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Long-term responses of bird populations to environmental and climatic changes

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Contents

Abstract

An extensive knowledge about population responses to ongoing environmental and climatic changes is a primary goal to enhance environmental policies and promote biodiversity conservation. The capacity of a population in responding to rapid changes occurring within ecosystems is one of the most important aspects that can determine its trajectory over space and time. Populations can show several types of responses to environmental pressures, which can also be interrelated. This thesis describes four studies that analyse some long-term responses of bird populations from both a methodological and applicative point of view, providing novel and valuable findings not only for bird studies but also in a broad ecological perspective. The first research focused on some methodological issues in population trend modelling. Changes in population size over time (i.e. population trends) are one of the clearest responses of populations to environmental changes, and represent a key tool for wildlife conservation. Thus, improving the capacity of estimating trends is pivotal. The study investigated the effects of the environmental bias, which may affect many existing surveys because of a variation in the sampling effort or design over space and time, and of two statistical properties of count data, namely overdispersion and zero inflation, on the estimation process of population trends. A multi-step modelling approach was proposed, and findings highlighted that the environmental bias was the most important factor that causes differences in trend estimates across models. Additionally, overdispersion and zero inflation can influence, also significantly, the estimates, and modelling frameworks should consider their evaluation in the statistical approach. In the second work, this modelling framework was applied to assess the long-term population trends for common breeding birds at regional scale (northern Italy). Additionally, through a trait-based approach, the study investigated whether species with similar life-history and ecological traits shared similar population dynamics. Findings allowed identifying species that need more conservation attention and for which management measures are required to avoid further population declines. The trait-based approach allowed identifying which ecological and functional groups need greater attention, emphasising the usefulness of traits' information to plan further studies aimed at identifying the drivers at the basis of the observed population changes. Then, the third study focused on niche modelling to understand whether a species can adapt its realised Grinnellian niche along relatively long-term periods as results of ongoing environmental changes. Moreover, the study assessed whether the observed changes were linked to population trends,

obtained from the previous work, and to species traits. The multi-species analysis on common breeding birds highlighted that niche conservatism is not a ubiquitous condition, and some species are changing their niches. Findings also showed the existence of non-random associations between niche changes and both population trends and groups of species sharing similar life-history and ecological traits. The last research dealt with assessing the effects of climate change on bird populations focusing on the extreme climatic events, which exacerbation and increase in frequency poses new global challenges for nature conservation. Using the UK Breeding Bird Survey, a long-term large-scale monitoring program, a multi-species analysis investigated how populations respond to extreme climatic events and which species are more sensitive to such climatic conditions. Findings highlighted widespread effects of extreme climatic events on the abundance of bird populations, suggesting that they could be a key driver for shaping future population dynamics. Long-term data revealed to be extremely important for assessing responses of populations in a changing environment and are essential to achieve a comprehensive perspective of ecological processes that can affect biocenoses and ecosystems.

Chapter 1

General introduction

1.1. Overview

A population is defined as a group of individuals of the same species inhabiting the same space during the same time (Berryman & Kindlmann, 2008). It is the level of organisation of living being where the natural selection occurs. A species is often distributed over separate populations. Its existence and dynamics are functions of exchanges and replacements among these interactive populations, which are called metapopulations (Pulliam, 1988; Hanski, 1998). The importance of studying population dynamics is crucial in ecology and conservation biology. Populations evolve, other than under pressures of both interspecific and intraspecific relationships, under environmental constraints (both natural and anthropogenic) often in a non-equilibrium state with the surrounding environment (Araújo & Pearson, 2005; Cheng et al., 2013; Brown & Carnaval, 2019). Human activities increased environmental changes on Earth at intolerable rates that imperil many species at all taxonomical levels (Steffen et al., 2015; Tilman et al., 2017). Habitat loss, fragmentation and degradation, pollution, climate change, invasive species, overhunting and overexploitation represent the major threats for the survival of wild populations (Butchart et al., 2010). The capacity to respond to rapid changes occurring in the environment is one of the most important factors that can determine the trajectory of a population over space and time. It depends on environmental pressures involved but also on intrinsic factors of the species and on the dynamics of interactions within ecosystems. Thus, populations of some species could negatively suffer from such changes, but others could benefit from it, with implications for biocenoses and ecosystem functioning (Şekercioğlu et al., 2004; Basile, 2022; Cavigliasso et al., 2022; Gruss et al., 2023). Populations can show several types of responses to environmental pressures. They can include variations in spatial distribution (Parmesan et al., 1999; Hickling et al., 2006; Chen et al., 2011; Brambilla et ., 2022), changes in population size over time (Newton, 2004; Stephens et al., 2016; Wan et al., 2022), adaptations to new or suboptimal environmental conditions or variations in environmental tolerances (i.e. changes in the realised ecological niche; Broennimann et al., 2014; Labisko et al., 2022), variations in phenology (Cleland et al., 2007; Vogt-Schilb et al., 2022), behaviour (Ventura et al., 2021; Islam et al., 2022), and fitness (Sergio et al., 2022). Our capacity in detecting such types of responses is pivotal to understand ecological processes affecting wild populations' dynamics, and, ultimately, to preserve biodiversity (Pereira et al., 2010).

1.1.1. Why birds

Birds provide all types of ecosystem services (Şekercioğlu et al., 2016), and they have proved to be good ecological indicators (Burger & Gochfeld, 2004; Morelli et al., 2021; Natsukawa, 2021; Reif et al., 2022). Birds are conspicuous and relatively easy to survey. Birds are widespread in most terrestrial habitats, their taxonomy is known and relatively well agreed and they are responsive to environmental and climatic changes (Pautasso, 2012; Chamberlain et al., 2016). The ecological relevance of avian species is well established, and they can provide valuable information about ecosystem processes (Mäntylä et al., 2011; Whelan et al., 2015), resulting to be important for conservation and environmental policies (Oettel & Lapin, 2021; Santangeli & Girardello, 2021; Virkkala et al., 2022). For example, bird data are used to produce some indicators for environmental assessment (e.g. the Common Farmland Bird Index and Common Forest Bird Index from the Pan European Common Bird Monitoring Scheme [PECBMS]; PECBMS, 2020) (Gregory et al., 2019; Kamp et al., 2021). Protecting birds does not just mean protecting avian species, but also safeguarding habitats on which they depend (e.g. Birds Directive 2009/147/EC in Europe). To date, over 13,600 Important Bird and Biodiversity Areas (IBAs) have been designed around the globe, covering 9% of Earth’s terrestrial area and 2% of its oceans (BirdLife International, 2022). Furthermore, the International Union for Conservation of Nature (IUCN) qualified the vast majority of IBAs as Key Biodiversity Areas (KBAs), and as a result 84% of KBAs have been recognised as important for birds (IUCN, 2016). Despite the great and increasing effort to promote their conservation, about 22% of the living bird species show significant conservation concern (BirdLife International, 2022). Thus, improving knowledge around species responses to rapid ongoing environmental changes is pivotal to implement and make effective conservation policies and to properly inform decision makers.

Birds have been attracting the attention of ecologists, conservationists and ordinary people for many decades. This led to a greater availability of data than other taxonomical groups, with considerable spatial and temporal coverage. Several sources of bird data are currently available, and they could be used for different purposes (Møller & Fiedler, 2010). Among them census data represent an important source of information that is mostly used for assessing population trends of breeding or wintering birds at national or continental level (e.g. PECBMS). Moreover, they have the potential to be used for several goals. In this context, one of the main advantages is the possibility to have a great amount of data over large temporal scale. Conversely, short-term and size-limited databases could prevent the ability of statistical models to detect significant effects of environmental variables on the response variable of interest, or the magnitude of such effects could remain ambiguous (Biró et al., 2018; González et al., 2022). Another significant advantage of bird census data is that they often contain information on multiple species. Indeed, they collect information on occurrence or abundance at a site for all co-occurring species. This allow investigating multiple species responses that can be used to address species-specific research questions as well as to have a more exhaustive perspective of ecological processes in avian communities. Moreover, multiple species surveys offer the edge of investigating whether groups of species with similar ecological and life-history characteristics (i.e. species traits) share similar responses. Over the past few decades, the trait-based approach is receiving increasing attention among ecologists, spreading out from plant ecology where it was originally proposed (Dawson et al., 2021). Despite the concept of "trait" is still debate (Dawson et al., 2021), the usefulness of embracing species traits in ecological studies is extensively recognised, also because of direct implications for nature conservation and landscape planning (Garcia-R. & Di Marco, 2020; Callaghan et al., 2020, 2021; Benedetti et al., 2022; Lakatos et al., 2022). Analysing responses across functional and ecological groups could permit highlighting the existence of analogous patterns across species with similar characteristics (Dumandan et al., 2021; Kamp et al., 2021; Hallman et al., 2022), providing the foundations to test specific hypotheses about the causes of the observed population responses in further studies.

1.2. Research questions

The main objective of the thesis was to assess some types of long-term responses of bird populations as results of environmental and climatic changes in order to provide valuable and novel evidence about the existing patterns of change. The investigation embraced methodological and applicative research whose results are transferable to other taxonomical groups with a broad ecological perspective.

Firstly, the assessment of population trends, i.e. the relative variation of population size over time, is critical for evaluating the status of wild populations (IUCN, 2012). It allows identifying species that need conservation attention as well as to evaluate the effectiveness of management strategies over time. Since the last century, several bird monitoring programs, both at national and continental scale, have been starting worldwide. For instance, in Europe a joint initiative of the European Bird Census Council and BirdLife International launched the PECBMS, in US and Canada the North American Breeding Bird Survey provide population trends for roughly 546 species (Sauer et al., 2017), and in many countries long-term monitoring programs at national level exist (e.g. the

Breeding Bird Surveys in UK, Harris et al., 2022). Large-scale collaborative projects allow implementing joint conservation policy with positive effects on biodiversity and environment. However, populations trends can vary across spatial and geographic gradients (Bowler et al., 2021) and their assessment at regional or local scale is worthy because they help local administrators and decision-makers for planning adequate environmental policies aimed at species and habitat conservation (Bani et al., 2009; Daskalova et al., 2019; Hughes et al., 2020). Population trend modelling has a long-running tradition in bird ecology and advances take place continuously (Link & Sauer, 1998; van Strien et al., 2000; Gregory et al., 2019; Fink et al., 2020). However, data used for assessing population trends may be affected by some sources of biases due to changes in methodologies in sampling, changes in quality of observers, and spatial or temporal heterogeneity in sampling effort. The latter situation can frequently occur in real cases, for example because of changes in funding allocation that limit the feasibility of maintaining a comparable spatial coverage across years. Furthermore, different bird census data deriving from different monitoring projects thought with distinct aims are often available for a specific geographic area. These data sets may be characterised by different survey designs, likely leading to source of heterogeneity that need to be taken into account. Anyway, they represent valuable source of data, especially when other sources are not available. Some recent works demonstrated that data integration can improve estimates of statistical parameters (Robinson et al., 2020; Strebel et al., 2022), and novel methodologies allow obtaining evaluation that are reliable also when data are characterised by biases inherited by differences in sampling design or variations in sampling effort over time (Massimino et al., 2008; Strebel et al., 2022). Additionally, statistical properties of count data, collected through bird census, need to be carefully taken into account. In this context, one of the major issues that is still overlooked in population trend modelling is the mutual interaction between overdispersion, i.e. the variance of a random variable is greater than the mean (Zuur et al., 2009) and the zero-inflation process (Ridout et al., 2001; Blasco-Moreno et al., 2019). The extent to which they could affect trend estimates is a significant issue that merits attentive consideration.

The second type of population responses I focused on concerns the assessment of niche changes that could be occurred in bird populations over time. The concept of ecological niche is of crucial importance in ecology (Hutchinson, 1957; Chase & Leibold, 2003; Soberón, 2007; Holt, 2009). One of the most established theoretic definitions of niche refers to the Hutchinson's idea of fundamental niche, defined as "an n-dimensional hypervolume […], every point in which corresponds to a state of the environment which would permit [a] species […] to exist indefinitely" (Hutchinson, 1957).

When biotic interactions occur, e.g. interspecific competition, the species is constrained within a subset of its fundamental niche, i.e. the realised niche (Hutchinson, 1957). Hutchinson (1978) referred to “scenopoetic” those variables that are invariant to species, and to “bionomic” for interactive and resource-related variables. This distinction, alongside the former contributions of Grinnell and Elton (Grinnell, 1914, 1917; Elton, 1927), led to recognise two types of niches: the Grinnellian niche, defined by the non-interactive environmental (scenopoetic) variables, and the Eltonian niche, focusing on biotic interactions and resource-consumer dynamics (bionomic variables) (James et al., 1984; Soberón, 2007; Soberón & Nakamura, 2009). However, considering the advances in the scientific and computational knowledges, the transfer of the term “niche” in applied ecology remains controversial and ambiguous (McInerny & Etienne, 2012a,b,c), and it is fundamental specifying which niche, or components of the niche, we are considering in the modelling approach. Niche modelling flourished in the last two decades, especially regarding niche evolution in related taxa (e.g. Losos, 2008; Hending et al., 2021; Liu et al., 2021) or niche analyses for invasive species (e.g. Broennimann et al., 2014; Liu et al., 2020; Tang et al., 2021). However, the assessment of within-species niche changes occurred in a specific population (or sub-populations) over time has received little attention in ecology. A critical question that remains extensively unanswered is if populations of a species are changing their ecological niche over relativey long-term periods (e.g. decades). This is important not only from a theoretical point of view, but also in applied ecology. For example, correlative species distribution models assume niche conservatism (i.e. niches are retained over time or appear to evolve relatively slowly within lineages; Wiens & Graham, 2005; Soberón & Nakamura, 2009) and assessing if a species is able to modify its niche is pivotal for future predictions under ongoing environmental changes (Brown & Carnaval, 2019). Furthermore, niche changes could be linked to other population responses (e.g. population trends, Ralston et al., 2017) or vary in relation to species traits (Zurell et al., 2018; but see Santangeli et al., 2022), but such questions need to be considered more thoroughly because they are currently rather neglected.

The third population response analysed and discussed in this thesis is linked to climate change. Climate change has been recognised as one of the major threats for biodiversity and species conservation (Bellard et al., 2012; Urban et al., 2015; Wiens, 2016; Manes et al., 2021). Most research effort had been focused on ecological and biological effects of long-term average change in climate, but in the last two decades extreme climatic events (e.g. extreme temperatures, heavy rainfall, prolonged drought) have attracted increasing concern among ecologists (Bailey & van de

Pol, 2016). Indeed, some studies showed that extreme climatic events can lead to greater biological consequences compared to changes in climatic means (Maron et al., 2015; Gardner et al., 2017; Harris et al., 2018; Marcelino et al., 2020), with widespread negative effects across all taxa and ecological levels (Maxwell et al., 2019). Extreme climatic events are expected to increase in frequency in the near future (IPCC, 2013), stressing the importance to assess their impact on ecological systems and biodiversity. However, well established methodologies for studying the effects of extreme climatic events effects on wild populations and assemblages (e.g. proxies of extreme climatic events, biological responses to be measured) have not been achieved yet, and extreme climatic events still represent a challenge that ecologists need to address extensively (Bailey & van de Pol, 2016).

1.3. Goals and thesis structure

The thesis addressed the following issues and pursued the following goals:

1. Methodological aspects in population trend modelling to provide novel insights for the trend estimation process (*Chapter 2*).
2. Assessment of long-term population trends at regional scale combining a species-by-species approach with a trait-based approach to provide findings for a conservation perspective (*Chapter 3*).
3. Assessment of long-term ecological niche changes and investigation of their relationship with both population trends and species traits (*Chapter 4*).
4. Investigation of the effects of extreme climatic events on populations over large spatial and temporal scales (*Chapter 5*).

The thesis consists in six chapters. This first chapter introduced a general and concise overview of the topics and outlined the motivations and the main research questions of the work. Then, a collection of four papers (three already published and one submitted), each of them is reported in a specific chapter (*Chapter 2-5*), extensively addresses the aforementioned topics. In the end, *Chapter 6* summarises the overall findings and future research perspectives.

In *Chapter 2*, I analysed some methodological questions in population trend modelling. Combining data collected from distinct structured monitoring programs, I suggested a methodological framework to improve population trend estimates taking into account issues linked to variation in sampling effort over space and time and to two statistical properties that could characterise count data, namely overdispersion and excess of zeroes. Correcting for biases deriving from variation in sampling effort represents a significant objective, also considering the increasing number of semi-strucured data currently available, and could allow using heterogenous data deriving from different surveys as well. Moreover, in the current widespread approaches, the excess of zero counts is too often overlooked or handled as a one of the sources leading to overdispersion, and the application of zero-inflated models for assessing population trends is mostly ignored. I discussed how these issues can affect the estimation process of population trends, and the importance of avoiding modelling choices based on supposed statistical assumptions in order improve the reliability of population trend estimates. In *Chapter 3*, I applied this modelling framework to assess population trends for common breeding birds at regional scale (northern Italy). Additionally, through a trait-based approach, I investigated whether species with similar life-history and ecological characteristics shared similar patterns of change in population trends. Findings allowed identifying species that need more conservation attention and for which management measures are required to avoid further population declines. The trait-based approach highlighted the importance to include species traits' information in population trend modelling, because it allows highlighting shared patterns of changes that are important to plan further studies aimed at identifying the drivers at the basis of the observed population changes. In *Chapter 4*, I focused on niche modelling to understand whether a species can adapt its realised niche along relatively long-term periods as response to ongoing environmental changes. I performed a multi-species niche analysis on common breeding birds to assess and quantify long-term changes occurred in their realised Grinnellian niche. Moreover, I examined whether the observed changes were linked to population trends, obtained from the previous work (*Chapter 3*), and to species traits. Findings represent a novelty in this research field and highlighted the existence of a non-random associations between niche changes and both population trends and groups of species sharing similar life-history and ecological characteristics. This study can contribute to improve the knowledge on niche dynamics providing valuable insights from both a theoretical and applied point of view. In *Chapter 5*, I dealt with climate change effects on bird populations with a focus on the effects of extreme climatic events, which is a topic of increasing interests among ecologists that needs to fill some gaps yet. This work is born from a collaboration with the British Trust for Ornithology (Thetford, UK), where I spent six months as visiting student. Using the UK Breeding Bird Survey, a long-term monitoring program collecting data since 1994, I performed a multi-species analysis at national scale in order to assess how populations respond to extreme climatic events and which species are more sensitive to such climatic conditions. Findings highlighted widespread effects of extreme climatic events on bird populations, suggesting that they could be a key driver for shaping future population dynamics. Lastly, in *Chapter 6*, concluding remarks from the previous chapters are summarised and future perspectives are discussed.

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Chapter 2

Population trends from count data: handling environmental bias, overdispersion and excess of zeroes

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Abstract

The assessment of population trends is a key point in wildlife conservation. Survey data collected over long period may not be comparable due to the presence of environmental biases (i.e. inadequate representation of the variability of environmental covariates in the study area). Moreover, count data may be affected by both overdispersion (i.e. the variance is larger than the mean) and excess of zero counts (potentially leading to zero inflation). The aim of this study was to define a modelling procedure to assess long-term population trends that addressed these three issues, and to shed light on the effects of environmental bias, overdispersion, and zero inflation on trend estimates. To test our procedure, we used six bird species whose data were collected in northern Italy from 1992 to 2019. We designed a multi-step approach. First, using generalised additive models (GAMs), we implemented a full factorial design of models (eight models per species) taking or not into account the environmental bias (including or not including environmental covariates, respectively), overdispersion (using a negative binomial distribution or a Poisson distribution, respectively), and zero inflation (using or not using zero-inflated models, respectively). Models were ranked according to the Akaike Information Criterion. Second, annual population indices (median and 95% confidence interval of the number of pairs per point count) were predicted through a parametric bootstrap procedure. Third, long-term population trends were assessed and tested for significance fitting weighted least square linear regression models to the predicted annual indices. To evaluate the effect of environmental bias, overdispersion, and zero inflation on trend estimates, an average discrepancy index was calculated for each model group. The results showed that environmental bias was the most important driver in determining different trend estimates, although overlooking overdispersion and zero inflation could lead to misleading results. For five species, zero-inflated GAMs resulted the best models to predict annual population indices. Our findings suggested a mutual interaction between zero inflation and overdispersion, with overdispersion arising in non-zero-inflated models. Moreover, for species having flocking foraging and/or colonial breeding behaviours, overdispersed and zero-inflated models may be more adequate. In conclusion, properly handling environmental bias, which may affect several data sets coming from long-term monitoring programs, is crucial to obtain reliable estimates of population trends. Furthermore, the extent to which overdispersion and zero inflation may affect trend estimates should be assessed by comparing different models, rather than presumed using statistical assumption.

2.1. Introduction

Knowledge about the status of wild populations is essential for actions aimed at conservation and management of species. The assessment of population trends, i.e. the relative variation of population size over time, allows evaluating whether a population requires conservation attention (Stanton et al., 2018). The estimation of population trends requires a well-defined sampling scheme, where sampling effort and survey methods follow a standardised protocol, which allows the collection of comparable data over time (Gregory et al., 2004; Tucker et al., 2005). Data used in trend assessment are usually represented by surrogate measurements of population size, such as indices of relative abundance (e.g. individuals detected per unit of effort; Buckland et al., 2008). Although for some animal groups standardised long-term monitoring programs exist, such as the North American Breeding Bird Survey (Sauer et al., 2017) and the UK Breeding Bird Survey (Harris et al., 2019), it is not uncommon that a long-term study presents variations in sampling scheme or survey design over time. This happens, for example, when variations in sampling effort occur in response to practical issues (e.g. reduction of funds or number of surveyors involved) that directly affect the possibility to compare data across years. Furthermore, many available data may derive from different surveys thought for different goals, citizen science observations, as well as opportunistic data collections. All these situations imply the presence of potential biases within a data set. Several types of biases have been described in ecological data. Geographical (Anderson et al., 2011) or spatial biases (Phillips et al., 2009; Kramer-Schadt et al., 2013; Gutierrez-Velez et al., 2020) are due to differences in sampling effort in the study area, resulting in a spatial clustering of sampling sites. They can lead to environmental biases (i.e. inadequate representation of the variability of environmental covariates in the study area; Phillips et al., 2009; Kramer-Schadt et al., 2013). Detection biases depend on imperfect detection of individuals, and they can occur because of differences in surveyor abilities, unequal survey conditions among samplings or differences in sampling effort for each site (Gutierrez-Velez et al., 2020). Several approaches have been suggested to handle biased data sets. They include, for example, data filtering (Yackulic et al., 2013), spatial thinning (Aiello-Lammens et al., 2015), resampling methods (Kubat and Matwin, 1997), model-based approaches using covariates to take into account the variation due to bias (Conn et al., 2017; Miller et at., 2019), or a mixture of some of the above-mentioned methods (Robinson et al., 2018; Johnston et al., 2021). Although bias-correction techniques found a broad application in species distribution models (SDMs; Guisan and Thuiller, 2005), their employment in estimating population trends has been poorly explored (but see for birds Massimino et al., 2008; Bani et al., 2009; Kamp et al., 2016; Fink et al., 2020).

