.0059)
β_{3st}	Sub/rur	0.0054	(-0.0047,0.0161)
β_{3bt}	Sub/rur	-0.0027	(-0.0077,0.0017)
ν_{hs}	Dens dep	NA	NA
ν_{st}	Dens dep	-0.0226	(-0.0284,-0.0173)
ν_{bt}	Dens dep	NA	NA
γ_{1hs}	Sparrowhawk	-0.0536	(-0.0598,-0.0475)
γ_{1st}	Sparrowhawk	-0.0257	(-0.0321,-0.0191)
γ_{1bt}	Sparrowhawk	-0.0079	(-0.0126,-0.0034)
γ_{2hs}	Collared dove	0.0032	(-0.0009,0.0082)
γ_{2st}	Collared dove	0.0075	(0.0032,0.0120)
γ_{2bt}	Collared dove	0.0014	(-0.0026,0.0048)
γ_{3hs}	Ground frost	0.0369	(0.0325,0.0424)
γ_{3st}	Ground frost	0.0367	(0.0321,0.0417)
γ_{3bt}	Ground frost	0.0081	(0.0023,0.0138)
ϕ	-	0.5538	(0.5421,0.5659)
p	-	1.3611	(1.3521,1.3706)
σ^2_ϵ	-	0.0008	(0.0004,0.0011)
σ^2_{hs}	-	0.0153	(0.0130,0.0179)
σ^2_{st}	-	0.0133	(0.0112,0.0157)
σ^2_{bt}	-	0.0006	(0.0004,0.0009)
ICC_{hs}	-	0.0497	(0.0262,0.0718)
ICC_{st}	-	0.0567	(0.0294,0.0822)
ICC_{bt}	-	0.5714	(0.3544,0.7336)

Table A.13: Density dependence marginal posterior probabilities.

Species	MPP
House sparrow	0.0000
Starling	1.0000
Blue tit	0.0000

Table A.14: $\boldsymbol{\beta}_s$ marginal posterior probabilities for each pair of species from the model in Table A.12, corresponding to northing easting, and suburban/rural respectively.

Parameters	MPP	Parameters	MPP	Parameters	MPP
$\beta_{1hs}, \beta_{1st}, \beta_{1bt}$	0.0133	$\beta_{2hs}, \beta_{2st}, \beta_{2bt}$	0.0560	$\beta_{hs}, \beta_{3st}, \beta_{3bt}$	0.0017
$\beta_{1st:bt}, \beta_{1hs}$	0.5272	$\beta_{2st:bt}, \beta_{2hs}$	0.9441	$\beta_{hs:bt}, \beta_{3st}$	0.8843
$\beta_{1hs:bt}, \beta_{1st}$	0.0832			$\beta_{hs:st}, \beta_{3bt}$	0.1141
$\beta_{1hs:st}, \beta_{1hs}$	0.3763				

Table A.15: $\boldsymbol{\gamma}_s$ marginal posterior probabilities for each pair of species from the model in Table A.12, corresponding to sparrowhawk collared dove and ground frost respectively.

Parameters	MPP	Parameters	MPP	Parameters	MPP
$\gamma_{1hs}, \gamma_{1st}, \gamma_{1bt}$	1.0000	$\gamma_{2hs}, \gamma_{2st}, \gamma_{2bt}$	0.0246	$\gamma_{3hs}, \gamma_{3st}, \gamma_{3bt}$	0.0290
		$\gamma_{2hs:bt}, \gamma_{2st}$	0.6677	$\gamma_{3hs:st}, \gamma_{3bt}$	0.9710
		$\gamma_{2hs:st}, \gamma_{2bt}$	0.3077		

Table A.16: House sparrow, greenfinch and chaffinch multi-species model. Intercept and density-dependence parameters are species-specific, with the reversible jump algorithm used to test for synchrony across the three species for all other regression covariate parameters. Posterior means and 95% symmetric credible intervals are presented. Covariate dependence is also conducted on the density-dependence parameters.