In addition to biases, overdispersion and excess of zeroes are two sources of heterogeneity that can potentially affect count data. In the last two decades, ecologists have paid increasing attention to these two issues (Ridout et al., 2001; Martin et al., 2005; Sólymos et al., 2012; Denes et al., 2015; Virgili et al., 2017; Blasco-Moreno et al, 2019), underlying the importance of including them in modelling framework to obtain more correct estimates of model parameters (Martin et al., 2005; Blasco-Moreno et al., 2019). Overdispersion occurs when, for a random variable Y, the variance is larger than the mean (Zuur et al., 2009). Zero counts may represent a lot of values in ecological data sets. They can be distinguished in false and true zeroes, depending on mechanisms involved in the generation process (Denes et al., 2015). False zeroes derive from the observational process and may be caused by imperfect detection (i.e. an individual is present at a site but not detected by the observer; Royle & Dorazio, 2008; MacKenzie et al., 2017) or by temporary absence (i.e. an individual may regularly occupy a site but be absent from it at the time of survey; Chandler et al., 2011). On the other hand, true zeroes can arise from ecological processes, such as species interactions (Martin et al., 2005; Blasco-Moreno et al., 2019) and habitat suitability (Martin et al., 2005; Denes et al., 2015), or from demographic stochasticity when the species fails to saturate all suitable habitats because of random local extinctions or dispersal limitations (Martin et al., 2005). In multispecies surveys performed at regional scale, for some species it is reasonable to expect a large number of true zeroes because some sampling units may fall outside the environmental range of the species. One way to handle the excess of zeroes is the reduction or filtering of data set by removing a part of zero counts in order to limit the loss of explanatory power of the model and the distortion of the shape of the response function (Austin & Meyers; 1996; Massimino et al., 2008). Nevertheless, the removal of a part of zeroes may result in a loss of information, because the distribution of the abundance of a species (counts) may include zeroes as outcome of the observational process (Blasco-Moreno et al., 2019). Zero-inflated models can be used to better manage the excess of zeroes by including in the model the sources of zero inflation (Lambert, 1992). However, their application in population trend analysis is often overlooked, also in widely used software such as TRIM (Pannekoek and van Strien, 2005; Boogart et al., 2020), and the excess of zero counts is usually managed as a specific case of overdispersion.

To our knowledge, the assessment of population trends using count data deriving from surveys in which changes in sampling effort and design occurred over time (i.e. with presence of environmental bias), and also accounting for the effects of overdispersion and excess of zeroes, has not been investigated in ecology. The aim of this study was to assess population trends by using a modelling approach that addressed these three issues, and to compare estimates of trends obtained from models that take into account or overlook environmental bias, overdispersion and excess of zeroes. We used count data coming from the dataset of breeding birds in Lombardy (northern Italy). We tested our modelling approach on six species, selected on the base of their representativeness in relation to habitat preferences, phenology, colonial behaviour and overall frequency in the dataset. Common Swift (*Apus apus*) and the Italian Sparrow (*Passer italiae*) mainly inhabit urban landscapes, the Barn Swallow (*Hirundo rustica*) and the Eurasian Skylark (*Alauda arvensis*) mostly prefer agricultural habitats, while the Great Spotted Woodpecker (*Dendrocopos major*) and the Eurasian Blue Tit (*Cyanistes caeruleus*) are species linked to forest habitats. In our study area, two species (Common Swift and Barn Swallow) are trans-Saharan migrants, the Eurasian Skylark is a partial short-distance migrant, while the Great Spotted Woodpecker, the Italian Sparrow and the Eurasian Blue Tit are sedentary species. Finally, the Common Swift and the Barn Swallow have a colonial breeding behaviour, and they usually forage in flock. The overall frequencies of the species, in the whole study area, were 0.26 for the Common Swift, 0.11 for the Great Spotted Woodpecker, 0.13 for the Eurasian Skylark, 0.36 for the Barn Swallow, 0.13 for the Eurasian Blue Tit, and 0.43 of the Italian Sparrow.

2.2. Materials and Methods

2.2.1. Study area

Lombardy is a region of 23,861 km^2 located in Northern Italy (45° N, 9° E; Figure 2.1A). Land use is mainly characterised by urban areas (14.7%), agricultural lands (42.2%), and natural and semi-natural lands (39.6%, of which 61.4% are forests) (data derived from digital land-cover map DUSAF; ERSAF, 2018). From North to South, four main sub-regions can be distinguished: 1) the Alps, whose peaks reach 4,000 m a.s.l.; 2) the Prealps, whose tops rarely exceed 3,000 m, and which are separated from the Alps by a wide glacial valley (Valtellina); 3) the alluvial plain of the Po River (the largest plain in Italy), with an altitude under 300 m; 4) a small portion of the northern Apennine located in the south-western corner of the region, characterised by a hilly region reaching 1,400 m (Figure 2.1B). Alps and Prealps are characterised by coniferous forests, natural shrublands and grasslands at higher altitudes, while broadleaved and mixed forests and meadows extend at lower ones. The Po Plain is intensively cultivated with cereals in the central and eastern part, while urban areas and paddy fields prevail in the western part. The Apennine area is characterised by vineyards, extensive farming and broadleaved and mixed forests (Figure 2.1C).

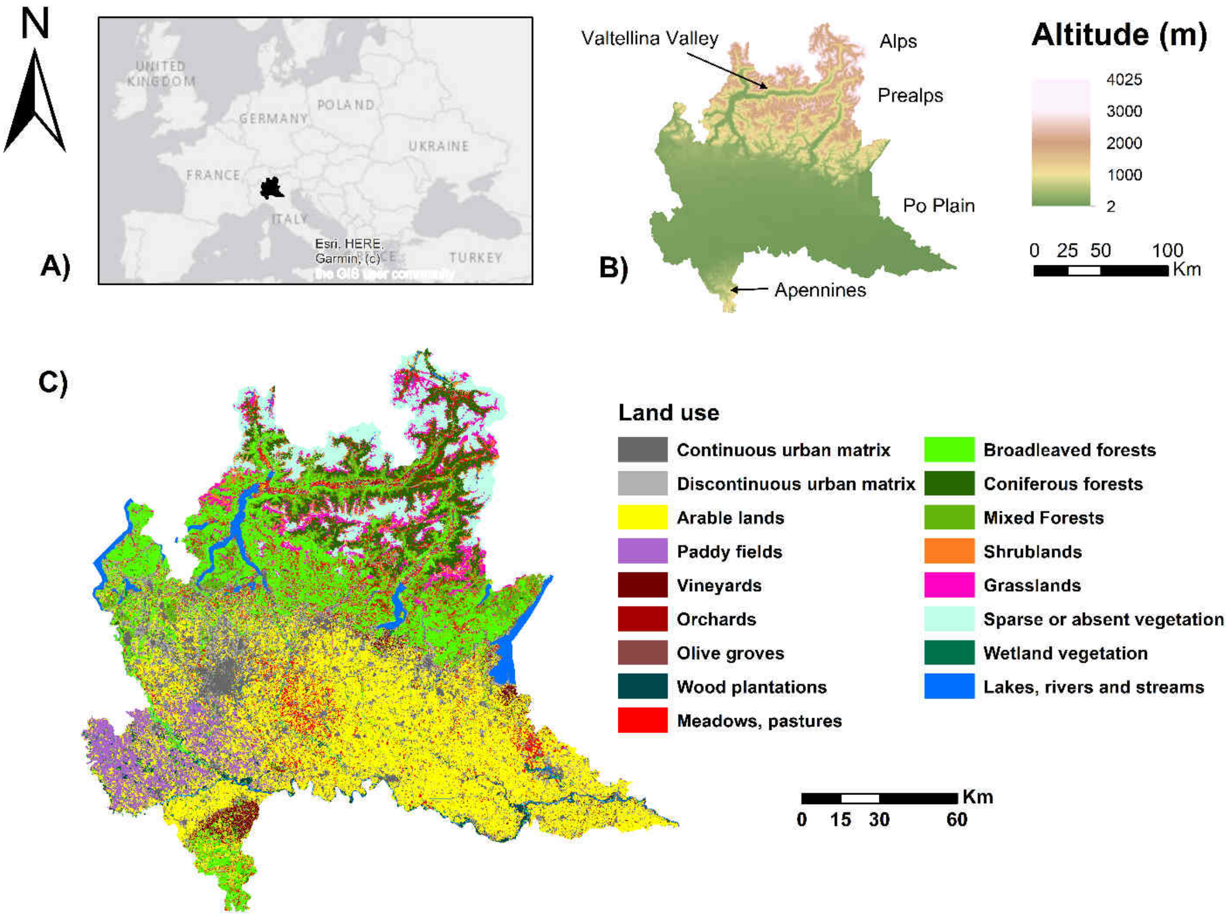


Figure 2.1. Location of the study area A), altitude B), and land uses C). Land uses are represented according to the third level of DUSAF land-cover map (ERSAF, 2018).

2.2.2. Bird data

We used data on breeding bird surveys collected from five different projects performed in Lombardy between 1992 and 2019 (Table 2.1). Overall, the dataset consists of 18,505 point counts, with an average of 771 point counts per year (range 373 - 1,443; SD = 244). No data are available for the years 1993, 1994, 1997, and 1998. All data were collected through a single-visit point-count method with unlimited distance (Blondel et al., 1981) and 10-min detection time (Fornasari et al., 1998). The minimum distance between sampling locations was at least 500 m. The technique is effective in detecting bird species belonging to the orders Columbiformes, Cuculiformes, Apodiformes, Coraciiformes, Piciformes, and Passeriformes (Bani et al., 2009), but can also be used to survey some other common species, such as the Common Buzzard (*Buteo buteo*) and the Common Kestrel (*Falco tinnunculus*). Bird surveys were carried out annually during the breeding season (10th May to 20th June), to minimise the count of migrants (birds not breeding in the study area) and to survey territorial birds. Surveys were conducted from sunrise to 11.00 a.m., only in good weather conditions, sunny to cloudy, without rain or strong wind (Bani et al., 2009). This technique provides a measure of relative bird abundance (Blondel et al., 1970; Bibby et al. 2000). All counts were expressed as number of breeding pairs, according to the method described by Blondel et al. (1981). Since the Italian Sparrow is a gregarious species (i.e. groups are composed of parental pairs and fledglings), to avoid an overestimation of the number of breeding pairs during the breading season, we considered a group of 14 individuals as one breeding pair (Bani, 1995).

Table 2.1. Summary of the five monitoring projects from which bird data were derived.

Project name	Project goal	Years	Sampling design	Number of point counts
Long-term Monitoring Program	Long-term survey at regional scale	1992, 1995 - 1996, 2005 - 2006	Stratified random sampling according to the different landscapes in the region.	2,756
		2007 - 2016	Stratified random sampling with random and fixed sampling units according to the different landscapes in the region.	7,885
		2017 - 2019	Stratified random sampling with fixed sampling units according to the different landscapes in the region.	1,622
Forest Biodiversity Survey	Survey of forest habitats	1999 - 2004	Random sampling in woodlands.	1,903
Lowland Biodiversity Survey	Survey of agricultural habitats	2000 - 2002	Random sampling in agricultural lands.	952
Regional Fauna Database	Survey at regional scale	2000 - 2006	Systematic stratified sampling at regional scale.	3,240
Greenway Project	Survey of Lombardy Apennines to draw an ecological greenway	2002 - 2003	Random sampling along river corridors in Apennine zone.	147

2.2.3. Environmental bias, overdispersion and zero inflation

The dataset was characterised by a spatial bias that led to an environmental bias due to the different allocation of sampling effort throughout years (S2.1 in Supplementary materials). Specifically, the spatial bias in the dataset derived from differences in sampling scheme between projects but also from changes in the sampling scheme for the “Long-Term Monitoring Program” along the time series (Table 2.1). To manage this bias, we applied a model-based approach that included environmental covariates to explain differences in bird counts caused by variations in the sampling effort (see Section 2.2.4.1). Species detection probability might represent an issue to be addressed in trend analysis based on density estimates (Kéry et al., 2009). Since our surveys did not include multiple visits within the same season, species detection probability could not be explicitly considered. Nevertheless, some studies highlighted that the effect of species detection on trend estimates for common and terrestrial birds may be considered negligible (Newson et al., 2013; Massimino et al., 2021). In fact, the species habitat-specific detection function is supposed to be constant over time (Newson et al., 2013), and it should not affect the estimation of population trends when correcting for the environmental bias (see also S3.3 in *Chapter 3*). Moreover, the large amount of data used in our study allowed limiting the noise caused by imperfect detection (Dondina et al., 2017), and surveys were performed by a restricted pool of expert surveyors, thus limiting the presence of inter-observer detection bias.

Overdispersion can arise in bird count data because of different processes, such as counting and sampling errors, flocking behaviour, environmental stochasticity or a mixture of them (Lindén & Mäntyniemi, 2011). Such sources of overdispersion may be present in a data set, due to the variability in sampling effort in space and time and in species ecological traits. Poisson distribution was often used to describe the error term structure for count data, but the negative binomial distribution was suggested as a suitable alternative, when the assumption about the equivalence between the mean and the variance is violated (i.e. overdispersion; Zuur et al., 2009; Blasco-Moreno et al., 2019; see S2.2 in Supplementary materials for details). Additionally, negative binomial distribution allows, to some extent, dealing with an extra-variation in the variance caused by an excess of zeroes (Warton et al., 2005).

To handle the potential excess of zeroes we used zero-inflated models (Cohen, 1963; Johnson & Kotz, 1969; Lambert, 1992). They are two-component mixture models combining a point mass at zero with a count distribution such as Poisson or negative binomial (see S2.2 for details). Zeroes can arise from one of two processes: a zero-process whereby only zero values are observed, and a count-process where both non-zero and zero values may be present. In both processes, unknown parameters can be constant or dependent on a combination of independent covariates.

2.2.4. Modelling framework and statistical analyses

To assess the effect of environmental bias, overdispersion and zero inflation on population trend estimates, and to compare differences in outcomes when at least one of these issues is overlooked, we applied a full factorial design of: presence/absence of environmental covariates, Poisson/negative binomial distribution, and using or not using zero-inflated models. This led to obtain eight different models for each species. Based on the output of these models we predicted annual population indices from which we assessed the long-term population trend. Finally, for each species, we compared the trend estimates deriving from the eight models.

All statistical analyses were conducted in R software version 4.0.2 (R Core Development Team, 2020). Since analyses were particularly resource-consuming, we used the supercomputer Marconi-A3 HPC (CINECA, 2020).

2.2.4.1. Estimation of the annual population index

We used generalised additive models (GAMs; Hastie & Tibshirani, 1986, 1990; Wood, 2017), which allow for relaxing parametric assumptions of generalised linear models (GLMs; McCullagh & Nelder, 1989), replacing some, or all, of the parametric terms by smooth functions of the covariates. Specifically, we formulated eight types of models, namely C-ZIP-GAM, C-ZINB-GAM, C-P-GAM, C-NB-GAM, nC-ZIP-GAM, nC-ZINB-GAM, nC-P-GAM, nC-NB-GAM (C= model with covariates that handle environmental bias; nC= model without covariates that do not handle environmental bias; ZIP= zero-inflated Poisson; ZINB= zero-inflated negative binomial; P=Poisson; NB= negative binomial) (Table 2.2). In all models, year of survey was considered as a categorical variable. In the count component of C-ZIP-GAM and C-ZINB-GAM, in addition to the variable “year”, we encompassed a set of covariates to account for environmental bias. We included 17 land-cover variables (S2.3 in Supplementary materials) and four topographic variables. Land-cover variables were recorded on the field and measured as percentage cover within a 250 m circular buffer around each survey site. Land cover was recorded according to the third level of the DUSAF land-use map (ERSAF, 2018; see S2.3 for details on classification). Topographic variables, namely elevation (meters), slope (grades), sine and cosine of aspect (adimensional, representing O-E and N-S exposure, respectively), were calculated in ArcMap version 10.7.1 (ESRI, 2019) using a DEM (Digital Elevation Model, downloadable from http://www.geoportale.regione.lombardia.it/) with a 20 m ground resolution, by averaging values within a 250 m circular buffer around each survey site. We also included the spatial trend (i.e. interaction between X and Y coordinates; UTM 32N, WGS84 Datum) to take into account geographical patterns (Dormann et al., 2007) and potential spatial autocorrelation (Bani et al., 2019). To account for the potential excess of true zeroes, we included three predictors in the binomial component of zero-inflated models, namely elevation and percentage cover of urban and forest area within a 2500 m circular buffer designed around the survey site. The computation of urban and forest cover were performed in ArcMap version 10.7.1 (ESRI, 2019) using 50 m resolution land-use raster maps (DUSAF and CORINE Land Cover, downloadable from http://www.geoportale.regione.lombardia.it/ and from https://land.copernicus.eu/pan-european/corine-land-cover as shapefiles, respectively), and to address temporal changes of environmental characteristics, survey sites were associated with the temporally closest maps (see S2.4 in Supplementary materials). We checked for linear correlation between covariates (absolute value for Pearson correlation coefficient > 0.70; Dormann et al., 2013; see S2.5 in Supplementary materials). The smooth estimation procedure in the *mgcv* R package guarantees the reliability of results even in the presence of concurvity, i.e. the presence of covariates which are themselves well modelled as smooth functions of other covariates (Wood, 2008).

C-P-GAM and C-NB-GAM were GAMs wherein the model structure was the same of the count component of C-ZIP-GAM and C-ZINB-GAM (i.e. equivalent models but which did not take into account for the zero inflation). nC-ZIP-GAM and nC-ZINB-GAM were zero-inflated GAMs with the same structure of C-ZIP-GAM and C-ZINB-GAM for the binomial component, and only accounting for the spatial trend in the count component. Finally, nC-P-GAM and nC-NB-GAM were GAMs that considered only the spatial trend. These models did not take into account any environmental bias, therefore they could likely lead to distorted population indices. Finally, by running both Poisson and negative binomial regressions, we obtained models that handled and did not handle overdispersion in both non-zero-inflated GAMs and zero-inflated GAMs.

Table 2.2. Description of models. Counts = response variable (number of pairs detected at each sampling site), Year = year of sampling; Sin = sine of the aspect; Cos = cosine of the aspect; X and Y = UTM coordinates; Elev = elevation; LC = land-cover variables; Urb_{2500} and For_{2500}= urban and forest cover

within a radius of 2500 m. See Section 2.2.4.1 and S2.3 for details. For zero-inflated models ω is the weight that represents the probability that an observation come from the specified count distribution (see S2.2). The "s" before the variable name indicates the use of a smooth function. The last three columns show the issues that the models took (Y) and did not take (N) into account: EB = environmental bias; OV = overdispersion; ZI = zero inflation.

Model name	Model type	Distribution	Count component	Binomial component	EB	OV	ZI
C-ZIP-GAM	Zero-inflated generalised additive model	Poisson	$Counts \sim Year + Sin + Cos + s(X,Y) + s(Elev) + s(Slope) + \sum_{i=1}^{k} s(LC_i)$	$\omega \sim s(Elev) + s(Urb_{2500}) + s(For_{2500})$	Y	N	Y
C-ZINB-GAM	Zero-inflated generalised additive model	Negative binomial	$Counts \sim Year + Sin + Cos + s(X,Y) + s(Elev) + s(Slope) + \sum_{i=1}^{k} s(LC_i)$	$\omega \sim s(Elev) + s(Urb_{2500}) + s(For_{2500})$	Y	Y	Y
C-P-GAM	Generalised additive model	Poisson	$Counts \sim Year + Sin + Cos + s(X,Y) + s(Elev) + s(Slope) + \sum_{i=1}^{k} s(LC_i)$		Y	N	N
C-NB-GAM	Generalised additive model	Negative binomial	$Counts \sim Year + Sin + Cos + s(X,Y) + s(Elev) + s(Slope) + \sum_{i=1}^{k} s(LC_i)$		Y	Y	N
nC-ZIP-GAM	Zero-inflated generalised additive model	Poisson	$Counts \sim Year + s(X,Y)$	$\omega \sim s(Elev) + s(Urb_{2500}) + s(For_{2500})$	N	N	Y
nC-ZINB-GAM	Zero-inflated generalised additive model	Negative binomial	$Counts \sim Year + s(X,Y)$	$\omega \sim s(Elev) + s(Urb_{2500}) + s(For_{2500})$	N	Y	Y
nC-P-GAM	Generalised additive model	Poisson	$Counts \sim Year + s(X,Y)$		N	N	N
nC-NB-GAM	Generalised additive model	Negative binomial	$Counts \sim Year + s(X,Y)$		N	Y	N

Except for sine and cosine of the aspect which were included as linear effects, land-cover and topographic variables, spatial trend, and covariates of the binomial component in zero-inflated GAMs were modelled as smooth functions. A thin plate regression spline was used as method of smoothing (Wood 2003, 2017), and a shrinkage method was applied to avoid overfitting and exclude non-significant variables. Shrinkage penalises the smoothing process decreasing the level of the estimated degree of freedom close to zero (Wood, 2017). To guarantee a good fit flexibility and a reasonable ecological interpretation of the relationship between the response and predictors, the maximum degree of freedom *k* was set at four. Similarly, the spatial smooth was limited to a maximum degree of freedom *k* at four to avoid an over-parameterisation of the models, preventing that the geographic coordinates replaced the predictive power of the other environmental variables.

As suggested by Wood (2011, 2017) and Wood et al. (2016), we used UBRE (Un-Biased Risk Estimation) as smoothing parameter estimation method for Poisson models and binomial component of zero-inflated models, and REML (Restricted Maximum Likelihood) for negative binomial models. We fitted GAMs and zero-inflated GAMs by using the R packages *mgcv* (Wood, 2019) and *zigam* (Wotherspoon and Burch, 2016), respectively. *Zigam* uses an expectation-maximization algorithm to implements GAMs performed in *mgcv* and allows including covariates for the binomial component of zero-inflated models.

The Akaike Information Criterion (AIC; Burnham & Anderson, 2002) was used to rank models and to identify the best model for each species (Dalrymple et al., 2003; Virgili et al., 2017), while the explained deviance was used as measure of goodness of fit (França et al., 2015).

In order to obtain estimates of the annual population index, we made a prediction based on a new data matrix for each model. To create the prediction dataset (S2.6 in Supplementary materials), we calculated for each year of survey the mean value at regional scale of each explanatory variable included in the models. For each land-cover predictor, starting from the six digital land-use vector maps available between 1980 and 2019 (DUSAF 1980, 1999, 2007, 2012, 2015, 2018, downloadable from http://www.geoportale.regione.lombardia.it/), a 50 m resolution raster map was created, by recoding each cell (0-1 values) with respect to the variable of interest. Then, for each raster map, a zonal statistic was applied and to align the spatial resolution with those used in the models, the values of each pixel were averaged within a radius of 250 m (or 2500 m in the case of urban and forest cover in the binomial component). The overall mean for the study area was obtained by averaging all pixel values. Finally, the values of each year of survey were obtained from a GAM wherein the annual average land cover was fitted as function of the year (continuous variable), using a thin plate regression spline as method of smoothing ($k = 4$) and generalised cross-validation (GCV) as smoothing parameter estimation (Wood, 2017). Model parameters were used to predict land-cover values for each year. The same procedure of zonal statistics with a radius of 250 m was applied to the topographic variables using the Digital Elevation Model (DEM) as raster map. Since topography is not influenced by temporal changes, the overall mean in the study area was used for each year. Finally, the centroid of the study area was used for coordinates. Raster analyses were performed in ArcMap version 10.7.1 (ESRI, 2019).

To obtain reliable estimates of the annual population indices, we applied a parametric bootstrap approach (Nelson, 2008). New datasets for the response variables (i.e. counts) were generated based on the parameters estimated from models with the original data, then each new sample was refitted and predicted 1,000 times. The median of the distribution of the bootstrapped predictions was used as estimator of the annual population index. Confidence intervals were computed using the percentile method (Davison & Hinkley, 2006; Nelson, 2008), which estimates the lower and upper limits as the $\alpha/2$ and $1-(\alpha/2)$ quantiles of the distribution, respectively (where α is the significance threshold at 0.05). The obtained population index indicates the estimated annual breeding pairs for a point count representative of the average environmental conditions across the whole study area within the specific sampling year.

2.2.4.2. Estimation of the long-term population trend

To assess the long-term population trend, we used a weighted least square linear regression (WLS), using the median of the annual population index as response variable and the year as continuous explanatory variable. To take into account uncertainty in the estimates of the indices, we weighted the indices by the reciprocal of the width of the confidence interval (CI) around the median. We acknowledge that annual indices are not temporally independent, but since our aim was to assess long-term trends, a linear regression can be considered adequate for the purpose (Byrkjedal et al., 2012; Lockerbie et al., 2016). The expected value is $I_t = \beta * Year + \varepsilon_i,\ w = 1/CI$, where the regression coefficient β represents the average variation of I_t over the whole period. The trend was considered statistically different from zero if $P(\beta) \leq 0.05$. The relative variation in population size from 1992 to 2019 (percentage of change: T%), was quantified by applying the following formula: $T\% = [(I_{2019} - I_{1992})/I_{1992}] * 100$. To evaluate differences among Ts% estimated by the several models, with respect to environmental bias (group 1: g_1), overdispersion (group 2: g_2) and zero inflation (group 3: g_3), we performed a pairwise comparison within each of these groups between: i) g_1: “COV” (i.e. models including covariates for environmental bias correction: C-ZIP-GAM, C-ZINB-GAM, C-P-GAM, C-NB-GAM) vs “nonCOV” (i.e. models without covariates: nC-ZIP-GAM, nC-ZINB-GAM, nC-P-GAM, nC-NB-GAM); ii) g_2: “OV” (i.e. overdispersed models: C-ZINB-GAM, C-NB-GAM, nC-ZINB-GAM, nC-NB-GAM) vs “nonOV” (i.e. equidispersed models: C-ZIP-GAM, C-P-GAM, nC-ZIP-GAM, nC-P-GAM), iii) g_3: “ZI” (i.e. zero-inflated models: C-ZIP-GAM, C-ZINB-GAM, nC-ZIP-GAM, nC-ZINB-GAM) vs “nonZI” (i.e. non-zero-inflated models: C-P-GAM, C-NB-GAM, nC-P-GAM, nC-NB-GAM).

Comparisons were performed by computing, for each group g_i, an index of average discrepancy (AD_{g_i}) between Ts% of the two opposite categories, defined as $AD_{g_i} = \sum_{k=1}^{n} AD_{s_k g_i}/n$, where n is the total number of species and $AD_{s_k g_i}$ is the average discrepancy for the species s_k within the group g_i, that is $AD_{s_k g_i} = mean(AD_{s_k g_{i,a}})/mean(AD_{s_k g_{i,b}})$, where a and b are the two categories within each group g_i. We defined “*a*” the categories “COV”, “OV”, and “ZI”, and “*b*” the other ones. When there are no differences in trend estimates between the two categories, AD_{g_i} and $AD_{s_k g_i}$ are equal to one. For the calculation of these indices, we assigned zero values to Ts% obtained from WLS models wherein β was not statistically different from zero.

2.3. Results

Overall, the mean explained deviance (Table 2.3) in C-ZIP-GAM was 62.11% for the binomial component (range: 7.87% - 97.20%), and 26.07% (range: 8.44% - 45.00%) for the count component, while in C-ZINB-GAM was 79.25% (range: 54.8% - 96.9%) and 25.87% (range: 9.61% - 44.5%) for the binomial and the count component, respectively. For the binomial component in nC-ZIP-GAM it was 56.17% (range: 7.81% - 79.20%), and it increased to 70.32% in nC-ZINB-GAM (range: 47.4% - 83.1%), while it were similar for the count component in both models (8.99 % in nC-ZIP-GAM, range: 3.09% - 22.20%; 7.73% in nC-ZINB-GAM, range: 2.84% - 20.4%). C-P-GAM and C-NB-GAM showed similar mean explained deviances (33.25%, range: 14.8% - 48.9% in the first one; 34.38%, range: 14.40% - 49.20% in the second one), as well as nC-P-GAM (11.67%, range: 3.09% - 21.5%) and nC-NB-GAM (12.28%, range: 4.65% - 21.5%).

Based on the AIC, the best model overall was C-ZIP-GAM for the Eurasian Skylark, the Eurasian Blue Tit, and the Italian Sparrow, C-ZINB-GAM for the Common Swift and the Barn Swallow, and C-P-GAM for the Great Spotted Woodpecker (Table 2.3; see S2.7 in Supplementary materials for details on models’ statistics).

For all species, models including land-cover and topographic covariates, namely C-(P/NB)-GAM and C-ZI(P/NB)-GAM, performed better than corresponding models nC-(P/NB)-GAM and nC-ZI(P/NB)-GAM that did not include covariates (e.g. C-P-GAM showed a lower value of AIC than nC-P-GAM, and so on; Table 2.3). Count data of the Common Swift and the Barn Swallow showed overdispersion in all models, of the Eurasian Skylark in non-zero-inflated models, and of the Italian Sparrow in models without the correction for the environmental bias (Table 2.3). Eurasian Blue Tit showed overdispersion only in the simplest model (nC-NB-GAM fit better than nC-P-GAM), while count data of the Great Spotted Woodpecker were never overdispersed (Table 2.3). Finally, zero-inflated models always performed better than corresponding non-zero-inflated models (Table 2.3), except for the Great Spotted Woodpecker for which the opposite was found in C-P-GAM and C-NB-GAM compared to C-ZIP-GAM and C-ZINB-GAM, respectively.

Table 2.3. Explained deviance (%) and the Akaike Information Criterion (AIC) of each model. For each species, models are ranked according to the AIC. In zero-inflated GAMs, explained deviances for both binomial and count component are shown. For negative binomial models, values of the estimated dispersion parameter θ (the smaller θ, the larger overdispersion) are indicated in parenthesis.

Species	Model	AIC	Explained deviance (%)	
Common Swift (*Apus apus*)	C-ZINB-GAM (0.30)	40,080	Binomial	54.80
			Count	9.61
	C-NB-GAM (0.18)	40,556		14.40
	nC-ZINB-GAM (0.31)	40,646	Binomial	47.4
			Count	2.84
	nC-NB-GAM (0.15)	41,647		4.65
	C-ZIP-GAM	55,397	Binomial	7.87
			Count	8.44
	nC-ZIP-GAM	56,324	Binomial	7.81
			Count	3.09
	C-P-GAM	79,149		14.80
	nC-P-GAM	86,771		4.79
Great Spotted Woodpecker (*Dendrocopos major*)	C-P-GAM	11,958		20.90
	C-NB-GAM (92,666)	12,021		20.20
	C-ZIP-GAM	12,023	Binomial	79.10
			Count	18.20
	C-ZINB-GAM (207,106)	12,076	Binomial	79.60
			Count	17.40
	nC-ZIP-GAM	12,728	Binomial	79.20
			Count	6.98
	nC-ZINB-GAM (65,553)	12,789	Binomial	78.50
			Count	6.25
	nC-P-GAM	13,278		6.53
	nC-NB-GAM (50,471)	13,298		6.29

Eurasian Skylark (*Alauda arvensis*)	C-ZIP-GAM	13,476	Binomial	77.60
			Count	45.00
	C-ZINB-GAM (14.49)	13,504	Binomial	78.70
			Count	44.50
	C-NB-GAM (2.36)	13,667		48.30
	C-P-GAM	13,742		47.00
	nC-ZIP-GAM	15,455	Binomial	62.00
			Count	22.20
	nC-ZINB-GAM (32.17)	15,524	Binomial	56.60
			Count	20.40
	nC-NB-GAM (0.56)	16,936		21.50
	nC-P-GAM	17,644		21.50
Barn Swallow (*Hirundo rustica*)	C-ZINB-GAM (0.80)	40,303	Binomial	87.20
			Count	25.20
	C-NB-GAM (0.71)	40,464		41.00
	nC-ZINB-GAM (0.75)	41,699	Binomial	82.50
			Count	5.20
	nC-NB-GAM (0.44)	44,591		19.30
	C-ZIP-GAM	47,492	Binomial	31.40
			Count	26.10
	nC-ZIP-GAM	49,370	Binomial	34.50
			Count	8.25
	C-P-GAM	51,918		35.00
	nC-P-GAM	61,827		16.10
Eurasian Blue Tit (*Cyanistes caeruleus*)	C-ZIP-GAM	13,764	Binomial	79.50
			Count	19.70
	C-ZINB-GAM (166.83)	13,844	Binomial	78.30
			Count	18.70
	C-P-GAM	13,997		32.90
	C-NB-GAM (2.66)	14,038		33.20
	nC-ZIP-GAM	14,411	Binomial	74.80
			Count	4.74
	nC-ZINB-GAM (217.84)	14,467	Binomial	73.80
			Count	3.73
	nC-NB-GAM (0.44)	17,173		3.44
	nC-P-GAM	17,819		3.09
Italian Sparrow (*Passer italiae*)	C-ZIP-GAM	30,881	Binomial	97.20
			Count	39.00
	C-ZINB-GAM (21.53)	30,913	Binomial	96.90
			Count	39.80
	C-P-GAM	30,937		48.90
	C-NB-GAM (19.29)	30,944		49.20
	nC-ZINB-GAM (7.28)	34,720	Binomial	83.10
			Count	7.97
	nC-ZIP-GAM	34,887	Binomial	78.70
			Count	8.68
	nC-NB-GAM (2.65)	37,928		18.50
	nC-P-GAM	38,688		18.00

For the Great Spotted Woodpecker, the Eurasian Skylark, the Barn Swallow and the Italian Sparrow, long-term trends assessed by WLS (Table 2.4, Figure 2.2A-B-C, and Figure 2.3A-B-C) showed similar results with respect to significance of the year coefficient (β) across all eight models. Conversely, for the Common Swift, five models (WLS C-ZINB-GAM, WLS C-(P/NB)-GAM and WLS nC-(P/NB)-GAM) highlighted significant negative trends, while for the Eurasian Blue Tit, four models (WLS C-ZI(P/NB)-GAM and WLS C-(P/NB)-GAM) showed significant positive trends. The percentage of change T% (in those cases wherein the trend was statistically significant) ranged from −38.38% to −61.78% for the Common Swift, from +561.42% to +1905.10% for the Great Spotted Woodpecker, from −95.51% to −99.73% for the Eurasian Skylark, from −52.90% to −69.88% for the Barn Swallow, from +48.78% to +70.78% for the Eurasian Blue Tit, and from −61.44% to −72.48% for the Italian Sparrow.

Table 2.4. Summary of weighted least square linear regression models (WLS) used to assess population trends. The "WLS model" column indicates, after "WLS", the GAM from which the predicted population indices and confidence intervals were used in the WLS. Β = estimate of regression coefficient for the explanatory variable "Year"; SE = standard error of β; t-value = t statistic; Adj-R^2 = adjusted R-square (in case of negative value it was round to zero); T% 1992-2019 = percentage of change in population dimension from 1992 to 2019 according to WLS model, (ns) indicates that change was not significance (α = 0.05). Estimates and standard errors for the intercept are not showed. For each species, the overall best model ranked by AIC is indicated in bold.

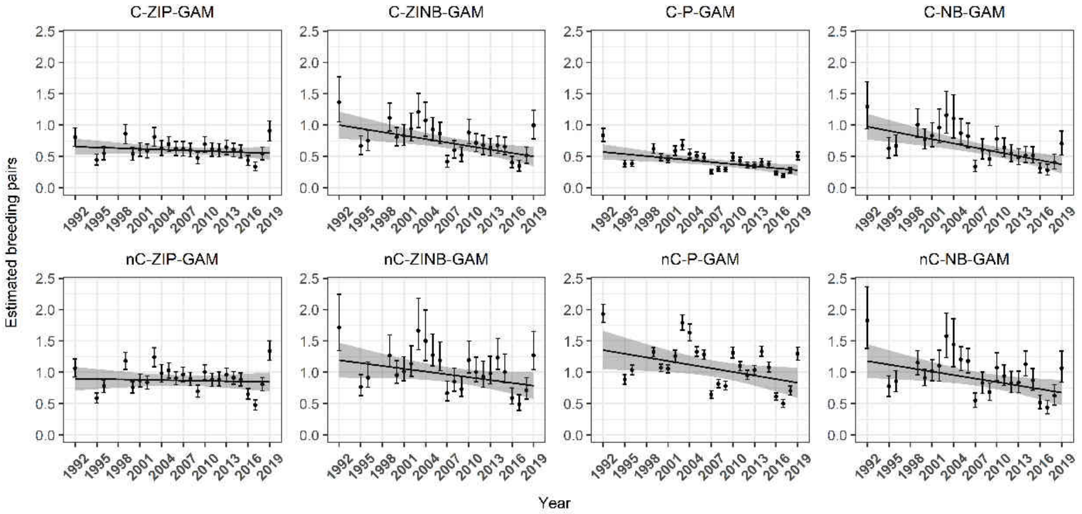
Species	WLS model	β^1	SE^1	t-value	p-value	T% 1992-2019	Adj-R^2
Common Swift (*Apus apus*)	WLS C-ZIP-GAM	−0.387	0.357	−1.085	0.289	−15.92 (ns)	0.008
	WLS C-ZINB-GAM	**−1.857**	**0.583**	**−3.187**	**0.004**	**−50.01**	**0.285**
	WLS C-P-GAM	−1.075	0.331	−3.246	0.004	−50.68	0.293
	WLS C-NB-GAM	−2.239	0.538	−4.158	<0.001	−61.78	0.415
	WLS nC-ZIP-GAM	−0.195	0.535	−0.365	0.719	−5.86 (ns)	0
	WLS nC-ZINB-GAM	−1.507	0.767	−1.966	0.062	−34.08 (ns)	0.111
	WLS nC-P-GAM	−1.926	0.863	−2.231	0.036	−38.38	0.147
	WLS nC-NB-GAM	−1.860	0.742	−2.506	0.020	−42.53	0.187

Table 2.4 (cont.)

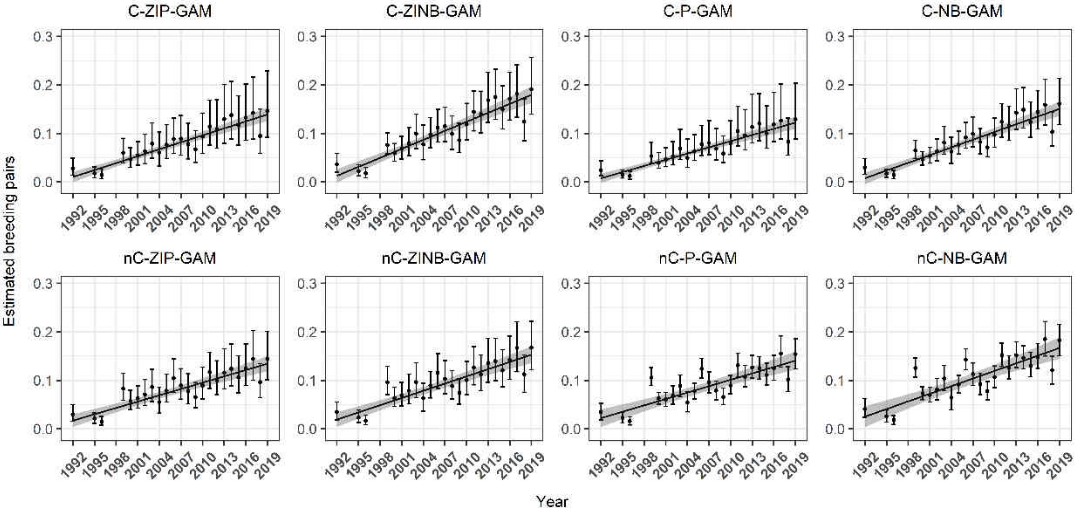
Great Spotted Woodpecker (*Dendrocopos major*)	WLS C-ZIP-GAM	0.478	0.038	12.640	<0.001	+1,272.34	0.873
	WLS C-ZINB-GAM	0.619	0.048	12.870	<0.001	+1,336.03	0.877
	WLS C-P-GAM	**0.425**	**0.034**	**12.450**	**<0.001**	**+1,530.25**	**0.870**
	WLS C-NB-GAM	0.531	0.042	12.68	<0.001	+1,905.10	0.874
	WLS nC-ZIP-GAM	0.434	0.045	9.758	<0.001	+685.15	0.804
	WLS nC-ZINB-GAM	0.496	0.050	9.858	<0.001	+701.99	0.807
	WLS nC-P-GAM	0.439	0.058	7.554	<0.001	+536.53	0.709
	WLS nC-NB-GAM	0.524	0.068	7.699	<0.001	+561.42	0.717
Eurasian Skylark (*Alauda arvensis*)	**WLS C-ZIP-GAM**	**−0.744**	**0.087**	**−8.521**	**<0.001**	**−99.65**	**0.757**
	WLS C-ZINB-GAM	−0.805	0.093	−8.665	<0.001	−99.48	0.763
	WLS C-P-GAM	−0.549	0.066	−8.293	<0.001	−99.13	0.747
	WLS C-NB-GAM	−0.462	0.059	−7.850	<0.001	−99.73	0.725
	WLS nC-ZIP-GAM	−0.761	0.079	−9.690	<0.001	−95.51	0.802
	WLS nC-ZINB-GAM	−0.701	0.068	−10.260	<0.001	−96.88	0.819
	WLS nC-P-GAM	−1.598	0.161	−9.958	<0.001	−98.14	0.810
	WLS nC-NB-GAM	−1.182	0.128	−9.214	<0.001	−95.92	0.785
Barn Swallow (*Hirundo rustica*)	WLS C-ZIP-GAM	−1.560	0.323	−4.833	<0.001	−57.53	0.493
	WLS C-ZINB-GAM	**−1.788**	**0.288**	**−6.209**	**<0.001**	**−67.41**	**0.620**
	WLS C-P-GAM	−1.839	0.308	−5.971	<0.001	−67.60	0.601
	WLS C-NB-GAM	−1.864	0.286	−6.527	<0.001	−69.88	0.644
	WLS nC-ZIP-GAM	−2.062	0.473	−4.362	<0.001	−52.90	0.439
	WLS nC-ZINB-GAM	−2.958	0.529	−5.589	<0.001	−58.85	0.568
	WLS nC-P-GAM	−5.148	0.755	−6.819	<0.001	−65.61	0.664
	WLS nC-NB-GAM	−5.010	0.858	−5.850	<0.001	−67.73	0.591
Eurasian Blue Tit (*Cyanistes caeruleus*)	**WLS C-ZIP-GAM**	**0.179**	**0.071**	**2.538**	**0.019**	**+48.78**	**0.191**
	WLS C-ZINB-GAM	0.242	0.084	2.878	0.009	+54.62	0.241
	WLS C-P-GAM	0.252	0.091	2.779	0.011	+60.31	0.226
	WLS C-NB-GAM	0.389	0.122	3.192	0.004	+70.78	0.286
	WLS nC-ZIP-GAM	0.180	0.121	1.487	0.151	+26.13 (ns)	0.050
	WLS nC-ZINB-GAM	0.245	0.161	1.525	0.142	+26.47 (ns)	0.055
	WLS nC-P-GAM	0.068	0.091	0.751	0.461	+14.77 (ns)	0
	WLS nC-NB-GAM	0.092	0.099	0.926	0.365	+18.95 (ns)	0
Italian Sparrow (*Passer italiae*)	**WLS C-ZIP-GAM**	**−1.902**	**0.236**	**−8.077**	**<0.001**	**−71.06**	**0.736**
	WLS C-ZINB-GAM	−1.582	0.196	−8.091	<0.001	−71.25	0.737
	WLS C-P-GAM	−1.699	0.208	−8.160	<0.001	−71.58	0.740
	WLS C-NB-GAM	−1.569	0.188	−8.364	<0.001	−72.48	0.750
	WLS nC-ZIP-GAM	−2.581	0.337	−7.660	<0.001	−61.44	0.715
	WLS nC-ZINB-GAM	−2.870	0.338	−8.486	<0.001	−62.17	0.755
	WLS nC-P-GAM	−3.845	0.410	−9.382	<0.001	−65.23	0.791
	WLS nC-NB-GAM	−3.707	0.404	−9.171	<0.001	−64.30	0.783

[1] Values are multiplied for 10^2 to ease comparisons

A) Common Swift



B) Great Spotted Woodpecker



C) Eurasian Skylark

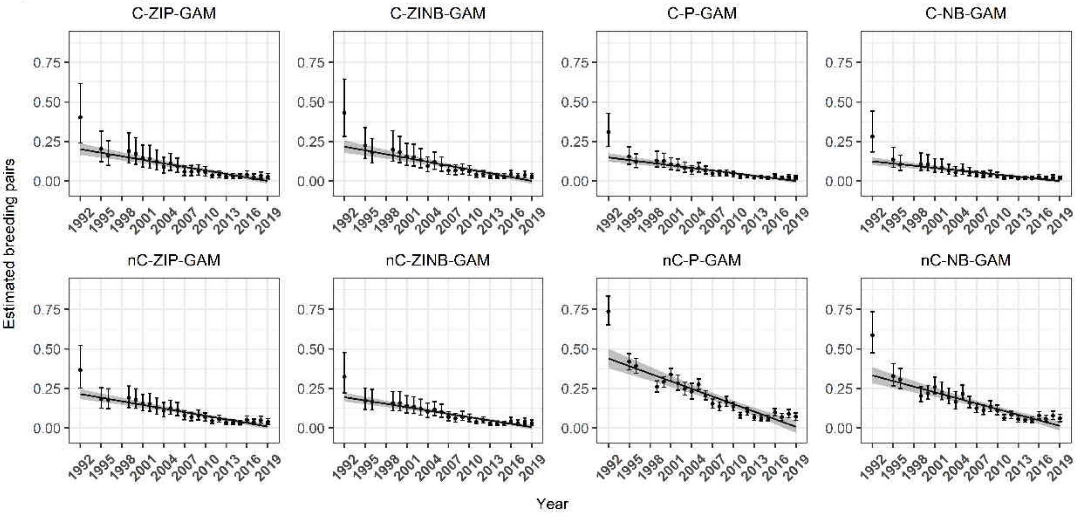


Figure 2.2. Long-term trends (regression line with confidence intervals) estimated by each model for the Common Swift in A), the Great Spotted Woodpecker in B), and the Eurasian Skylark in C). The Y-axis represents the number of estimated annual breeding pairs (dots) with confidence interval (bars) per point count (see Section 2.2.4.1).