Parameter	Covariate	Posterior mean	95%CI
α_{hs}	Intercept	-0.0600	(-0.0720,-0.0485)
α_{gf}	Intercept	-0.0353	(-0.0453,-0.0250)
α_{cf}	Intercept	-0.0058	(-0.0138,0.0021)
β_{1hs}	Northing	-0.0060	(-0.0192,0.0048)
β_{1gf}	Northing	-0.0012	(-0.0102,0.0076)
β_{1cf}	Northing	-0.0008	(-0.0084,0.0072)
β_{2hs}	Easting	-0.0285	(-0.0400,-0.0178)
β_{2gf}	Easting	-0.0246	(-0.0360,-0.0146)
β_{2cf}	Easting	-0.0226	(-0.0315,-0.0138)
β_{3hs}	Sub/rur	-0.0156	(-0.0252,-0.0043)
β_{3gf}	Sub/rur	-0.0181	(-0.0266,-0.0087)
β_{3cf}	Sub/rur	-0.0202	(-0.0277,-0.0129)
$\nu_{hs,hs}$	Dens dep	NA	NA
$\nu_{gf,gf}$	Dens dep	**-0.0142**	(-0.0195,-0.0093)
$\nu_{cf,cf}$	Dens dep	**-0.0282**	(-0.0330,-0.0228)
$\nu_{gf,hs}$	Interaction	**0.0327**	(0.0258,0.0401)
$\nu_{cf,hs}$	Interaction	**-0.0462**	(-0.0555,-0.0367)
γ_{1hs}	Sparrowhawk	-0.0459	(-0.0532,-0.0387)
γ_{1gf}	Sparrowhawk	-0.0016	(-0.0064,0.0035)
γ_{1cf}	Sparrowhawk	-0.0016	(-0.0063,0.0036)
γ_{2hs}	Collared dove	0.0037	(0.0003,0.0071)
γ_{2gf}	Collared dove	0.0036	(0.0001,0.0071)
γ_{2cf}	Collared dove	0.0118	(0.0070,0.0175)
γ_{3hs}	Ground frost	0.0375	(0.0321,0.0431)
γ_{3gf}	Ground frost	0.0145	(0.0046,0.0238)
γ_{3cf}	Ground frost	0.0375	(0.0321,0.0431)
ϕ_{hs}	-	0.6867	(0.6619,0.7121)
ϕ_{gf}	-	0.5360	(0.5182,0.5545)
ϕ_{cf}	-	0.3890	(0.3754,0.4029)
p_{hs}	-	1.3534	(1.3407,1.3639)
p_{gf}	-	1.4218	(1.4069,1.4370)
p_{cf}	-	1.3563	(1.3450,1.3731)

Table A.17: House sparrow, greenfinch and chaffinch multi-species model. Intercept and density-dependence parameters are species-specific, with the reversible jump algorithm used to test for synchrony across the three species for all other regression covariate parameters. Posterior means and 95% symmetric credible intervals are presented. Covariate dependence is also conducted on the density-dependence parameters.

Parameter	Posterior mean	95%CI
σ^2_ϵ	0.0037	(0.0027,0.0050)
σ^2_{hs}	0.0145	(0.0120,0.0173)
σ^2_{gf}	0.0084	(0.0068,0.0103)
σ^2_{cf}	0.0039	(0.0025,0.0055)
ICC_{hs}	0.205	(0.154,0.256)
ICC_{gf}	0.308	(0.221,0.398)
ICC_{cf}	0.495	(0.344,0.648)

Table A.18: $\boldsymbol{\beta}_s$ marginal posterior probabilities testing for synchrony in response to environmental covariates from the model in Table A.16, corresponding to northing, easting, and suburban/rural respectively. $\{hs, gf\}$ denotes that the parameter shared across house sparrow and greenfinch.

Northing		Easting		Sub/rur	
Model	MPP	Model	MPP	Model	MPP
$\beta_1 gf : cf, \beta_1 hs$	0.591	$\beta_2 gf, cf, \beta_2 hs$	0.649	$\beta_3 gf, cf, \beta_3 hs$	0.494
$\beta_1 hs, cf, \beta_1 gf$	0.223	$\beta_2 hs, gf, \beta_2 cf$	0.238	$\beta_3 hs, cf, \beta_3 gf$	0.252
$\beta_1 hs, gf, \beta_1 cf$	0.175	$\beta_2 hs, cf, \beta_2 gf$	0.105	$\beta_3 hs, gf, \beta_3 cf$	0.250
$\beta_1 hs, \beta_1 gf, \beta_1 cf$	0.010	$\beta_2 hs, \beta_2 gf, \beta_2 cf$	0.008	$\beta_3 hs, \beta_3 gf, \beta_3 cf$	0.003

Table A.19: $\boldsymbol{\gamma}_s$ marginal posterior probabilities testing for synchrony in response to environmental covariates from the model in Table A.16, corresponding to sparrowhawk collared dove and ground frost respectively. $\{hs, gf\}$ denotes the parameter shared across house sparrow and greenfinch.

Sparrowhawk		Collared dove		Ground frost	
Model	MPP	Model	MPP	Model	MPP
$\gamma_1 gf, cf, \gamma_1 hs$	0.991	$\gamma_2 hs, gf, \gamma_2 cf$	0.981	$\gamma_3 hs, cf, \gamma_3 gf$	0.994
$\gamma_1 hs, \gamma_1 gf, \gamma_1 cf$	0.009	$\gamma_2 hs, \gamma_2 gf, \gamma_2 cf$	0.019	$\gamma_3 hs, \gamma_3 gf, \gamma_3 cf$	0.006

Table A.20: Marginal posterior probabilities relating to the sharing of the two Tweedie variance parameters across tit species from the model in Table A.16. $\{hs, gt\}$ denotes the parameter shared across blue tit and great tit.

ϕ		p	
Model	MPP	Model	MPP
$\phi_{hs}, \phi_{gf}, \phi_{cf}$	1.000	$p_{hs,cf}, p_{gf}$	0.835
		p_{hs}, p_{gf}, p_{cf}	0.165

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