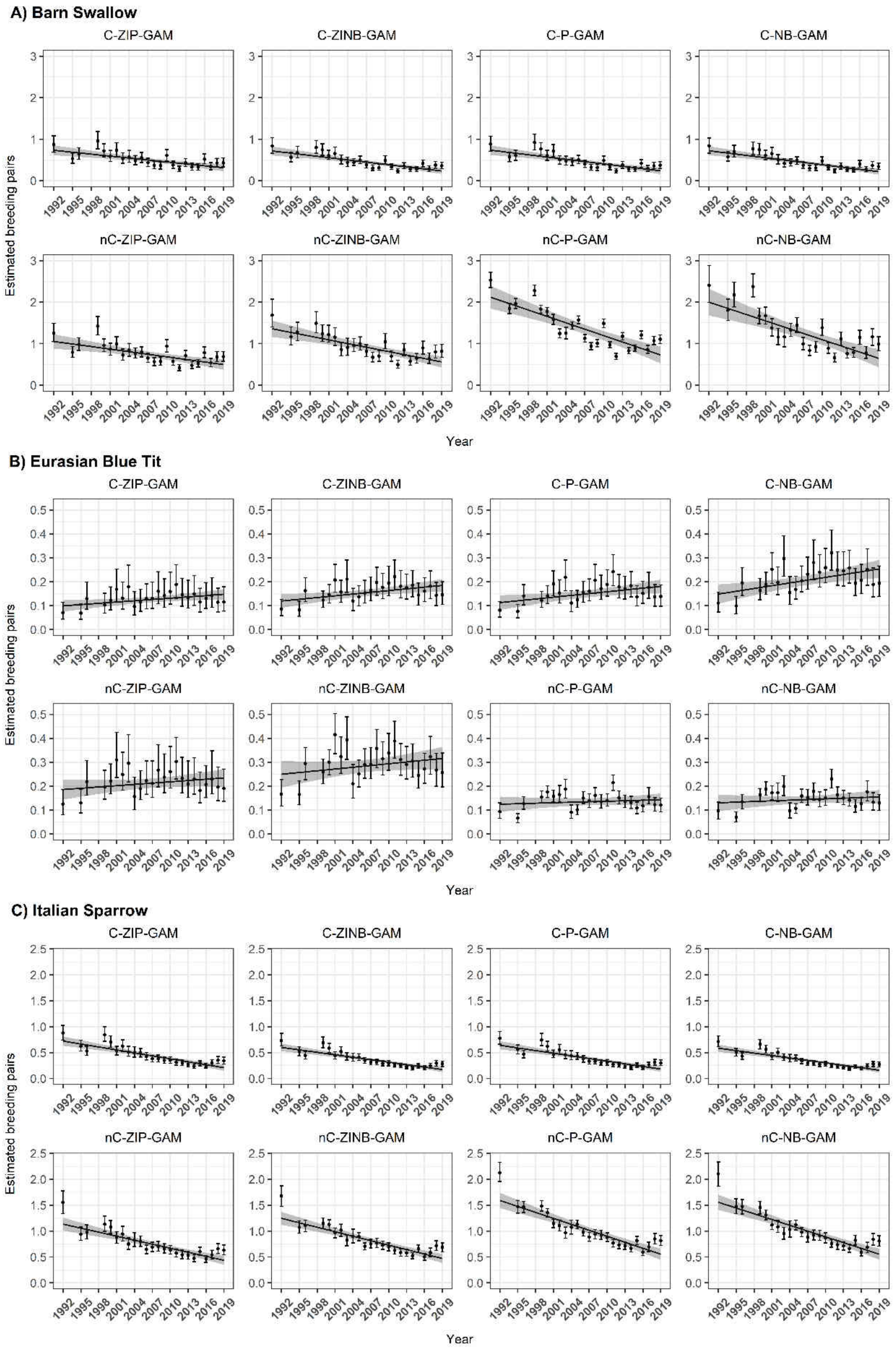


Figure 2.3. Long-term trends (regression line with confidence intervals) estimated by each model for the Barn Swallow in A), the Eurasian Blue Tit in B) and the Italian Sparrow in C). The Y-axis represents the number of estimated annual breeding pairs (dots) with confidence interval (bars) per point count (see Section 2.2.4.1).

The index of the average discrepancy (AD_{g_i}) was the highest for g₁, where the magnitude of variation in trend estimates was 1.534 times higher in models belonging to the category "COV" compared to the category "nonCOV" (Table 2.5). AD_{g_2} (i.e. "OV" vs "nonOV") was 1.181, with three species (Common Swift, Great Spotted Woodpecker and Eurasian Blue Tit) that showed values of $AD_{s_k g_2}$ greater than 1.10, while AD_{g_3}(i.e. "ZI" vs "nonZI") was 0.795, with the Common Swift, the Great Spotted Woodpecker, the Barn Swallow and the Eurasian Blue Tit that showed values lower than 0.90 (Table 2.5).

Table 2.5. Index of average discrepancy for each species within each group ($AD_{s_k g_i}$) and for each group overall (AD_{g_i}). Zero values were assigned to statistically non-significant trends. The number of significant trends for each category and species are shown in parenthesis.

Group	$AD_{s_k g_i}$						AD_{g_i}
	Common Swift	Great Spotted Woodpecker	Eurasian Skylark	Barn Swallow	Eurasian Blue Tit	Italian Sparrow	
g_1: COV vs nonCOV	2.008 (3 vs 2)	2.432 (4 vs 4)	1.030 (4 vs 4)	1.071 (4 vs 4)	NA (4 vs 0)	1.131 (4 vs 4)	1.534
g_2: OV vs nonOV	1.733 (3 vs 2)	1.119 (4 vs 4)	0.999 (4 vs 4)	1.083 (4 vs 4)	1.150 (2 vs 2)	1.003 (4 vs 4)	1.181
g_3: ZI vs nonZI	0.257 (1 vs 4)	0.881 (4 vs 4)	0.996 (4 vs 4)	0.874 (4 vs 4)	0.789 (2 vs 2)	0.972 (4 vs 4)	0.795

2.4. Discussion

The use of environmental biased data sets to estimate population trends requires attention in modelling conceptualisation in order to avoid misleading findings. A model-based approach that includes environmental covariates may represent a good solution to control for environmental biases derived from variations in sampling effort or design over time. In addition to the explanatory variable "year", which represents the variable of interest to explain temporal changes in population size in trend analysis, environmental covariates can be used to produce unbiased estimates of annual population indices when the predictions are made on an independent and non-distorted data set. The abundance of a species is often affected by environmental factors in a non-linear way, and the ability of GAMs to capture this non-linearity enhances the response-covariates relationship (Guisan et al., 2002), allowing to obtain a greater predictive capacity. Considering the limit for the maximum degrees of freedom we set in models (important to keep a plausible ecological interpretation), the shrinkage method to avoid overfitting and exclude non-significant variables, and the large dimension of the dataset, we obtained a good trade-off between complexity and goodness of fit for bias-corrected models.

Findings suggested that overdispersion was high in species showing large variability in abundance throughout the study area (e.g. the Barn Swallow and the Common Swift). Indeed, in some sampling sites these species counted a few breeding pairs, but in others they counted some tens of pairs. This variability, caused by flocking foraging and colonial breeding behaviours, led to a count distribution with the variance greater than the mean. When pairs occur in aggregations, assumptions of Poisson distribution are violated, and negative binomial distribution is recommended (Zuur et al., 2009). Despite the inclusion of the dispersion parameter θ (i.e. negative binomial distribution was used to describe the error structure), these species still showed an excess of zero counts, which led to select the zero-inflated negative binomial GAMs as best models. This probably occurred because the only dispersion parameter was not able to handle the large variance of the count distribution deriving from both the excess of zeroes and the high abundance of individuals in some sampling sites. Overall, these findings suggested that for colonial species (e.g. the House Martin *Delichon urbicum*), and for species living and foraging in aggregations (e.g. the Common Starling *Sturnus vulgaris*, and crows), zero-inflated negative binomial models should be considered when modelling count data obtained by multispecies surveys. For the Italian Sparrow, the selection of C-ZIP-GAM as best model was consistent with the conversion factor used to determine the number of observed breeding pairs, which resulted in lacking of overdispersion. Results for the Eurasian Skylark showed a mutual interaction between overdispersion and zero inflation. In this species, overdispersion only arose in non-zero-inflated models. Indeed, excess of zeroes can be a source of overdispersion (Wagh & Kamalja, 2018). However, overdispersion disappeared when zero-inflated Poisson models were used, because the excess of zeroes that caused overdispersion was better handled by the binomial component of zero-inflated models.

Zero-inflated models can be used to manage both true and false zeroes (Martin et al., 2005). Therefore, the choice of adequate predictors is crucial to define the source of zero inflation. In our study, the use of two variables at landscape scale (percentage cover of urban and forest area within a 2500 m circular buffer around the survey site) and elevation as predictors of the binomial component revealed a good performance, suggesting their eligibility to explain the arise of zero counts. Indeed, in multi-species surveys performed at broad spatial scale, most of true zero values can arise by sampling in poor suitable habitats, and the altitudinal gradient and landscape characteristics may represent important drivers leading to zero inflation. In our study, only for the Great Spotted Woodpecker a non-zero-inflated model was selected as best model. The species is mainly associated with forest habitats, from plains to mountains, but it can also inhabit fragmented landscapes (Chiatante et al., 2019), as well as tree stands in urban and rural areas (Michalczuk & Michalczuk, 2016; Canedoli et al., 2017). Because of these reasons, the species is probably characterised by widespread spatial distribution, and the observed zero counts did not imply zero inflation linked to elevation and habitat characteristics at landscape scale.

Population trends assessed through the optimal models (i.e. WLS models based on best GAMs selected by the AIC), highlighted a decline for the Common Swift, the Eurasian Skylark, the Barn Swallow, and the Italian Sparrow. These results were largely in accordance with the status of these species throughout Europe, where farmland (Gregory et al., 2019) and insectivorous bird species (Bowler et al., 2019) are decreasing. In our study, the Great Spotted Woodpecker and the Eurasian Blue Tit showed an increasing population trend that was consistent with known trends in Europe for these two species (PECBMS, 2020). In some areas of Northern Italy, the Barn Swallow declined by 53.1% from 2001 to 2010 (Ambrosini et al., 2012) and by 56.6% from 1999 to 2011 (Sicurella et al., 2014). In Lombardy, from 1992 to 2007, the Barn Swallow showed a reduction of 48%, the Italian Sparrow decreased by 64% and the Eurasian Skylark by 75%; conversely, the Great Spotted Woodpecker and the Eurasian Blue Tit showed significant increasing trends (Bani et al., 2009). Contrariwise, Bani et al. (2009) did not detect a significant trend for the Common Swift from 1992 to 2007 in the same study area, while our results showed a reduction of about 50% from 1992 to 2019. It may be due to different timescales considered between the two studies, but also to the ability of the presented modelling approach to provide more accurate estimates of population indices and therefore also of trend.

The inclusion of environmental covariates to correct the environmental bias was the most important factor to determine different trend estimates. The average discrepancy in the group 1 (AD_{g_1}), where we compared the percentage of change in population size (Ts%) between "COV" vs "nonCOV" models (models with environmental covariates and without them, respectively), showed that biased models (i.e. "nonCOV") led to a relevant underestimation of the magnitude of the trend (AD_{g_1}= 1.534). As expected, the exclusion of an approach to correct the environmental bias led to distorted trend estimates. In addition, overlooking the environmental bias could lead to an even more extreme misinterpretation of results (see results for the Eurasian Blue Tit where none of "nonCOV" models was able to detect statistically significant trends). Our results also highlighted that using overdispersed or zero-inflated models could cause moderately higher or lower trend estimates compared to non-overdispersed or non-zero-inflated model, respectively (see AD_{g_2} and AD_{g_3}). This means that the inappropriate use or non-use of the negative binomial distribution or zero-inflated models could produce, in general, moderate distortions in assessment of trend estimates. However, predefining the distribution to describe the mean-variance relationship or whether data are affected by an excessive number of zero counts may be misleading (Blasco-Moreno et al., 2019). Count data may exhibit species-specific statistical properties, and applying a robust statistical framework to decide the model to be used is a crucial point. In our work, only for two species (Eurasian Skylark and Italian Sparrow) the estimated trends were roughly similar in the four WLS models using bias-corrected annual indices (i.e. WLS C-ZIP-GAM, WLS C-ZINB-GAM, WLS C-P-GAM, and WLS C-NB-GAM). For the other four species the trends were markedly different in several cases. For instance, looking at the Eurasian Blue Tit, WLS C-ZIP-GAM (the best model for this species) estimated +48.78 of T%, but the percentage of change in population size was +54.62% for WLS C-ZINB-GAM, +60.31% for WLS C-P-GAM and +70.78% for WLS C-NB-GAM. An over or underestimation of population trends, or, even more, failures to detect real significant trends, represent critical issues for species management and conservation. Misleading estimates can lead to jeopardise species conservation plans (especially for threatened species), with negative effects on biodiversity.

2.5. Conclusions

In this study, we proposed a statistical approach to assess population trends from count data taking into account environmental bias, overdispersion and zero inflation. We also highlighted implications deriving from the interpretation of trends that are estimated from models that do not address these issues. As expected, findings showed that environmental bias was the main driver in determining differences in trend estimates. Moreover, assuming that the distribution function of a random count variable has an identical error structure across all species can lead to distorted estimates of trends. In addition, the excess of zeroes can lead to a zero-inflation process. To date, zero-inflated models are underused in population trend analysis. When there are many zero counts, such as in multi-species survey data, these models can effectively deal with both the excess of zeroes and the overdispersion resulting from zero counts. Additionally, zero-inflated negative binomial models may be needed to manage count data characterised by large variance (e.g. species with colonial breeding or flocking foraging behaviours).

Accurately estimating population trends is crucial to monitor temporal dynamics of wild populations and to plan management actions aimed at conserving species (see Tirozzi et al., 2021 and *Chapter 3*). Future research should aim at the implementation of modelling approaches capable of correcting environmental distortions resulting from temporal changes in the sampling effort or design, as well as from the collection of non-standardised data (e.g. citizen science data). This would allow obtaining more accurate estimates of population trends and exploiting the large amount of new data now available from citizen science projects (Dickinson et al., 2010). Furthermore, the inclusion of zero-inflated models in population trend analysis should be a primary goal. At the time of writing, little software is able to implement zero-inflated models with the ability to specify the variables causing the zero-inflation process (e.g. R packages *pscl* [Zeileis et al., 2008] and *detect* [Sólymos et al., 2018] for GLMs, *zigam* [Wotherspoon & Burch, 2016] for GAMs), and even rarer is the possibility to use less common statistical distributions (e.g. quasi-Poisson, adjusted-Poisson or Hermite distributions [Kemp & Kemp, 1965]). Future research should aim to address these limitations in order to provide a more comprehensive toolset for analysing long-term count data.

Supplementary materials

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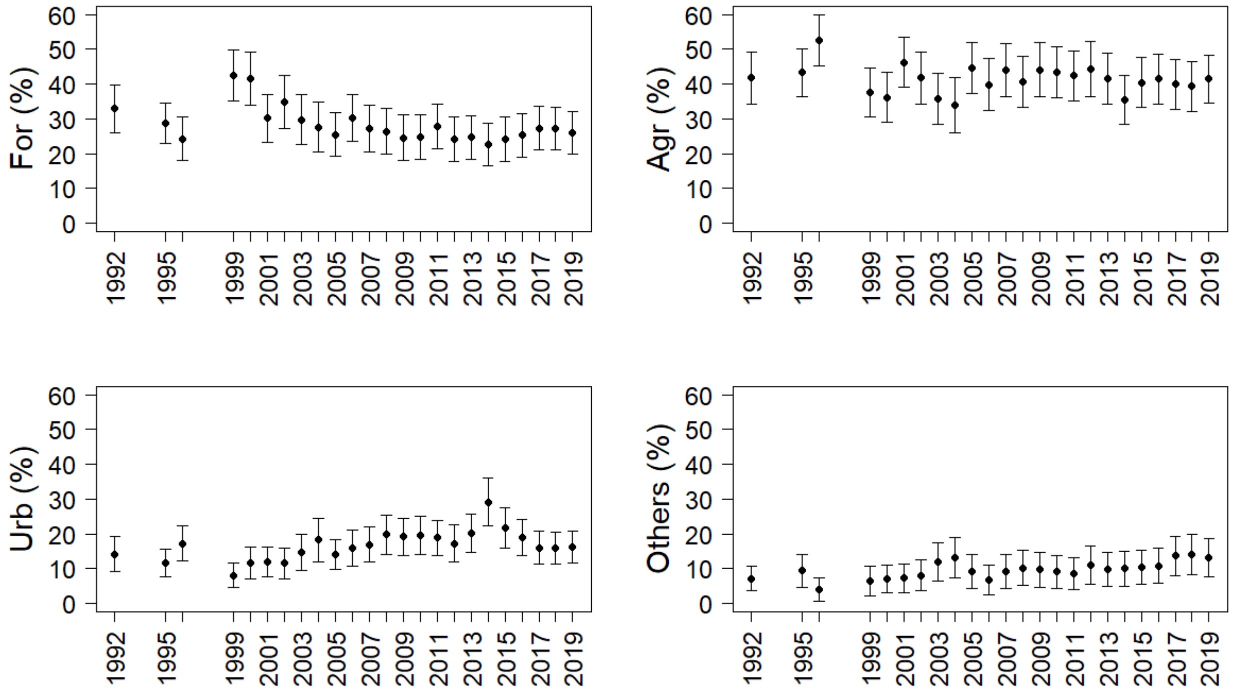
S2.1

Sampling effort (mean ± standard error) over time in relation to the main types of habitats. Values (%) were averaged within a 250 m-radius around each point count. For = forest habitats (C311, C312, C313); Agr = agricultural habitats (C211, C213, C221, C222, C223, C224, C231); Urb = urban habitats (C110, C112); Others = shrublands, and shrub and grass vegetation under evolution (C320), grasslands (C321), natural-open habitats with sparse or absente vegetation (C330). Wetland vegetation (C410) and rivers and streams (C511) were not included. See S2.3 for further details on variables' codes.



S2.2

Details on overdispersion and zero-inflated models.

a) Overdispersion

Abundance derived from count data is often estimated assuming the error term follows a Poisson distribution, where given Y_i an observed integer value, the expected value is $E(Y) = \mu$ and the variance function is $V(Y) = \mu$ (i.e. the mean is equal to the variance) (Zuur et al., 2009). However, when count data show overdispersion (i.e. variance is larger than the mean), Poisson models are inadequate because of the restrictive assumption of the mean-variance relationship. In this case, a suitable alternative is the negative binomial distribution (Zuur et al., 2009). This distribution function has two parameters, μ and θ (also called dispersion parameter); the mean and variance of Y_i are given by $E(Y) = \mu$ and $Var(Y) = \mu + \frac{\mu^2}{\theta}$, respectively (Zuur et al., 2009). Thus, the variance is a quadratic function of the mean, and the smaller θ (relatively to μ^2), the larger overdispersion.

b) Zero-inflated models

For a random variable Y with a zero-inflated distribution, the probability mass function is equal to

$$f(y) \coloneqq f(y|\omega, \psi_{count}) = (1-\omega) f_{zero} + \omega f_{count}(y|\psi_{count}) \qquad \text{(I)}$$

where f_{zero} is the point mass at zero, ψ_{count} are the model parameters of the count distribution, and ω is the weight that represents the probability of observation y coming from the count distribution f_{count}. In the case of Poisson distribution with parameter λ, the zero-inflated Poisson model (ZIP) has probability mass function equal to

$$\Pr(Y = y|\omega, \lambda) = \begin{cases} (1-\omega) + (\omega)\exp(-\lambda), & if\ y = 0 \\ \frac{(\omega)\exp(-\lambda)\lambda^y}{y!}, & if\ y > 0 \end{cases} \qquad \text{(II)}$$

For the negative binomial distribution with mean parameter λ and dispersion parameter θ, the probability mass function of the zero-inflated model (ZINB) is equal to

$$\Pr(Y = y|\omega, \lambda, \theta) = \begin{cases} (1-\omega) + \omega\left(\frac{1}{1+\lambda/\theta}\right)^{\theta}, & if\ y = 0 \\ \omega\ \frac{\Gamma(y+\theta)}{\Gamma(\theta)*\Gamma(y+1)}\left(\frac{1}{1+\lambda/\theta}\right)^{\theta}\left(\frac{\lambda/\theta}{1+\lambda/\theta}\right)^{y}, & if\ y > 0 \end{cases} \qquad \text{(III)}$$

where Γ corresponds to a Gamma function (Blasco-Moreno et al., 2019).

S2.3

Description of land-cover variables included in the models and correspondence with land covers according to the third level of DUSAF classification (ERSAF, 2018).

Land-cover variables		
DUSAF code	Description	Variable code
111	Continuous urban matrix	C110
121	Industrial areas and large production plants	
122	Road and rail networks	
123	Harbours	
124	Airports	
131	Quarries	
132	Dumps	
133	Building sites	
134	Degraded areas	
141	Green urban areas	
142	Recreational areas	
112	Discontinuous urban matrix	C112
211	Arable lands (e.g. maize, wheat, horticulture)	C211
213	Paddy fields	C213
221	Vineyards	C221
222	Orchards	C222
223	Olive groves	C223
224	Wood plantations	C224
231	Meadows and pastures	C231
311	Broadleaved forests	C311
312	Coniferous forests	C312
313	Mixed forests	C313
321	Grasslands	C321
322	Shrublands	C320
324	Shrub and grass vegetation under evolution	
331	Areas around waterbodies without vegetation	C330
332	Debris covers and rocks	
333	Rock areas with sparse vegetation	
334	Glaciers and perennial snow	
411	Wetland vegetation	C410
511	Rivers and streams	C511

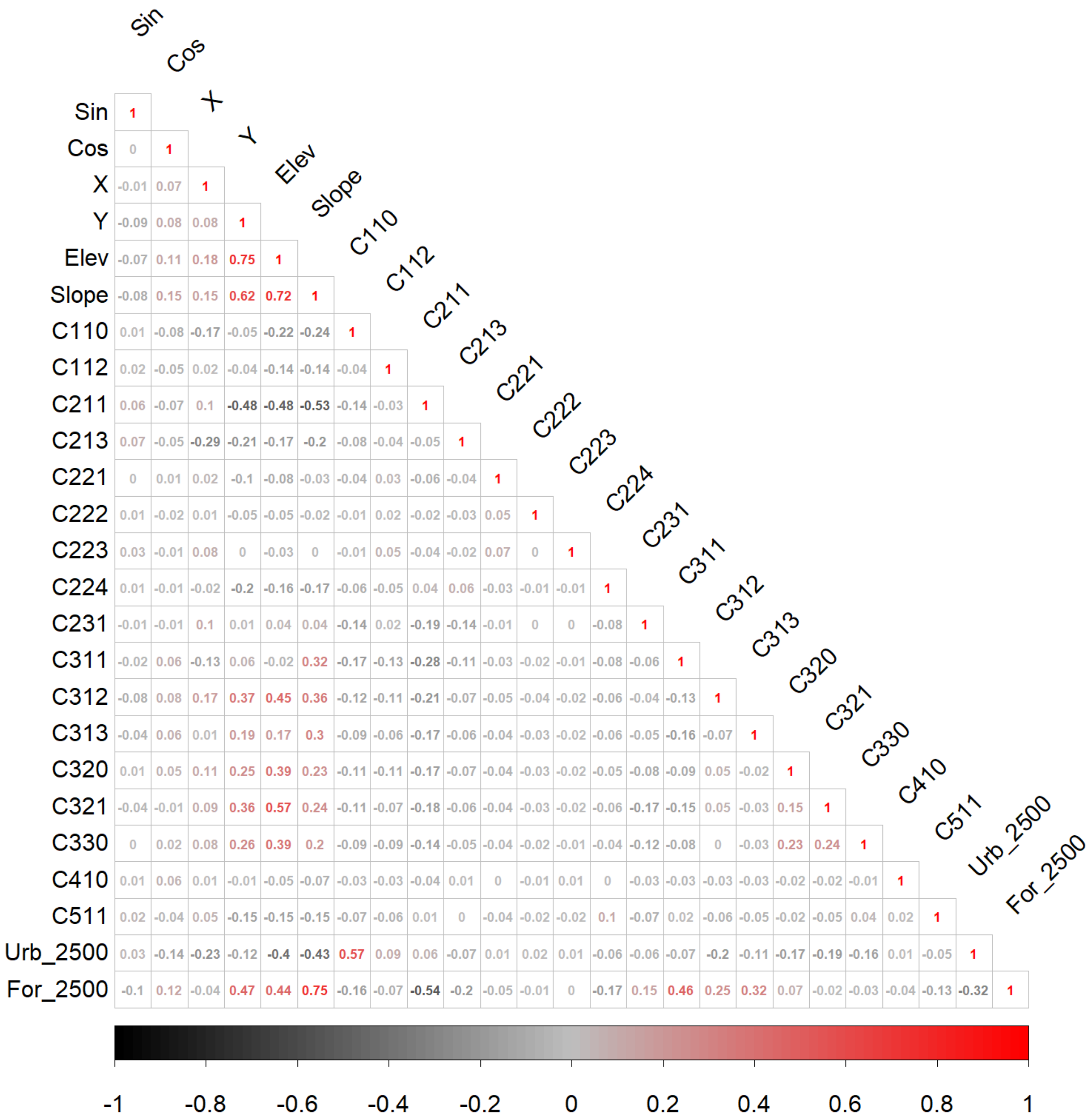
S2.4

Association between digital land-cover maps and bird data for the variables Urb_{2500} and For_{2500}.

Digital land-cover map	Bird data
CORINE Land Cover 1990	1992
DUSAF 1999	1995-2002
DUSAF 2007	2003-2009
DUSAF 2012	2010-2013
DUSAF 2015	2014-2016
DUSAF 2018	2017-2019

S2.5

Pearson correlation analysis between covariates and correlation plot. Triangular matrix showing linear correlation between covariates considered in the study. Only for three couples of variables (Y-Elev; Slope-Elev; Slope-For$_{2500}$) the Pearson coefficient was greater than the threshold of 0.7 (Dormann et al., 2013). However, considering that GAMs also performed well at high level of collinearity (Dorman et al., 2013), and the large dimension of the dataset (Yu et al., 2015), this did not significantly affect models' performance and reliability of models' parameters.



	Sin	Cos	X	Y	Elev	Slope	C110	C112	C211	C213	C221	C222	C223	C224	C231	C311	C312	C313	C320	C321	C330	C410	C511	Urb_2500	For_2500
Sin	1																								
Cos	0	1																							
X	-0.01	0.07	1																						
Y	-0.09	0.08	0.08	1																					
Elev	-0.07	0.11	0.18	0.75	1																				
Slope	-0.08	0.15	0.15	0.62	0.72	1																			
C110	0.01	-0.08	-0.17	-0.05	-0.22	-0.24	1																		
C112	0.02	-0.05	0.02	-0.04	-0.14	-0.14	-0.04	1																	
C211	0.06	-0.07	0.1	-0.48	-0.48	-0.53	-0.14	-0.03	1																
C213	0.07	-0.05	-0.29	-0.21	-0.17	-0.2	-0.08	-0.04	-0.05	1															
C221	0	0.01	0.02	-0.1	-0.08	-0.03	-0.04	0.03	-0.06	-0.04	1														
C222	0.01	-0.02	0.01	-0.05	-0.05	-0.02	-0.01	0.02	-0.02	-0.03	0.05	1													
C223	0.03	-0.01	0.08	0	-0.03	0	-0.01	0.05	-0.04	-0.02	0.07	0	1												
C224	0.01	-0.01	-0.02	-0.2	-0.16	-0.17	-0.06	-0.05	0.04	0.06	-0.03	-0.01	-0.01	1											
C231	-0.01	-0.01	0.1	0.01	0.04	0.04	-0.14	0.02	-0.19	-0.14	-0.01	0	0	-0.08	1										
C311	-0.02	0.06	-0.13	0.06	-0.02	0.32	-0.17	-0.13	-0.28	-0.11	-0.03	-0.02	-0.01	-0.08	-0.06	1									
C312	-0.08	0.08	0.17	0.37	0.45	0.36	-0.12	-0.11	-0.21	-0.07	-0.05	-0.04	-0.02	-0.06	-0.04	-0.13	1								
C313	-0.04	0.06	0.01	0.19	0.17	0.3	-0.09	-0.06	-0.17	-0.06	-0.04	-0.03	-0.02	-0.06	-0.05	-0.16	-0.07	1							
C320	0.01	0.05	0.11	0.25	0.39	0.23	-0.11	-0.11	-0.17	-0.07	-0.04	-0.03	-0.02	-0.05	-0.08	-0.09	0.05	-0.02	1						
C321	-0.04	-0.01	0.09	0.36	0.57	0.24	-0.11	-0.07	-0.18	-0.06	-0.04	-0.03	-0.02	-0.06	-0.17	-0.15	0.05	-0.03	0.15	1					
C330	0	0.02	0.08	0.26	0.39	0.2	-0.09	-0.09	-0.14	-0.05	-0.04	-0.02	-0.01	-0.04	-0.12	-0.08	0	-0.03	0.23	0.24	1				
C410	0.01	0.06	0.01	-0.01	-0.05	-0.07	-0.03	-0.03	-0.04	0.01	0	-0.01	0.01	0	-0.03	-0.03	-0.03	-0.03	-0.02	-0.02	-0.01	1			
C511	0.02	-0.04	0.05	-0.15	-0.15	-0.15	-0.07	-0.06	0.01	0	-0.04	-0.02	-0.02	0.1	-0.07	0.02	-0.06	-0.05	-0.02	-0.05	0.04	0.02	1		
Urb_2500	0.03	-0.14	-0.23	-0.12	-0.4	-0.43	0.57	0.09	0.06	-0.07	0.01	0.02	0.01	-0.06	-0.06	-0.07	-0.2	-0.11	-0.17	-0.19	-0.16	0.01	-0.05	1	
For_2500	-0.1	0.12	-0.04	0.47	0.44	0.75	-0.16	-0.07	-0.54	-0.2	-0.05	-0.01	0	-0.17	0.15	0.46	0.25	0.32	0.07	-0.02	-0.03	-0.04	-0.13	-0.32	1

S2.6

Dataset used for the prediction in the parametric bootstrap procedure. See Section 2.2.4.1 in the main text and S2.3 for details on explanatory variables.

Year	C110	C112	C211	C213	C221	C222	C223	C224	C231	C311	C312	C313	C320	C321	C330	C410	C511	Urb$_{2500}$	For$_{2500}$	Elev	Sin	Cos	Slope	Y (UTM_WGS84_N)	X (UTM_WGS84_E)
1992	6.29	4.66	35.12	4.57	1.01	0.19	0.09	1.82	5.70	14.48	5.84	3.45	3.46	3.26	7.45	0.14	0.59	10.99	23.82	611.69	0.02	–0.20	12.16	5052016	559952
1995	6.35	5.26	33.97	4.89	1.00	0.20	0.09	1.74	5.71	14.71	5.78	3.69	3.45	3.07	7.61	0.14	0.61	11.66	24.23	611.69	0.02	–0.20	12.16	5052016	559952
1996	6.40	5.44	33.61	4.97	1.00	0.20	0.09	1.72	5.71	14.77	5.77	3.75	3.45	3.03	7.65	0.13	0.61	11.88	24.34	611.69	0.02	–0.20	12.16	5052016	559952
1999	6.62	5.85	32.62	5.14	1.02	0.21	0.09	1.66	5.72	14.88	5.73	3.87	3.45	2.99	7.71	0.13	0.63	12.51	24.53	611.69	0.02	–0.20	12.16	5052016	559952
2000	6.72	5.95	32.31	5.16	1.03	0.21	0.09	1.64	5.73	14.90	5.72	3.89	3.45	3.00	7.72	0.13	0.63	12.72	24.55	611.69	0.02	–0.20	12.16	5052016	559952
2001	6.84	6.03	32.03	5.18	1.04	0.22	0.09	1.63	5.73	14.91	5.71	3.90	3.45	3.03	7.71	0.13	0.64	12.92	24.56	611.69	0.02	–0.20	12.16	5052016	559952
2002	6.97	6.09	31.75	5.17	1.05	0.22	0.09	1.62	5.74	14.90	5.70	3.90	3.45	3.06	7.70	0.13	0.64	13.11	24.55	611.69	0.02	–0.20	12.16	5052016	559952
2003	7.10	6.15	31.50	5.16	1.07	0.22	0.10	1.61	5.74	14.90	5.69	3.90	3.45	3.10	7.68	0.13	0.65	13.29	24.53	611.69	0.02	–0.20	12.16	5052016	559952
2004	7.24	6.19	31.25	5.13	1.08	0.23	0.10	1.60	5.74	14.89	5.69	3.89	3.44	3.15	7.66	0.13	0.65	13.47	24.51	611.69	0.02	–0.20	12.16	5052016	559952
2005	7.38	6.22	31.02	5.10	1.10	0.23	0.10	1.59	5.75	14.89	5.69	3.87	3.44	3.20	7.64	0.13	0.65	13.63	24.49	611.69	0.02	–0.20	12.16	5052016	559952
2006	7.51	6.24	30.81	5.05	1.11	0.23	0.10	1.58	5.75	14.89	5.68	3.86	3.44	3.25	7.61	0.13	0.66	13.79	24.47	611.69	0.02	–0.20	12.16	5052016	559952
2007	7.63	6.25	30.60	5.00	1.12	0.23	0.10	1.58	5.76	14.89	5.68	3.85	3.44	3.29	7.59	0.13	0.66	13.93	24.47	611.69	0.02	–0.20	12.16	5052016	559952
2008	7.75	6.27	30.41	4.94	1.13	0.24	0.11	1.57	5.76	14.91	5.69	3.84	3.44	3.33	7.56	0.13	0.66	14.05	24.47	611.69	0.02	–0.20	12.16	5052016	559952
2009	7.85	6.28	30.23	4.88	1.14	0.24	0.11	1.56	5.76	14.93	5.69	3.83	3.44	3.36	7.54	0.14	0.67	14.16	24.49	611.69	0.02	–0.20	12.16	5052016	559952
2010	7.94	6.28	30.07	4.81	1.15	0.24	0.11	1.54	5.77	14.96	5.69	3.82	3.44	3.38	7.53	0.14	0.67	14.26	24.52	611.69	0.02	–0.20	12.16	5052016	559952
2011	8.01	6.29	29.91	4.74	1.15	0.24	0.11	1.53	5.77	15.00	5.70	3.82	3.44	3.40	7.51	0.14	0.67	14.34	24.57	611.69	0.02	–0.20	12.16	5052016	559952
2012	8.07	6.30	29.76	4.66	1.16	0.25	0.12	1.52	5.78	15.06	5.70	3.83	3.43	3.41	7.50	0.14	0.67	14.41	24.64	611.69	0.02	–0.20	12.16	5052016	559952
2013	8.11	6.31	29.62	4.59	1.16	0.25	0.12	1.50	5.78	15.12	5.71	3.84	3.43	3.40	7.50	0.14	0.68	14.46	24.73	611.69	0.02	–0.20	12.16	5052016	559952
2014	8.15	6.33	29.48	4.51	1.16	0.25	0.12	1.49	5.78	15.20	5.72	3.85	3.43	3.39	7.49	0.14	0.68	14.51	24.83	611.69	0.02	–0.20	12.16	5052016	559952
2015	8.16	6.34	29.35	4.43	1.15	0.25	0.12	1.47	5.79	15.28	5.73	3.87	3.43	3.37	7.50	0.14	0.68	14.54	24.95	611.69	0.02	–0.20	12.16	5052016	559952
2016	8.18	6.36	29.22	4.35	1.15	0.25	0.13	1.45	5.79	15.37	5.74	3.89	3.43	3.34	7.50	0.14	0.68	14.57	25.08	611.69	0.02	–0.20	12.16	5052016	559952
2017	8.18	6.38	29.10	4.28	1.14	0.26	0.13	1.44	5.80	15.47	5.75	3.92	3.43	3.31	7.51	0.14	0.69	14.60	25.22	611.69	0.02	–0.20	12.16	5052016	559952
2018	8.18	6.40	28.97	4.20	1.14	0.26	0.13	1.42	5.80	15.57	5.76	3.94	3.43	3.28	7.52	0.14	0.69	14.62	25.36	611.69	0.02	–0.20	12.16	5052016	559952
2019	8.18	6.42	28.85	4.12	1.13	0.26	0.13	1.40	5.80	15.67	5.77	3.97	3.43	3.25	7.52	0.14	0.69	14.64	25.50	611.69	0.02	–0.20	12.16	5052016	559952

S2.7

Summary of GAMs performed for each species. In each table the common and scientific name of the species, the type of model, summary statistics for both parametric and smooth terms are shown. Edf = estimated degree of freedom. See Section 2.2.4.1 in the main text and S2.3 for further details on explanatory variables.

Common Swift (*Apus apus*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.073	0.018	−58.660	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.947	224.936	<0.001
s(Urb$_{2500}$)		1.780	482.821	<0.001
s(For$_{2500}$)		1.841	4.933	0.057
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	1.512	0.040	38.094	<0.001
Year 1995	−0.608	0.057	−10.593	<0.001
Year 1996	−0.406	0.054	−7.565	<0.000
Year 1999	0.028	0.048	0.589	0.556
Year 2000	−0.434	0.046	−9.390	<0.001
Year 2001	−0.314	0.049	−6.388	<0.001
Year 2002	−0.351	0.053	−6.684	<0.001
Year 2003	−0.047	0.050	−0.936	0.349
Year 2004	−0.294	0.057	−5.181	<0.001
Year 2005	−0.200	0.047	−4.267	<0.001
Year 2006	−0.314	0.047	−6.670	<0.001
Year 2007	−0.321	0.060	−5.317	<0.001
Year 2008	−0.350	0.057	−6.118	<0.001
Year 2009	−0.588	0.056	−10.419	<0.001
Year 2010	−0.216	0.050	−4.342	<0.001
Year 2011	−0.334	0.050	−6.696	<0.001
Year 2012	−0.359	0.054	−6.636	<0.001
Year 2013	−0.291	0.052	−5.574	<0.001
Year 2014	−0.354	0.049	−7.261	<0.001
Year 2015	−0.395	0.052	−7.565	<0.001
Year 2016	−0.678	0.060	−11.253	<0.001
Year 2017	−0.939	0.073	−12.908	<0.001
Year 2018	−0.463	0.065	−7.120	<0.001
Year 2019	0.044	0.054	0.809	0.419
Sin	0.030	0.012	2.574	0.010
Cos	−0.065	0.017	−3.745	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.923	67.145	<0.001
s(Elev)		2.954	102.059	<0.001
S(Slope)		2.822	10.567	0.010
s(C110)		2.203	38.416	<0.001
s(C112)		2.732	50.987	<0.001
s(C211)		2.907	123.371	<0.001
s(C213)		2.647	93.105	<0.001
s(C221)		2.916	81.962	<0.001
s(C222)		2.841	55.542	<0.001
s(C223)		0.914	9.608	0.001
s(C224)		2.897	116.731	<0.001
s(C231)		1.963	40.502	<0.001
s(C311)		2.990	307.131	<0.001
s(C312)		2.933	134.208	<0.001
s(C313)		1.131	236.344	<0.001
s(C320)		1.013	48.695	<0.001
s(C321)		2.951	42.923	<0.001
s(C330)		2.585	27.391	<0.001
s(C410)		2.975	54.744	<0.001
s(C511)		2.908	24.056	<0.001

Common Swift (*Apus apus*) — Model C-ZINB-GAM

Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.831	0.022	37.700	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		1.170	665.070	<0.001
s(Urb$_{2500}$)		1.112	1027.400	<0.001
s(For$_{2500}$)		2.833	60.010	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.922	0.127	7.258	<0.001
Year 1995	−0.780	0.159	−4.908	<0.001
Year 1996	−0.669	0.156	−4.284	<0.001
Year 1999	−0.278	0.147	−1.887	0.059
Year 2000	−0.601	0.142	−4.237	<0.001
Year 2001	−0.594	0.148	−4.005	<0.001
Year 2002	−0.458	0.162	−2.834	0.005
Year 2003	−0.217	0.163	−1.334	0.182
Year 2004	−0.335	0.178	−1.884	0.060
Year 2005	−0.485	0.146	−3.319	<0.001
Year 2006	−0.601	0.144	−4.167	<0.001
Year 2007	−1.300	0.162	−8.042	<0.001
Year 2008	−0.949	0.159	−5.971	<0.001
Year 2009	−1.072	0.157	−6.836	<0.001
Year 2010	−0.561	0.154	−3.644	<0.001
Year 2011	−0.793	0.150	−5.298	<0.001
Year 2012	−0.834	0.156	−5.341	<0.001
Year 2013	−0.886	0.155	−5.710	<0.001
Year 2014	−0.848	0.150	−5.646	<0.001
Year 2015	−0.853	0.155	−5.520	<0.001
Year 2016	−1.361	0.159	−8.573	<0.001
Year 2017	−1.510	0.175	−8.652	<0.001
Year 2018	−1.113	0.171	−6.503	<0.001
Year 2019	−0.453	0.167	−2.716	0.007
Sin	0.065	0.030	2.214	0.027
Cos	−0.127	0.044	−2.889	0.004
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.906	52.724	<0.001
s(Elev)		2.895	50.998	<0.001
s(Slope)		0.411	0.680	0.194
s(C110)		1.022	16.871	0.000
s(C112)		0.876	6.340	0.005
s(C211)		1.979	29.953	0.000
s(C213)		0.903	7.950	0.002
s(C221)		0.956	19.609	0.000
s(C222)		0.800	4.087	0.023
s(C223)		0.851	5.823	0.009
s(C224)		0.905	9.191	0.001
s(C231)		0.619	1.562	0.094
s(C311)		2.679	160.801	0.000
s(C312)		1.237	108.943	0.000
s(C313)		1.269	147.769	0.000
s(C320)		0.956	16.345	0.000
s(C321)		0.001	0.000	0.907
s(C330)		0.003	0.002	0.411
s(C410)		0.002	0.000	0.755
s(C511)		0.002	0.000	0.811

Common Swift (*Apus apus*) — Model C-P-GAM				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.346	0.040	8.740	<0.001
Year 1995	−0.788	0.057	−13.834	<0.001
Year 1996	−0.780	0.053	−14.633	<0.001
Year 1999	−0.305	0.047	−6.486	<0.001
Year 2000	−0.557	0.046	−12.168	<0.001
Year 2001	−0.628	0.049	−12.896	<0.001
Year 2002	−0.364	0.052	−7.007	<0.001
Year 2003	−0.220	0.050	−4.443	<0.001
Year 2004	−0.454	0.056	−8.126	<0.001
Year 2005	−0.515	0.047	−11.068	<0.001
Year 2006	−0.561	0.047	−12.064	<0.001
Year 2007	−1.205	0.060	−20.122	<0.001
Year 2008	−1.044	0.057	−18.371	<0.001
Year 2009	−1.077	0.056	−19.180	<0.001
Year 2010	−0.559	0.049	−11.339	<0.001
Year 2011	−0.680	0.050	−13.720	<0.001
Year 2012	−0.859	0.053	−16.092	<0.001
Year 2013	−0.852	0.052	−16.446	<0.001
Year 2014	−0.743	0.048	−15.458	<0.001
Year 2015	−0.833	0.052	−16.105	<0.001
Year 2016	−1.316	0.060	−21.998	<0.001
Year 2017	−1.463	0.073	−20.165	<0.001
Year 2018	−1.132	0.065	−17.530	<0.001
Year 2019	−0.531	0.054	−9.858	<0.001
Sin	0.057	0.011	4.949	<0.001
Cos	−0.160	0.018	−9.068	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.993	591.150	<0.001
s(Elev)		2.981	465.620	<0.001
s(Slope)		2.767	19.390	<0.001
s(C110)		1.098	98.710	<0.001
s(C112)		0.958	17.570	<0.001
s(C211)		2.944	235.120	<0.001
s(C213)		2.367	216.130	<0.001
s(C221)		2.889	80.940	<0.001
s(C222)		2.859	62.070	<0.001
s(C223)		1.005	27.140	<0.001
s(C224)		2.947	165.680	<0.001
s(C231)		0.901	24.750	<0.001
s(C311)		2.979	771.390	<0.001
s(C312)		2.544	514.520	<0.001
s(C313)		2.089	594.620	<0.001
s(C320)		2.535	62.420	<0.001
s(C321)		2.959	64.700	<0.001
s(C330)		2.569	84.910	<0.001
s(C410)		2.262	13.270	<0.001
s(C511)		2.874	42.280	<0.001

Common Swift (*Apus apus*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.344	0.135	2.547	0.011
Year 1995	−0.727	0.169	−4.289	<0.001
Year 1996	−0.670	0.166	−4.032	<0.001
Year 1999	−0.269	0.155	−1.729	0.084
Year 2000	−0.537	0.150	−3.570	<0.001
Year 2001	−0.474	0.157	−3.024	0.002
Year 2002	−0.331	0.171	−1.936	0.053
Year 2003	−0.138	0.170	−0.811	0.418
Year 2004	−0.201	0.186	−1.078	0.281
Year 2005	−0.436	0.155	−2.823	0.005
Year 2006	−0.502	0.155	−3.240	0.001
Year 2007	−1.381	0.171	−8.094	<0.001
Year 2008	−0.805	0.167	−4.811	<0.001
Year 2009	−1.083	0.167	−6.501	<0.001
Year 2010	−0.561	0.164	−3.424	0.001
Year 2011	−0.762	0.160	−4.763	<0.001
Year 2012	−0.923	0.166	−5.576	<0.001
Year 2013	−1.037	0.165	−6.289	<0.001
Year 2014	−0.973	0.161	−6.029	<0.001
Year 2015	−0.977	0.164	−5.941	<0.001
Year 2016	−1.466	0.169	−8.702	<0.001
Year 2017	−1.569	0.185	−8.483	<0.001
Year 2018	−1.218	0.181	−6.748	<0.001
Year 2019	−0.659	0.175	−3.761	<0.001
Sin	0.103	0.030	3.391	<0.001
Cos	−0.173	0.046	−3.806	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.900	57.639	<0.001
s(Elev)		2.883	88.774	<0.001
s(Slope)		0.006	0.006	0.305
s(C110)		1.135	50.502	<0.001
s(C112)		1.017	28.798	<0.001
s(C211)		1.446	37.115	<0.001
s(C213)		0.969	17.764	<0.001
s(C221)		0.934	13.578	<0.001
s(C222)		0.823	4.808	0.016
s(C223)		0.825	4.850	0.015
s(C224)		0.920	10.910	<0.001
s(C231)		0.003	0.000	0.830
s(C311)		2.605	209.590	<0.001
s(C312)		1.460	176.720	<0.001
s(C313)		1.274	175.295	<0.001
s(C320)		0.997	32.743	<0.001
s(C321)		0.003	0.000	0.786
s(C330)		0.936	12.866	<0.001
s(C410)		0.002	0.000	0.827
s(C511)		0.007	0.005	0.380

Common Swift (*Apus apus*) — Model nC-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.117	0.019	−60.040	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.914	326.800	<0.001
s(Urb$_{2500}$)		1.776	540.800	<0.001
s(For$_{2500}$)		0.001	0.000	0.495
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	1.592	0.037	42.634	<0.001
Year 1995	−0.597	0.057	−10.547	<0.001
Year 1996	−0.328	0.053	−6.225	<0.001
Year 1999	0.076	0.046	1.654	0.098
Year 2000	−0.367	0.045	−8.074	<0.001
Year 2001	−0.241	0.048	−4.987	<0.001
Year 2002	−0.285	0.052	−5.517	<0.001
Year 2003	0.108	0.049	2.220	0.026
Year 2004	−0.127	0.055	−2.296	0.022
Year 2005	−0.085	0.046	−1.852	0.064
Year 2006	−0.215	0.046	−4.666	<0.001
Year 2007	−0.156	0.060	−2.624	0.009
Year 2008	−0.236	0.057	−4.177	<0.001
Year 2009	−0.485	0.056	−8.681	<0.001
Year 2010	−0.124	0.049	−2.528	0.011
Year 2011	−0.254	0.049	−5.151	<0.001
Year 2012	−0.252	0.053	−4.752	<0.001
Year 2013	−0.172	0.052	−3.330	<0.001
Year 2014	−0.224	0.048	−4.708	<0.001
Year 2015	−0.257	0.051	−4.999	<0.001
Year 2016	−0.560	0.060	−9.408	<0.001
Year 2017	−0.870	0.072	−12.022	<0.001
Year 2018	−0.348	0.064	−5.395	<0.001
Year 2019	0.157	0.054	2.929	0.003
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.828	17.100	<0.001

Common Swift (*Apus apus*) — Model nC-ZINB-GAM

Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.438	0.019	22.870	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.962	811.800	<0.001
s(Urb$_{2500}$)		1.202	1089.800	<0.001
s(For$_{2500}$)		0.001	0.000	0.815
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	1.172	0.126	9.325	<0.001
Year 1995	−0.896	0.161	−5.581	<0.001
Year 1996	−0.701	0.158	−4.437	<0.001
Year 1999	−0.346	0.149	−2.322	0.020
Year 2000	−0.611	0.143	−4.265	<0.001
Year 2001	−0.584	0.150	−3.894	<0.001
Year 2002	−0.399	0.163	−2.447	0.014
Year 2003	−0.029	0.165	−0.178	0.859
Year 2004	−0.167	0.179	−0.933	0.351
Year 2005	−0.365	0.148	−2.471	0.013
Year 2006	−0.523	0.146	−3.590	<0.001
Year 2007	−1.023	0.162	−6.296	<0.001
Year 2008	−0.811	0.160	−5.057	<0.001
Year 2009	−0.948	0.158	−6.001	<0.001
Year 2010	−0.460	0.156	−2.956	0.003
Year 2011	−0.659	0.151	−4.357	<0.001
Year 2012	−0.705	0.158	−4.468	<0.001
Year 2013	−0.638	0.157	−4.075	<0.001
Year 2014	−0.490	0.151	−3.255	0.001
Year 2015	−0.644	0.156	−4.130	<0.001
Year 2016	−1.151	0.160	−7.205	<0.001
Year 2017	−1.336	0.175	−7.634	<0.001
Year 2018	−0.964	0.173	−5.562	<0.001
Year 2019	−0.376	0.170	−2.210	0.027
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.917	51.360	<0.001

Common Swift (*Apus apus*) — Model nC-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.564	0.037	15.104	<0.001
Year 1995	−0.780	0.057	−13.793	<0.001
Year 1996	−0.621	0.053	−11.776	<0.001
Year 1999	−0.377	0.046	−8.200	<0.001
Year 2000	−0.585	0.045	−12.882	<0.001
Year 2001	−0.604	0.048	−12.501	<0.001
Year 2002	−0.428	0.052	−8.306	<0.001
Year 2003	−0.077	0.049	−1.568	0.117
Year 2004	−0.167	0.055	−3.031	0.002
Year 2005	−0.371	0.046	−8.061	<0.001
Year 2006	−0.409	0.046	−8.851	<0.001
Year 2007	−1.096	0.060	−18.391	<0.001
Year 2008	−0.857	0.057	−15.167	<0.001
Year 2009	−0.900	0.056	−16.120	<0.001
Year 2010	−0.387	0.049	−7.903	<0.001
Year 2011	−0.561	0.049	−11.373	<0.001
Year 2012	−0.702	0.053	−13.238	<0.001
Year 2013	−0.620	0.052	−12.041	<0.001
Year 2014	−0.370	0.047	−7.782	<0.001
Year 2015	−0.582	0.051	−11.313	<0.001
Year 2016	−1.147	0.060	−19.272	<0.001
Year 2017	−1.340	0.072	−18.529	<0.001
Year 2018	−1.004	0.064	−15.590	<0.001
Year 2019	−0.396	0.054	−7.385	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.970	1974.000	<0.001

Common Swift (*Apus apus*) — Model nC-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.639	0.139	4.583	<0.001
Year 1995	−0.858	0.178	−4.814	<0.001
Year 1996	−0.761	0.175	−4.342	<0.001
Year 1999	−0.465	0.163	−2.863	0.004
Year 2000	−0.697	0.158	−4.419	<0.001
Year 2001	−0.585	0.165	−3.545	<0.001
Year 2002	−0.502	0.179	−2.796	0.005
Year 2003	−0.147	0.178	−0.825	0.409
Year 2004	−0.227	0.195	−1.162	0.245
Year 2005	−0.418	0.162	−2.575	0.010
Year 2006	−0.445	0.163	−2.727	0.006
Year 2007	−1.205	0.176	−6.829	<0.001
Year 2008	−0.793	0.175	−4.522	<0.001
Year 2009	−0.986	0.174	−5.669	<0.001
Year 2010	−0.532	0.172	−3.087	0.002
Year 2011	−0.667	0.168	−3.978	<0.001
Year 2012	−0.797	0.173	−4.616	<0.001
Year 2013	−0.784	0.172	−4.568	<0.001
Year 2014	−0.484	0.168	−2.890	0.004
Year 2015	−0.736	0.171	−4.298	<0.001
Year 2016	−1.259	0.174	−7.227	<0.001
Year 2017	−1.423	0.190	−7.487	<0.001
Year 2018	−1.064	0.187	−5.689	<0.001
Year 2019	−0.541	0.183	−2.950	0.003
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.999	398.000	<0.001

Great Spotted Woodpecker (*Dendrocopos major*) — Model C-ZIP-GAM

		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.978	0.021	46.720	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.985	2718.000	<0.001
s(Urb$_{2500}$)		0.001	0.000	0.748
s(For$_{2500}$)		2.992	1434.000	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.082	0.245	−12.588	<0.001
Year 1995	−0.478	0.338	−1.412	0.158
Year 1996	−0.699	0.361	−1.936	0.053
Year 1999	0.725	0.256	2.826	0.005
Year 2000	0.483	0.260	1.858	0.063
Year 2001	0.626	0.268	2.338	0.019
Year 2002	0.767	0.277	2.767	0.006
Year 2003	1.017	0.272	3.734	<0.001
Year 2004	0.735	0.308	2.386	0.017
Year 2005	0.992	0.262	3.792	<0.001
Year 2006	1.143	0.255	4.481	<0.001
Year 2007	1.148	0.264	4.339	<0.001
Year 2008	1.013	0.270	3.746	<0.001
Year 2009	0.862	0.273	3.160	0.002
Year 2010	1.179	0.264	4.461	<0.001
Year 2011	1.420	0.256	5.539	<0.001
Year 2012	1.347	0.262	5.144	<0.001
Year 2013	1.497	0.258	5.798	<0.001
Year 2014	1.560	0.257	6.073	<0.001
Year 2015	1.391	0.261	5.326	<0.001
Year 2016	1.528	0.259	5.907	<0.001
Year 2017	1.559	0.261	5.971	<0.001
Year 2018	1.156	0.270	4.278	<0.001
Year 2019	1.592	0.261	6.095	<0.001
Sin	−0.015	0.032	−0.469	0.639
Cos	0.056	0.048	1.163	0.245
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.955	97.659	<0.001
s(Elev)		1.940	9.652	0.003
S(Slope)		0.914	22.397	<0.001
s(C110)		2.216	14.829	<0.001
s(C112)		1.736	10.581	0.002
s(C211)		2.083	9.671	0.004
s(C213)		0.926	19.094	<0.001
s(C221)		0.000	0.000	0.917
s(C222)		0.001	0.000	0.421
s(C223)		0.852	5.104	0.014
s(C224)		1.784	65.088	<0.001
s(C231)		0.841	5.134	0.009
s(C311)		2.925	176.327	<0.001
s(C312)		1.032	52.313	<0.001
s(C313)		2.405	128.915	<0.001
s(C320)		0.654	1.554	0.115
s(C321)		0.815	4.538	0.015
s(C330)		1.569	4.196	0.066
s(C410)		0.000	0.000	0.800
s(C511)		0.007	0.004	0.430

Great Spotted Woodpecker (*Dendrocopos major*) — Model C-ZINB-GAM

		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.965	0.021	45.290	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.990	2765.000	<0.001
s(Urb$_{2500}$)		0.002	0.000	0.831
s(For$_{2500}$)		2.995	1694.000	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.022	0.245	−12.352	<0.001
Year 1995	−0.504	0.338	−1.490	0.136
Year 1996	−0.712	0.361	−1.972	0.049
Year 1999	0.709	0.256	2.766	0.006
Year 2000	0.461	0.260	1.774	0.076
Year 2001	0.594	0.268	2.219	0.026
Year 2002	0.759	0.277	2.740	0.006
Year 2003	0.984	0.272	3.613	<0.001
Year 2004	0.756	0.308	2.452	0.014
Year 2005	0.990	0.262	3.785	<0.001
Year 2006	1.117	0.255	4.383	<0.001
Year 2007	1.154	0.264	4.364	<0.001
Year 2008	1.004	0.270	3.713	<0.001
Year 2009	0.876	0.273	3.213	0.001
Year 2010	1.180	0.264	4.467	<0.001
Year 2011	1.380	0.256	5.385	<0.001
Year 2012	1.348	0.262	5.148	<0.001
Year 2013	1.530	0.258	5.929	<0.001
Year 2014	1.570	0.257	6.110	<0.001
Year 2015	1.403	0.261	5.375	<0.001
Year 2016	1.528	0.259	5.909	<0.001
Year 2017	1.583	0.261	6.063	<0.001
Year 2018	1.182	0.270	4.374	<0.001
Year 2019	1.617	0.261	6.190	<0.001
Sin	−0.026	0.032	−0.812	0.417
Cos	0.095	0.048	1.990	0.047
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.902	47.217	<0.001
s(Elev)		0.000	0.000	0.685
S(Slope)		1.288	78.182	<0.001
s(C110)		0.988	10.584	<0.001
s(C112)		0.906	8.162	0.002
s(C211)		2.121	10.876	0.001
s(C213)		0.926	10.557	<0.001
s(C221)		0.000	0.000	0.981
s(C222)		0.209	0.274	0.249
s(C223)		0.874	5.452	0.012
s(C224)		1.030	83.429	<0.001
s(C231)		0.879	5.490	0.005
s(C311)		2.825	199.506	<0.001
s(C312)		1.123	72.811	<0.001
s(C313)		2.404	141.695	<0.001
s(C320)		0.639	1.807	0.084
s(C321)		0.840	4.759	0.015
s(C330)		0.414	0.670	0.198
s(C410)		0.000	0.000	0.897
s(C511)		0.576	1.368	0.113

Great Spotted Woodpecker (*Dendrocopos major*) — Model C-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.562	0.245	−14.544	<0.001
Year 1995	−0.514	0.338	−1.518	0.129
Year 1996	−0.714	0.361	−1.977	0.048
Year 1999	0.768	0.256	2.993	0.003
Year 2000	0.481	0.260	1.847	0.065
Year 2001	0.630	0.268	2.351	0.019
Year 2002	0.767	0.277	2.766	0.006
Year 2003	1.032	0.273	3.788	<0.001
Year 2004	0.724	0.308	2.350	0.019
Year 2005	0.967	0.262	3.695	<0.001
Year 2006	1.155	0.255	4.531	<0.001
Year 2007	1.195	0.265	4.519	<0.001
Year 2008	1.035	0.270	3.827	<0.001
Year 2009	0.880	0.273	3.227	0.001
Year 2010	1.196	0.264	4.525	<0.001
Year 2011	1.465	0.256	5.715	<0.001
Year 2012	1.369	0.262	5.227	<0.001
Year 2013	1.535	0.258	5.943	<0.001
Year 2014	1.584	0.257	6.163	<0.001
Year 2015	1.405	0.261	5.380	<0.001
Year 2016	1.567	0.259	6.055	<0.001
Year 2017	1.623	0.261	6.213	<0.001
Year 2018	1.201	0.270	4.443	<0.001
Year 2019	1.631	0.261	6.240	<0.001
Sin	−0.025	0.032	−0.773	0.440
Cos	0.055	0.048	1.147	0.251
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.984	116.397	<0.001
s(Elev)		2.976	124.603	<0.001
s(Slope)		0.975	17.158	<0.001
s(C110)		2.162	18.054	<0.001
s(C112)		1.721	10.527	0.001
s(C211)		2.118	11.104	0.001
s(C213)		0.931	25.415	<0.001
s(C221)		1.302	0.432	0.667
s(C222)		0.000	0.000	0.357
s(C223)		0.844	4.641	0.019
s(C224)		1.849	61.231	<0.001
s(C231)		0.762	5.004	0.006
s(C311)		2.924	192.659	<0.001
s(C312)		1.044	63.092	<0.001
s(C313)		2.439	141.736	<0.001
s(C320)		0.642	1.448	0.122
s(C321)		0.869	9.923	<0.001
s(C330)		0.772	4.357	0.016
s(C410)		0.000	0.000	0.901
s(C511)		0.000	0.000	0.541

Great Spotted Woodpecker (*Dendrocopos major*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	–3.533	0.245	–14.429	<0.001
Year 1995	–0.543	0.338	–1.604	0.109
Year 1996	–0.713	0.361	–1.973	0.049
Year 1999	0.769	0.257	2.999	0.003
Year 2000	0.462	0.260	1.776	0.076
Year 2001	0.596	0.268	2.224	0.026
Year 2002	0.755	0.277	2.726	0.006
Year 2003	1.022	0.272	3.750	<0.001
Year 2004	0.763	0.308	2.475	0.013
Year 2005	0.972	0.262	3.714	<0.001
Year 2006	1.133	0.255	4.445	<0.001
Year 2007	1.222	0.264	4.619	<0.001
Year 2008	1.034	0.270	3.826	<0.001
Year 2009	0.905	0.273	3.317	0.001
Year 2010	1.204	0.264	4.556	<0.001
Year 2011	1.444	0.256	5.635	<0.001
Year 2012	1.386	0.262	5.295	<0.001
Year 2013	1.588	0.258	6.150	<0.001
Year 2014	1.613	0.257	6.276	<0.001
Year 2015	1.432	0.261	5.485	<0.001
Year 2016	1.580	0.259	6.106	<0.001
Year 2017	1.664	0.261	6.373	<0.001
Year 2018	1.237	0.270	4.578	<0.001
Year 2019	1.668	0.261	6.383	<0.001
Sin	–0.035	0.032	–1.102	0.271
Cos	0.091	0.048	1.887	0.059
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.909	54.575	<0.001
s(Elev)		2.913	102.775	<0.001
s(Slope)		1.137	17.392	<0.001
s(C110)		1.072	17.128	<0.001
s(C112)		0.908	8.245	0.002
s(C211)		2.068	10.280	0.002
s(C213)		0.969	18.018	0.000
s(C221)		0.002	0.000	0.671
s(C222)		0.314	0.482	0.212
s(C223)		0.867	5.105	0.015
s(C224)		1.031	77.159	<0.001
s(C231)		0.879	5.383	0.007
s(C311)		2.873	228.140	<0.001
s(C312)		1.140	72.301	<0.001
s(C313)		2.520	163.497	<0.001
s(C320)		0.658	1.932	0.078
s(C321)		0.928	10.173	0.001
s(C330)		0.805	3.838	0.027
s(C410)		0.001	0.000	0.991
s(C511)		0.488	0.953	0.154

Great Spotted Woodpecker (*Dendrocopos major*) — Model nC-ZIP-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.4583	0.021	21.930	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.977	2595.400	<0.001
s(Urb$_{2500}$)		2.986	101.700	<0.001
s(For$_{2500}$)		2.994	1954.300	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.580	0.243	−10.631	<0.001
Year 1995	−0.376	0.338	−1.111	0.267
Year 1996	−0.742	0.361	−2.056	0.040
Year 1999	0.966	0.256	3.779	<0.001
Year 2000	0.590	0.260	2.271	0.023
Year 2001	0.669	0.267	2.500	0.012
Year 2002	0.794	0.276	2.871	0.004
Year 2003	0.998	0.272	3.668	<0.001
Year 2004	0.539	0.308	1.753	0.080
Year 2005	0.920	0.261	3.521	<0.001
Year 2006	1.201	0.255	4.719	<0.001
Year 2007	1.039	0.264	3.931	<0.001
Year 2008	0.922	0.270	3.414	<0.001
Year 2009	0.731	0.272	2.682	0.007
Year 2010	1.034	0.264	3.918	<0.001
Year 2011	1.305	0.256	5.094	<0.001
Year 2012	1.137	0.262	4.347	<0.001
Year 2013	1.298	0.258	5.035	<0.001
Year 2014	1.352	0.257	5.271	<0.001
Year 2015	1.192	0.261	4.571	<0.001
Year 2016	1.357	0.258	5.252	<0.001
Year 2017	1.484	0.261	5.689	<0.001
Year 2018	1.074	0.270	3.976	<0.001
Year 2019	1.486	0.261	5.696	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.982	154.300	<0.001

Great Spotted Woodpecker (*Dendrocopos major*) — Model nC-ZINB-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.475	0.021	23.060	<0.001
Smooth terms		**edf**	**Chi square**	**p-value**
s(Elev)		2.987	2570.700	<0.001
s(Urb$_{2500}$)		2.940	25.460	<0.001
s(For$_{2500}$)		2.997	2194.990	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.578	0.243	−10.621	<0.001
Year 1995	−0.404	0.338	−1.196	0.232
Year 1996	−0.757	0.361	−2.097	0.036
Year 1999	0.958	0.256	3.746	<0.001
Year 2000	0.570	0.260	2.194	0.028
Year 2001	0.644	0.267	2.407	0.016
Year 2002	0.765	0.276	2.767	0.006
Year 2003	0.978	0.272	3.597	<0.001
Year 2004	0.566	0.308	1.842	0.066
Year 2005	0.923	0.261	3.533	<0.001
Year 2006	1.166	0.255	4.583	<0.001
Year 2007	1.047	0.264	3.961	<0.001
Year 2008	0.907	0.270	3.359	<0.001
Year 2009	0.737	0.272	2.705	0.007
Year 2010	1.033	0.264	3.911	<0.001
Year 2011	1.252	0.256	4.888	<0.001
Year 2012	1.133	0.262	4.332	<0.001
Year 2013	1.320	0.258	5.122	<0.001
Year 2014	1.347	0.257	5.251	<0.001
Year 2015	1.196	0.261	4.584	<0.001
Year 2016	1.354	0.258	5.241	<0.001
Year 2017	1.497	0.261	5.739	<0.001
Year 2018	1.084	0.270	4.013	<0.001
Year 2019	1.493	0.261	5.720	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.963	103.300	<0.001

Great Spotted Woodpecker (*Dendrocopos major*) — Model nC-P-GAM

Parametric terms	Estimate	Standard error	z-value	p-value
Intercept	−3.154	0.243	−12.996	<0.001
Year 1995	−0.457	0.338	−1.352	0.176
Year 1996	−0.802	0.361	−2.221	0.026
Year 1999	1.111	0.256	4.345	<0.001
Year 2000	0.590	0.260	2.270	0.023
Year 2001	0.547	0.267	2.047	0.041
Year 2002	0.675	0.276	2.442	0.015
Year 2003	0.916	0.272	3.367	<0.001
Year 2004	0.438	0.308	1.423	0.155
Year 2005	0.796	0.261	3.045	0.002
Year 2006	1.263	0.255	4.963	<0.001
Year 2007	1.001	0.264	3.787	<0.001
Year 2008	0.810	0.270	3.000	0.003
Year 2009	0.633	0.272	2.322	0.020
Year 2010	0.940	0.264	3.558	<0.001
Year 2011	1.319	0.256	5.152	<0.001
Year 2012	1.116	0.262	4.270	<0.001
Year 2013	1.289	0.258	4.997	<0.001
Year 2014	1.271	0.257	4.957	<0.001
Year 2015	1.150	0.261	4.408	<0.001
Year 2016	1.272	0.258	4.923	<0.001
Year 2017	1.490	0.261	5.711	<0.001
Year 2018	1.068	0.270	3.953	<0.001
Year 2019	1.479	0.261	5.668	<0.001
Smooth terms		**edf**	**Ch- square**	**p-value**
s(X, Y)		2.946	270.300	<0.001

Great Spotted Woodpecker (*Dendrocopos major*) — Model nC-NB-GAM

Parametric terms	Estimate	Standard error	z-value	p-value
Intercept	−3.158	0.243	−13.013	<0.001
Year 1995	−0.464	0.338	−1.372	0.170
Year 1996	−0.803	0.361	−2.224	0.026
Year 1999	1.121	0.256	4.385	<0.001
Year 2000	0.588	0.260	2.263	0.024
Year 2001	0.538	0.267	2.012	0.044
Year 2002	0.679	0.276	2.455	0.014
Year 2003	0.935	0.272	3.437	<0.001
Year 2004	0.454	0.308	1.476	0.140
Year 2005	0.811	0.261	3.103	0.002
Year 2006	1.250	0.255	4.911	<0.001
Year 2007	1.013	0.264	3.835	<0.001
Year 2008	0.820	0.270	3.036	0.002
Year 2009	0.645	0.272	2.369	0.018
Year 2010	0.954	0.264	3.612	<0.001
Year 2011	1.314	0.256	5.130	<0.001
Year 2012	1.128	0.262	4.316	<0.001
Year 2013	1.311	0.258	5.085	<0.001
Year 2014	1.275	0.257	4.971	<0.001
Year 2015	1.163	0.261	4.458	<0.001
Year 2016	1.283	0.258	4.963	<0.001
Year 2017	1.510	0.261	5.790	<0.001
Year 2018	1.087	0.270	4.027	<0.001
Year 2019	1.498	0.261	5.741	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.988	234.000	<0.001

Eurasian Skylark (*Alauda arvensis*) — Model C-ZIP-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.168	0.018	9.125	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.991	618.800	<0.001
s(Urb$_{2500}$)		1.121	295.900	<0.001
s(For$_{2500}$)		2.110	193.900	<0.001

Count component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.124	0.107	−10.466	<0.001
Year 1995	−0.645	0.085	−7.623	<0.001
Year 1996	−0.861	0.084	−10.286	<0.001
Year 1999	−0.661	0.094	−7.067	<0.001
Year 2000	−0.748	0.082	−9.161	<0.001
Year 2001	−0.919	0.084	−10.953	<0.001
Year 2002	−0.939	0.101	−9.250	<0.001
Year 2003	−1.083	0.103	−10.488	<0.001
Year 2004	−1.391	0.127	−10.973	<0.001
Year 2005	−1.163	0.082	−14.132	<0.001
Year 2006	−1.349	0.093	−14.544	<0.001
Year 2007	−1.777	0.113	−15.709	<0.001
Year 2008	−1.767	0.121	−14.652	<0.001
Year 2009	−1.676	0.108	−15.491	<0.001
Year 2010	−1.836	0.122	−15.035	<0.001
Year 2011	−2.245	0.134	−16.783	<0.001
Year 2012	−2.199	0.128	−17.136	<0.001
Year 2013	−2.506	0.147	−17.029	<0.001
Year 2014	−2.463	0.152	−16.191	<0.001
Year 2015	−2.564	0.154	−16.608	<0.001
Year 2016	−2.146	0.130	−16.560	<0.001
Year 2017	−2.586	0.181	−14.321	<0.001
Year 2018	−2.280	0.161	−14.195	<0.001
Year 2019	−2.513	0.176	−14.259	<0.001
Sin	0.020	0.026	0.793	0.428
Cos	0.040	0.038	1.063	0.288
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.979	267.814	<0.001
s(Elev)		2.940	183.753	<0.001
S(Slope)		2.553	170.265	<0.001
s(C110)		1.048	81.880	<0.001
s(C112)		2.736	50.882	<0.001
s(C211)		2.742	62.335	<0.001
s(C213)		1.671	31.182	<0.001
s(C221)		1.955	6.344	0.029
s(C222)		0.001	0.000	0.871
s(C223)		0.878	5.259	0.014
s(C224)		2.638	40.149	<0.001
s(C231)		0.992	44.294	<0.001
s(C311)		1.849	117.667	<0.001
s(C312)		2.820	54.836	<0.001
s(C313)		2.941	32.039	<0.001
s(C320)		1.635	42.053	<0.001
s(C321)		2.641	104.323	<0.001
s(C330)		2.376	59.652	<0.001
s(C410)		0.884	8.908	0.001
s(C511)		0.246	0.389	0.201

Eurasian Skylark (*Alauda arvensis*) — Model C-ZINB-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.179	0.019	9.629	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.988	632.500	<0.001
s(Urb$_{2500}$)		1.122	299.200	<0.001
s(For$_{2500}$)		1.940	186.200	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.049	0.104	−10.040	<0.001
Year 1995	−0.655	0.089	−7.350	<0.001
Year 1996	−0.861	0.088	−9.787	<0.001
Year 1999	−0.693	0.097	−7.112	<0.001
Year 2000	−0.783	0.086	−9.115	<0.001
Year 2001	−0.942	0.088	−10.707	<0.001
Year 2002	−0.947	0.106	−8.955	<0.001
Year 2003	−1.097	0.107	−10.218	<0.001
Year 2004	−1.418	0.131	−10.791	<0.001
Year 2005	−1.187	0.086	−13.755	<0.001
Year 2006	−1.367	0.097	−14.167	<0.001
Year 2007	−1.799	0.117	−15.431	<0.001
Year 2008	−1.791	0.124	−14.429	<0.001
Year 2009	−1.692	0.112	−15.151	<0.001
Year 2010	−1.853	0.125	−14.763	<0.001
Year 2011	−2.273	0.137	−16.601	<0.001
Year 2012	−2.228	0.132	−16.935	<0.001
Year 2013	−2.540	0.150	−16.939	<0.001
Year 2014	−2.493	0.155	−16.076	<0.001
Year 2015	−2.585	0.157	−16.452	<0.001
Year 2016	−2.161	0.133	−16.268	<0.001
Year 2017	−2.614	0.184	−14.218	<0.001
Year 2018	−2.299	0.164	−14.032	<0.001
Year 2019	−2.548	0.179	−14.207	<0.001
Sin	0.023	0.027	0.877	0.381
Cos	0.047	0.039	1.210	0.226
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.927	282.553	<0.001
s(Elev)		2.933	213.018	<0.001
S(Slope)		1.820	170.972	<0.001
s(C110)		1.243	74.311	<0.001
s(C112)		1.040	40.167	<0.001
s(C211)		2.552	86.119	<0.001
s(C213)		1.002	23.633	<0.001
s(C221)		0.000	0.000	0.793
s(C222)		0.001	0.001	0.350
s(C223)		0.865	4.877	0.018
s(C224)		0.976	26.036	<0.001
s(C231)		1.364	69.292	<0.001
s(C311)		1.778	112.822	<0.001
s(C312)		1.117	58.412	<0.001
s(C313)		2.823	29.856	<0.001
s(C320)		0.999	32.718	<0.001
s(C321)		2.263	125.446	<0.001
s(C330)		2.466	61.418	<0.001
s(C410)		0.893	7.761	0.003
s(C511)		0.024	0.021	0.341

Eurasian Skylark (*Alauda arvensis*) — Model C-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.850	0.106	−17.451	<0.001
Year 1995	−0.658	0.085	−7.765	<0.001
Year 1996	−0.876	0.084	−10.484	<0.001
Year 1999	−0.778	0.093	−8.347	<0.001
Year 2000	−0.799	0.082	−9.781	<0.001
Year 2001	−0.974	0.084	−11.631	<0.001
Year 2002	−1.026	0.101	−10.168	<0.001
Year 2003	−1.216	0.103	−11.758	<0.001
Year 2004	−1.439	0.127	−11.328	<0.001
Year 2005	−1.206	0.082	−14.664	<0.001
Year 2006	−1.416	0.093	−15.284	<0.001
Year 2007	−1.756	0.113	−15.578	<0.001
Year 2008	−1.765	0.120	−14.684	<0.001
Year 2009	−1.683	0.108	−15.607	<0.001
Year 2010	−1.855	0.122	−15.241	<0.001
Year 2011	−2.286	0.133	−17.131	<0.001
Year 2012	−2.213	0.128	−17.283	<0.001
Year 2013	−2.514	0.147	−17.121	<0.001
Year 2014	−2.441	0.152	−16.101	<0.001
Year 2015	−2.580	0.154	−16.738	<0.001
Year 2016	−2.151	0.129	−16.690	<0.001
Year 2017	−2.579	0.180	−14.337	<0.001
Year 2018	−2.258	0.160	−14.126	<0.001
Year 2019	−2.488	0.176	−14.176	<0.001
Sin	0.054	0.026	2.080	0.038
Cos	0.042	0.037	1.128	0.259
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.984	270.037	<0.001
s(Elev)		1.695	94.584	<0.001
s(Slope)		2.776	187.987	<0.001
s(C110)		1.048	90.208	<0.001
s(C112)		2.665	50.747	<0.001
s(C211)		2.808	76.534	<0.001
s(C213)		1.831	32.090	<0.001
s(C221)		2.045	9.547	0.005
s(C222)		0.006	0.001	0.676
s(C223)		0.875	5.178	0.015
s(C224)		2.679	43.160	<0.001
s(C231)		0.997	48.348	<0.001
s(C311)		2.162	130.212	<0.001
s(C312)		2.824	56.716	<0.001
s(C313)		2.916	22.774	<0.001
s(C320)		1.684	33.177	<0.001
s(C321)		2.918	161.998	<0.001
s(C330)		2.577	75.094	<0.001
s(C410)		0.879	8.399	0.002
s(C511)		0.290	0.481	0.191

Eurasian Skylark (*Alauda arvensis*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.780	0.113	−15.713	<0.001
Year 1995	−0.684	0.106	−6.451	<0.001
Year 1996	−0.906	0.104	−8.705	<0.001
Year 1999	−0.835	0.112	−7.455	<0.001
Year 2000	−0.865	0.101	−8.537	<0.001
Year 2001	−1.031	0.103	−9.998	<0.001
Year 2002	−1.032	0.121	−8.558	<0.001
Year 2003	−1.265	0.123	−10.297	<0.001
Year 2004	−1.510	0.149	−10.161	<0.001
Year 2005	−1.275	0.102	−12.550	<0.001
Year 2006	−1.472	0.111	−13.283	<0.001
Year 2007	−1.819	0.129	−14.102	<0.001
Year 2008	−1.845	0.137	−13.475	<0.001
Year 2009	−1.754	0.125	−14.010	<0.001
Year 2010	−1.924	0.138	−13.965	<0.001
Year 2011	−2.379	0.148	−16.024	<0.001
Year 2012	−2.302	0.144	−16.029	<0.001
Year 2013	−2.616	0.161	−16.263	<0.001
Year 2014	−2.534	0.165	−15.318	<0.001
Year 2015	−2.660	0.167	−15.883	<0.001
Year 2016	−2.210	0.144	−15.388	<0.001
Year 2017	−2.655	0.193	−13.772	<0.001
Year 2018	−2.323	0.174	−13.377	<0.001
Year 2019	−2.565	0.188	−13.642	<0.001
Sin	0.046	0.029	1.582	0.114
Cos	0.044	0.043	1.015	0.310
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.922	265.394	<0.001
s(Elev)		1.876	94.771	<0.001
s(Slope)		2.463	181.358	<0.001
s(C110)		1.272	84.805	<0.001
s(C112)		1.044	43.159	<0.001
s(C211)		2.623	79.106	<0.001
s(C213)		1.024	27.004	<0.001
s(C221)		0.001	0.000	0.557
s(C222)		0.002	0.002	0.375
s(C223)		0.855	4.456	0.022
s(C224)		0.983	29.482	<0.001
s(C231)		1.299	52.828	<0.001
s(C311)		1.871	131.117	<0.001
s(C312)		1.104	61.545	<0.001
s(C313)		2.737	25.390	<0.001
s(C320)		0.987	25.590	<0.001
s(C321)		2.727	163.155	<0.001
s(C330)		2.585	74.681	<0.001
s(C410)		0.892	7.705	0.003
s(C511)		0.329	0.490	0.219

Eurasian Skylark (*Alauda arvensis*) — Model nC-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.200	0.029	−42.060	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.808	264.200	<0.001
s(Urb$_{2500}$)		1.160	501.100	<0.001
s(For$_{2500}$)		2.969	861.100	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.449	0.060	7.427	<0.001
Year 1995	−0.670	0.084	−7.997	<0.001
Year 1996	−0.686	0.082	−8.413	<0.001
Year 1999	−0.590	0.089	−6.603	<0.001
Year 2000	−0.646	0.079	−8.162	<0.001
Year 2001	−0.794	0.082	−9.672	<0.001
Year 2002	−0.787	0.099	−7.938	<0.001
Year 2003	−0.945	0.101	−9.354	<0.001
Year 2004	−1.110	0.125	−8.902	<0.001
Year 2005	−0.975	0.080	−12.164	<0.001
Year 2006	−1.054	0.091	−11.563	<0.001
Year 2007	−1.447	0.111	−13.065	<0.001
Year 2008	−1.560	0.119	−13.133	<0.001
Year 2009	−1.419	0.106	−13.434	<0.001
Year 2010	−1.557	0.121	−12.911	<0.001
Year 2011	−1.971	0.132	−14.926	<0.001
Year 2012	−1.769	0.127	−13.975	<0.001
Year 2013	−2.222	0.146	−15.261	<0.001
Year 2014	−2.219	0.150	−14.759	<0.001
Year 2015	−2.332	0.153	−15.255	<0.001
Year 2016	−1.817	0.127	−14.282	<0.001
Year 2017	−2.126	0.179	−11.891	<0.001
Year 2018	−1.857	0.159	−11.713	<0.001
Year 2019	−2.083	0.174	−11.942	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.987	343.500	<0.001

Eurasian Skylark (*Alauda arvensis*) — Model nC-ZINB-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.375	0.030	−45.690	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.937	72.320	<0.001
s(Urb$_{2500}$)		2.050	381.020	<0.001
s(For$_{2500}$)		2.964	569.420	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.658	0.062	10.641	<0.001
Year 1995	−0.666	0.086	−7.754	<0.001
Year 1996	−0.663	0.084	−7.924	<0.001
Year 1999	−0.650	0.091	−7.146	<0.001
Year 2000	−0.674	0.081	−8.309	<0.001
Year 2001	−0.810	0.084	−9.635	<0.001
Year 2002	−0.805	0.101	−7.975	<0.001
Year 2003	−0.940	0.103	−9.142	<0.001
Year 2004	−1.097	0.127	−8.655	<0.001
Year 2005	−0.998	0.082	−12.158	<0.001
Year 2006	−1.086	0.093	−11.681	<0.001
Year 2007	−1.450	0.112	−12.897	<0.001
Year 2008	−1.599	0.120	−13.283	<0.001
Year 2009	−1.465	0.107	−13.655	<0.001
Year 2010	−1.612	0.122	−13.223	<0.001
Year 2011	−2.016	0.133	−15.114	<0.001
Year 2012	−1.813	0.128	−14.170	<0.001
Year 2013	−2.268	0.147	−15.450	<0.001
Year 2014	−2.273	0.151	−15.007	<0.001
Year 2015	−2.377	0.154	−15.430	<0.001
Year 2016	−1.866	0.129	−14.511	<0.001
Year 2017	−2.196	0.180	−12.201	<0.001
Year 2018	−1.924	0.160	−12.039	<0.001
Year 2019	−2.156	0.176	−12.275	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.969	157.900	<0.001

Eurasian Skylark (*Alauda arvensis*) — Model nC-P-GAM				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.677	0.061	−11.173	<0.001
Year 1995	−0.573	0.084	−6.832	<0.001
Year 1996	−0.634	0.082	−7.766	<0.001
Year 1999	−1.039	0.089	−11.691	<0.001
Year 2000	−0.927	0.079	−11.711	<0.001
Year 2001	−0.781	0.082	−9.533	<0.001
Year 2002	−0.957	0.099	−9.701	<0.001
Year 2003	−1.092	0.101	−10.825	<0.001
Year 2004	−1.160	0.125	−9.303	<0.001
Year 2005	−0.981	0.080	−12.239	<0.001
Year 2006	−1.282	0.091	−14.070	<0.001
Year 2007	−1.570	0.111	−14.186	<0.001
Year 2008	−1.683	0.119	−14.183	<0.001
Year 2009	−1.479	0.106	−14.013	<0.001
Year 2010	−1.700	0.120	−14.143	<0.001
Year 2011	−2.213	0.132	−16.772	<0.001
Year 2012	−1.952	0.126	−15.441	<0.001
Year 2013	−2.388	0.146	−16.406	<0.001
Year 2014	−2.451	0.150	−16.323	<0.001
Year 2015	−2.467	0.153	−16.155	<0.001
Year 2016	−2.002	0.127	−15.756	<0.001
Year 2017	−2.384	0.179	−13.348	<0.001
Year 2018	−2.107	0.158	−13.306	<0.001
Year 2019	−2.333	0.174	−13.390	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.986	1535.000	<0.001

Eurasian Skylark (*Alauda arvensis*) — Model nC-NB-GAM				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.639	0.097	−6.613	<0.001
Year 1995	−0.587	0.129	−4.558	<0.001
Year 1996	−0.651	0.126	−5.162	<0.001
Year 1999	−1.045	0.127	−8.241	<0.001
Year 2000	−0.985	0.118	−8.352	<0.001
Year 2001	−0.815	0.123	−6.645	<0.001
Year 2002	−0.941	0.139	−6.747	<0.001
Year 2003	−1.091	0.143	−7.653	<0.001
Year 2004	−1.230	0.171	−7.189	<0.001
Year 2005	−0.988	0.121	−8.172	<0.001
Year 2006	−1.309	0.129	−10.108	<0.001
Year 2007	−1.539	0.146	−10.531	<0.001
Year 2008	−1.639	0.152	−10.775	<0.001
Year 2009	−1.463	0.142	−10.292	<0.001
Year 2010	−1.666	0.153	−10.924	<0.001
Year 2011	−2.219	0.163	−13.636	<0.001
Year 2012	−1.955	0.159	−12.257	<0.001
Year 2013	−2.348	0.173	−13.579	<0.001
Year 2014	−2.422	0.176	−13.729	<0.001
Year 2015	−2.441	0.180	−13.546	<0.001
Year 2016	−1.989	0.159	−12.510	<0.001
Year 2017	−2.286	0.200	−11.409	<0.001
Year 2018	−2.008	0.184	−10.912	<0.001
Year 2019	−2.239	0.197	−11.361	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.853	998.700	<0.001

Barn Swallow (*Hirundo rustica*) — Model C-ZIP-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.209	0.018	−11.560	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.955	822.000	<0.001
s(Urb$_{2500}$)		2.946	239.200	<0.001
s(For$_{2500}$)		2.978	173.400	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.240	0.071	3.408	<0.001
Year 1995	−0.521	0.050	−10.498	<0.001
Year 1996	−0.338	0.047	−7.121	<0.001
Year 1999	0.048	0.046	1.051	0.293
Year 2000	−0.248	0.044	−5.632	<0.001
Year 2001	−0.460	0.046	−9.992	<0.001
Year 2002	−0.237	0.053	−4.488	<0.001
Year 2003	−0.568	0.058	−9.868	<0.001
Year 2004	−0.491	0.068	−7.264	<0.001
Year 2005	−0.659	0.047	−14.015	<0.001
Year 2006	−0.535	0.047	−11.367	<0.001
Year 2007	−0.775	0.055	−14.206	<0.001
Year 2008	−0.937	0.059	−15.910	<0.001
Year 2009	−0.959	0.056	−17.042	<0.001
Year 2010	−0.443	0.051	−8.656	<0.001
Year 2011	−0.918	0.054	−17.044	<0.001
Year 2012	−1.224	0.063	−19.406	<0.001
Year 2013	−0.790	0.053	−14.860	<0.001
Year 2014	−1.062	0.057	−18.483	<0.001
Year 2015	−1.060	0.058	−18.423	<0.001
Year 2016	−0.611	0.053	−11.538	<0.001
Year 2017	−1.019	0.067	−15.317	<0.001
Year 2018	−0.798	0.062	−12.915	<0.001
Year 2019	−0.789	0.061	−12.930	<0.001
Sin	0.056	0.012	4.654	<0.001
Cos	−0.124	0.019	−6.648	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.931	60.491	<0.001
s(Elev)		2.978	84.980	<0.001
S(Slope)		2.634	53.548	<0.001
s(C110)		2.629	253.536	<0.001
s(C112)		2.962	172.330	<0.001
s(C211)		1.774	74.358	<0.001
s(C213)		2.753	57.189	<0.001
s(C221)		1.449	78.288	<0.001
s(C222)		0.871	6.704	0.005
s(C223)		0.866	5.700	0.010
s(C224)		2.632	93.847	<0.001
s(C231)		1.844	8.980	0.005
s(C311)		2.887	525.078	<0.001
s(C312)		2.941	46.721	<0.001
s(C313)		2.231	230.225	<0.001
s(C320)		1.704	72.098	<0.001
s(C321)		2.688	21.373	<0.001
s(C330)		0.001	0.000	0.590
s(C410)		2.977	138.591	<0.001
s(C511)		0.916	17.610	<0.001

Barn Swallow (*Hirundo rustica*) — Model C-ZINB-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	2.130	0.043	50.000	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		1.248	1648.500	<0.001
s(Urb$_{2500}$)		2.925	697.400	<0.001
s(For$_{2500}$)		2.991	1062.300	<0.001

Count component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.224	0.097	−2.315	0.021
Year 1995	−0.432	0.101	−4.271	<0.001
Year 1996	−0.245	0.098	−2.492	0.013
Year 1999	−0.074	0.097	−0.764	0.445
Year 2000	−0.158	0.092	−1.710	0.087
Year 2001	−0.366	0.095	−3.844	<0.001
Year 2002	−0.294	0.107	−2.738	0.006
Year 2003	−0.556	0.110	−5.051	<0.001
Year 2004	−0.656	0.127	−5.182	<0.001
Year 2005	−0.697	0.095	−7.325	<0.001
Year 2006	−0.567	0.095	−5.969	<0.001
Year 2007	−0.838	0.104	−8.031	<0.001
Year 2008	−1.053	0.108	−9.788	<0.001
Year 2009	−1.040	0.104	−9.989	<0.001
Year 2010	−0.595	0.101	−5.882	<0.001
Year 2011	−0.998	0.101	−9.889	<0.001
Year 2012	−1.343	0.108	−12.394	<0.001
Year 2013	−0.910	0.103	−8.871	<0.001
Year 2014	−1.155	0.104	−11.140	<0.001
Year 2015	−1.169	0.105	−11.130	<0.001
Year 2016	−0.765	0.103	−7.452	<0.001
Year 2017	−1.153	0.117	−9.844	<0.001
Year 2018	−0.858	0.113	−7.593	<0.001
Year 2019	−0.908	0.114	−8.003	<0.001
Sin	0.052	0.021	2.532	0.011
Cos	−0.172	0.031	−5.485	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.951	63.796	<0.001
s(Elev)		2.887	94.594	<0.001
S(Slope)		1.292	32.069	<0.001
s(C110)		2.466	140.681	<0.001
s(C112)		2.873	109.102	<0.001
s(C211)		1.308	33.685	<0.001
s(C213)		1.020	35.423	<0.001
s(C221)		0.984	37.342	<0.001
s(C222)		0.039	0.037	0.330
s(C223)		0.337	0.463	0.240
s(C224)		1.016	72.137	<0.001
s(C231)		0.301	0.405	0.223
s(C311)		2.538	463.975	<0.001
s(C312)		2.700	62.920	<0.001
s(C313)		1.508	215.796	<0.001
s(C320)		1.012	48.342	<0.001
s(C321)		0.916	9.275	0.001
s(C330)		0.864	6.274	0.007
s(C410)		0.007	0.005	0.411
s(C511)		0.694	2.240	0.068

Barn Swallow (*Hirundo rustica*) — Model C-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.671	0.068	−9.804	<0.001
Year 1995	−0.443	0.050	−8.916	<0.001
Year 1996	−0.385	0.048	−8.102	<0.001
Year 1999	0.022	0.046	0.470	0.638
Year 2000	−0.171	0.044	−3.880	<0.001
Year 2001	−0.405	0.046	−8.810	<0.001
Year 2002	−0.243	0.053	−4.610	<0.001
Year 2003	−0.604	0.057	−10.511	<0.001
Year 2004	−0.652	0.068	−9.655	<0.001
Year 2005	−0.686	0.047	−14.583	<0.001
Year 2006	−0.589	0.047	−12.511	<0.001
Year 2007	−0.827	0.055	−15.161	<0.001
Year 2008	−1.051	0.059	−17.843	<0.001
Year 2009	−1.060	0.056	−18.850	<0.001
Year 2010	−0.635	0.051	−12.424	<0.001
Year 2011	−1.013	0.054	−18.792	<0.001
Year 2012	−1.364	0.063	−21.622	<0.001
Year 2013	−0.884	0.053	−16.626	<0.001
Year 2014	−1.180	0.057	−20.563	<0.001
Year 2015	−1.202	0.058	−20.865	<0.001
Year 2016	−0.785	0.053	−14.833	<0.001
Year 2017	−1.124	0.067	−16.904	<0.001
Year 2018	−0.934	0.062	−15.127	<0.001
Year 2019	−0.892	0.061	−14.610	<0.001
Sin	0.054	0.012	4.474	<0.001
Cos	−0.151	0.019	−8.141	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.984	241.384	<0.001
s(Elev)		2.892	361.878	<0.001
s(Slope)		2.274	116.787	<0.001
s(C110)		2.665	280.262	<0.001
s(C112)		2.980	333.665	<0.001
s(C211)		2.649	45.041	<0.001
s(C213)		1.798	36.099	<0.001
s(C221)		1.816	59.877	<0.001
s(C222)		0.503	0.922	0.175
s(C223)		0.830	4.555	0.019
s(C224)		2.523	138.848	<0.001
s(C231)		1.579	2.165	0.235
s(C311)		2.741	712.073	<0.001
s(C312)		2.921	97.396	<0.001
s(C313)		2.150	276.489	<0.001
s(C320)		1.875	89.257	<0.001
s(C321)		2.806	16.042	<0.001
s(C330)		1.448	17.052	<0.001
s(C410)		2.972	88.555	<0.001
s(C511)		2.776	16.005	<0.001

Barn Swallow (*Hirundo rustica*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.678	0.098	−6.932	<0.001
Year 1995	−0.386	0.103	−3.730	<0.001
Year 1996	−0.196	0.100	−1.948	0.051
Year 1999	−0.100	0.098	−1.023	0.306
Year 2000	−0.130	0.094	−1.379	0.168
Year 2001	−0.329	0.097	−3.387	<0.001
Year 2002	−0.270	0.109	−2.466	0.014
Year 2003	−0.528	0.112	−4.701	<0.001
Year 2004	−0.720	0.128	−5.620	<0.001
Year 2005	−0.690	0.097	−7.103	<0.001
Year 2006	−0.571	0.097	−5.902	<0.001
Year 2007	−0.833	0.106	−7.829	<0.001
Year 2008	−1.053	0.110	−9.599	<0.001
Year 2009	−1.045	0.106	−9.834	<0.001
Year 2010	−0.595	0.103	−5.768	<0.001
Year 2011	−0.986	0.103	−9.589	<0.001
Year 2012	−1.339	0.110	−12.125	<0.001
Year 2013	−0.910	0.105	−8.701	<0.001
Year 2014	−1.168	0.105	−11.079	<0.001
Year 2015	−1.190	0.107	−11.130	<0.001
Year 2016	−0.764	0.104	−7.316	<0.001
Year 2017	−1.156	0.119	−9.682	<0.001
Year 2018	−0.850	0.115	−7.399	<0.001
Year 2019	−0.926	0.116	−8.010	<0.001
Sin	0.053	0.021	2.527	0.012
Cos	−0.184	0.032	−5.763	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.958	78.766	<0.001
s(Elev)		2.810	309.632	<0.001
s(Slope)		1.421	39.579	<0.001
s(C110)		2.532	130.684	<0.001
s(C112)		2.855	101.381	<0.001
s(C211)		1.246	18.978	<0.001
s(C213)		0.992	22.065	<0.001
s(C221)		0.973	27.382	<0.001
s(C222)		0.051	0.046	0.336
s(C223)		0.297	0.380	0.256
s(C224)		1.009	59.826	<0.001
s(C231)		0.680	1.942	0.074
s(C311)		2.521	442.859	<0.001
s(C312)		2.742	77.266	<0.001
s(C313)		1.443	232.409	<0.001
s(C320)		1.017	52.085	<0.001
s(C321)		0.895	7.512	0.003
s(C330)		0.899	8.626	0.002
s(C410)		0.002	0.000	0.623
s(C511)		0.726	2.609	0.054

Barn Swallow (*Hirundo rustica*) — Model nC-ZIP-GAM

		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.964	0.046	−20.840	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.800	457.500	<0.001
s(Urb_{2500})		2.946	230.900	<0.001
s(For_{2500})		2.956	190.400	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	1.335	0.037	36.211	<0.001
Year 1995	−0.474	0.049	−9.618	<0.001
Year 1996	−0.264	0.047	−5.621	<0.001
Year 1999	0.092	0.045	2.064	0.039
Year 2000	−0.307	0.044	−7.057	<0.001
Year 2001	−0.413	0.046	−9.051	<0.001
Year 2002	−0.280	0.052	−5.357	<0.001
Year 2003	−0.597	0.057	−10.520	<0.001
Year 2004	−0.450	0.067	−6.735	<0.001
Year 2005	−0.553	0.047	−11.885	<0.001
Year 2006	−0.513	0.047	−11.031	<0.001
Year 2007	−0.721	0.054	−13.340	<0.001
Year 2008	−0.867	0.058	−14.823	<0.001
Year 2009	−0.852	0.056	−15.288	<0.001
Year 2010	−0.363	0.051	−7.143	<0.001
Year 2011	−0.854	0.053	−15.979	<0.001
Year 2012	−1.171	0.063	−18.722	<0.001
Year 2013	−0.640	0.053	−12.131	<0.001
Year 2014	−1.036	0.057	−18.200	<0.001
Year 2015	−0.947	0.057	−16.565	<0.001
Year 2016	−0.542	0.052	−10.333	<0.001
Year 2017	−0.914	0.066	−13.791	<0.001
Year 2018	−0.682	0.062	−11.078	<0.001
Year 2019	−0.668	0.061	−10.989	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.981	100.900	<0.001

Barn Swallow (*Hirundo rustica*) — Model nC-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	1.129	0.063	18.040	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.967	1045.700	<0.001
s(Urb$_{2500}$)		2.890	585.500	<0.001
s(For$_{2500}$)		2.998	640.900	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	1.068	0.082	13.098	<0.001
Year 1995	−0.428	0.103	−4.174	<0.001
Year 1996	−0.305	0.101	−3.036	0.002
Year 1999	−0.091	0.098	−0.924	0.356
Year 2000	−0.302	0.094	−3.221	0.001
Year 2001	−0.369	0.097	−3.811	<0.001
Year 2002	−0.347	0.109	−3.187	0.001
Year 2003	−0.675	0.112	−6.039	<0.001
Year 2004	−0.602	0.129	−4.652	<0.001
Year 2005	−0.624	0.097	−6.461	<0.001
Year 2006	−0.565	0.097	−5.836	<0.001
Year 2007	−0.772	0.106	−7.309	<0.001
Year 2008	−0.981	0.109	−9.026	<0.001
Year 2009	−0.965	0.105	−9.172	<0.001
Year 2010	−0.532	0.103	−5.155	<0.001
Year 2011	−0.933	0.103	−9.090	<0.001
Year 2012	−1.279	0.110	−11.668	<0.001
Year 2013	−0.731	0.104	−7.034	<0.001
Year 2014	−1.124	0.105	−10.728	<0.001
Year 2015	−1.029	0.106	−9.669	<0.001
Year 2016	−0.667	0.104	−6.386	<0.001
Year 2017	−1.022	0.118	−8.636	<0.001
Year 2018	−0.792	0.116	−6.848	<0.001
Year 2019	−0.771	0.116	−6.671	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.895	61.830	<0.001

Barn Swallow (*Hirundo rustica*) — Model nC-P-GAM

Parametric terms	Estimate	Standard error	z-value	p-value
Intercept	0.340	0.037	9.210	<0.001
Year 1995	−0.316	0.049	−6.417	<0.001
Year 1996	−0.252	0.047	−5.366	<0.001
Year 1999	−0.104	0.045	−2.325	<0.001
Year 2000	−0.320	0.044	−7.331	<0.001
Year 2001	−0.355	0.046	−7.789	<0.001
Year 2002	−0.469	0.052	−8.981	<0.001
Year 2003	−0.710	0.057	−12.526	<0.001
Year 2004	−0.702	0.067	−10.503	<0.001
Year 2005	−0.566	0.047	−12.168	<0.001
Year 2006	−0.474	0.047	−10.179	<0.001
Year 2007	−0.810	0.054	−14.991	<0.001
Year 2008	−0.992	0.058	−16.968	<0.001
Year 2009	−0.922	0.056	−16.542	<0.001
Year 2010	−0.532	0.051	−10.480	<0.001
Year 2011	−0.952	0.053	−17.811	<0.001
Year 2012	−1.297	0.063	−20.731	<0.001
Year 2013	−0.766	0.053	−14.547	<0.001
Year 2014	−1.116	0.057	−19.596	<0.001
Year 2015	−1.045	0.057	−18.277	<0.001
Year 2016	−0.738	0.052	−14.075	<0.001
Year 2017	−1.077	0.066	−16.263	<0.001
Year 2018	−0.858	0.062	−13.946	<0.001
Year 2019	−0.828	0.061	−13.637	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.995	4825.000	<0.001

Barn Swallow (*Hirundo rustica*) — Model nC-NB-GAM

Parametric terms	Estimate	Standard error	z-value	p-value
Intercept	0.292	0.090	3.247	0.001
Year 1995	−0.285	0.115	−2.492	0.013
Year 1996	−0.101	0.112	−0.901	0.367
Year 1999	−0.013	0.105	−0.125	0.900
Year 2000	−0.367	0.102	−3.586	<0.001
Year 2001	−0.364	0.107	−3.395	<0.001
Year 2002	−0.555	0.118	−4.697	<0.001
Year 2003	−0.737	0.121	−6.065	<0.001
Year 2004	−0.730	0.136	−5.368	<0.001
Year 2005	−0.599	0.107	−5.610	<0.001
Year 2006	−0.512	0.107	−4.809	<0.001
Year 2007	−0.888	0.116	−7.635	<0.001
Year 2008	−1.060	0.119	−8.907	<0.001
Year 2009	−0.967	0.116	−8.329	<0.001
Year 2010	−0.556	0.114	−4.896	<0.001
Year 2011	−0.990	0.112	−8.808	<0.001
Year 2012	−1.288	0.120	−10.775	<0.001
Year 2013	−0.764	0.114	−6.714	<0.001
Year 2014	−1.152	0.115	−10.033	<0.001
Year 2015	−1.116	0.117	−9.519	<0.001
Year 2016	−0.740	0.114	−6.508	<0.001
Year 2017	−1.130	0.128	−8.798	<0.001
Year 2018	−0.727	0.124	−5.868	<0.001
Year 2019	−0.896	0.125	−7.150	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.994	2565.000	<0.001

Eurasian Blue Tit (*Cyanistes caeruleus*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.432	0.022	−19.920	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.796	1698.100	<0.001
s(Urb$_{2500}$)		2.943	306.300	<0.001
s(For$_{2500}$)		2.962	1448.100	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.293	0.166	−13.834	<0.001
Year 1995	−0.026	0.214	−0.122	0.903
Year 1996	0.584	0.188	3.105	0.002
Year 1999	0.352	0.174	2.017	0.044
Year 2000	0.534	0.170	3.142	0.002
Year 2001	0.869	0.176	4.937	<0.001
Year 2002	0.608	0.184	3.306	<0.001
Year 2003	0.937	0.182	5.144	<0.001
Year 2004	0.329	0.220	1.495	0.135
Year 2005	0.478	0.183	2.614	0.009
Year 2006	0.599	0.175	3.423	<0.001
Year 2007	0.620	0.184	3.374	<0.001
Year 2008	0.830	0.181	4.580	<0.001
Year 2009	0.696	0.184	3.791	<0.001
Year 2010	0.819	0.182	4.500	<0.001
Year 2011	0.992	0.172	5.753	<0.001
Year 2012	0.717	0.181	3.962	<0.001
Year 2013	0.621	0.182	3.406	<0.001
Year 2014	0.716	0.180	3.973	<0.001
Year 2015	0.450	0.189	2.385	0.017
Year 2016	0.572	0.186	3.071	0.002
Year 2017	0.654	0.188	3.468	<0.001
Year 2018	0.418	0.196	2.136	0.033
Year 2019	0.423	0.196	2.154	0.031
Sin	−0.052	0.026	−1.996	0.046
Cos	0.093	0.039	2.387	0.017
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.984	155.942	<0.001
s(Elev)		2.372	48.588	<0.001
S(Slope)		1.856	4.496	0.071
s(C110)		0.979	17.841	<0.001
s(C112)		2.833	10.779	0.009
s(C211)		2.241	30.049	<0.001
s(C213)		0.980	19.241	<0.001
s(C221)		2.410	16.012	<0.001
s(C222)		0.793	6.065	0.005
s(C223)		0.553	1.106	0.156
s(C224)		1.864	13.713	<0.001
s(C231)		1.765	4.958	0.041
s(C311)		2.608	69.971	<0.001
s(C312)		1.867	8.433	0.007
s(C313)		2.221	30.566	<0.001
s(C320)		2.501	2.874	0.314
s(C321)		1.414	9.298	0.003
s(C330)		0.723	2.752	0.048
s(C410)		0.770	4.851	0.011
s(C511)		0.000	0.000	0.902

Eurasian Blue Tit (*Cyanistes caeruleus*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.442	0.020	−21.970	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.110	1715.300	<0.001
s(Urb$_{2500}$)		2.948	346.900	<0.001
s(For$_{2500}$)		2.963	1999.800	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.290	0.166	−13.787	<0.001
Year 1995	−0.042	0.214	−0.198	0.843
Year 1996	0.619	0.188	3.292	<0.001
Year 1999	0.332	0.174	1.906	0.057
Year 2000	0.514	0.169	3.031	0.002
Year 2001	0.870	0.176	4.955	<0.001
Year 2002	0.586	0.184	3.191	0.001
Year 2003	0.909	0.182	4.996	<0.001
Year 2004	0.329	0.220	1.497	0.134
Year 2005	0.482	0.183	2.636	0.008
Year 2006	0.580	0.175	3.312	<0.001
Year 2007	0.657	0.184	3.578	<0.001
Year 2008	0.844	0.181	4.657	<0.001
Year 2009	0.722	0.184	3.933	<0.001
Year 2010	0.828	0.182	4.549	<0.001
Year 2011	0.962	0.173	5.573	<0.001
Year 2012	0.745	0.181	4.118	<0.001
Year 2013	0.691	0.182	3.793	<0.001
Year 2014	0.760	0.180	4.219	<0.001
Year 2015	0.504	0.189	2.672	0.008
Year 2016	0.599	0.186	3.217	0.001
Year 2017	0.716	0.188	3.805	<0.001
Year 2018	0.466	0.196	2.385	0.017
Year 2019	0.476	0.196	2.430	0.015
Sin	−0.058	0.026	−2.221	0.026
Cos	0.120	0.039	3.117	0.002
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.958	106.523	<0.001
s(Elev)		2.655	58.073	<0.001
S(Slope)		0.001	0.000	0.851
s(C110)		1.104	36.323	<0.001
s(C112)		0.755	2.959	0.040
s(C211)		2.263	43.143	<0.001
s(C213)		0.979	21.776	<0.001
s(C221)		0.001	0.000	0.597
s(C222)		0.879	7.566	0.003
s(C223)		0.666	1.721	0.107
s(C224)		0.930	12.675	<0.001
s(C231)		0.703	2.142	0.063
s(C311)		2.637	115.895	<0.001
s(C312)		0.911	7.383	0.003
s(C313)		2.088	42.196	<0.001
s(C320)		0.000	0.000	0.959
s(C321)		0.922	9.410	0.001
s(C330)		0.789	3.547	0.032
s(C410)		0.793	4.110	0.021
s(C511)		0.000	0.000	0.734

Eurasian Blue Tit (*Cyanistes caeruleus*) — Model C-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.274	0.165	−19.816	<0.001
Year 1995	−0.090	0.214	−0.422	0.673
Year 1996	0.518	0.188	2.756	0.006
Year 1999	0.363	0.174	2.082	0.037
Year 2000	0.512	0.170	3.016	0.003
Year 2001	0.806	0.176	4.586	<0.001
Year 2002	0.582	0.184	3.168	0.002
Year 2003	0.951	0.182	5.225	<0.001
Year 2004	0.276	0.220	1.255	0.210
Year 2005	0.383	0.183	2.096	0.036
Year 2006	0.591	0.175	3.376	<0.001
Year 2007	0.623	0.184	3.391	<0.001
Year 2008	0.872	0.181	4.815	<0.001
Year 2009	0.683	0.184	3.722	<0.001
Year 2010	0.775	0.182	4.261	<0.001
Year 2011	1.017	0.172	5.902	<0.001
Year 2012	0.705	0.181	3.895	<0.001
Year 2013	0.659	0.182	3.618	<0.001
Year 2014	0.725	0.180	4.022	<0.001
Year 2015	0.426	0.189	2.260	0.024
Year 2016	0.522	0.186	2.805	0.005
Year 2017	0.673	0.188	3.569	<0.001
Year 2018	0.407	0.196	2.076	0.038
Year 2019	0.407	0.196	2.071	0.038
Sin	−0.055	0.026	−2.109	0.035
Cos	0.088	0.039	2.267	0.023
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.986	203.600	<0.001
s(Elev)		2.765	281.365	<0.001
s(Slope)		2.301	14.725	<0.001
s(C110)		1.014	61.210	<0.001
s(C112)		2.776	16.960	<0.001
s(C211)		2.262	116.350	<0.001
s(C213)		1.000	51.952	<0.001
s(C221)		2.594	14.614	<0.001
s(C222)		0.821	5.458	0.010
s(C223)		0.014	0.014	0.308
s(C224)		2.372	9.341	0.010
s(C231)		0.004	0.006	0.166
s(C311)		2.782	168.059	<0.001
s(C312)		1.654	12.084	<0.001
s(C313)		2.403	62.877	<0.001
s(C320)		2.693	4.488	0.171
s(C321)		1.675	19.245	<0.001
s(C330)		0.794	4.427	0.018
s(C410)		0.762	3.189	0.040
s(C511)		0.000	0.000	1.000

Eurasian Blue Tit (*Cyanistes caeruleus*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.280	0.171	−19.144	<0.001
Year 1995	−0.118	0.222	−0.530	0.596
Year 1996	0.544	0.197	2.766	0.006
Year 1999	0.354	0.181	1.953	0.051
Year 2000	0.498	0.176	2.828	0.005
Year 2001	0.782	0.184	4.260	<0.001
Year 2002	0.540	0.193	2.801	0.005
Year 2003	0.949	0.191	4.970	<0.001
Year 2004	0.306	0.229	1.335	0.182
Year 2005	0.381	0.190	2.003	0.045
Year 2006	0.563	0.182	3.088	0.002
Year 2007	0.679	0.192	3.538	<0.001
Year 2008	0.876	0.190	4.610	<0.001
Year 2009	0.717	0.192	3.730	<0.001
Year 2010	0.790	0.190	4.155	<0.001
Year 2011	1.004	0.180	5.573	<0.001
Year 2012	0.738	0.189	3.901	<0.001
Year 2013	0.724	0.190	3.799	<0.001
Year 2014	0.776	0.188	4.121	<0.001
Year 2015	0.479	0.197	2.432	0.015
Year 2016	0.534	0.194	2.751	0.006
Year 2017	0.731	0.197	3.711	<0.001
Year 2018	0.437	0.205	2.137	0.033
Year 2019	0.449	0.205	2.193	0.028
Sin	−0.063	0.028	−2.241	0.025
Cos	0.114	0.042	2.745	0.006
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.966	109.952	<0.001
s(Elev)		2.905	222.919	<0.001
s(Slope)		2.411	15.023	<0.001
s(C110)		1.185	71.286	<0.001
s(C112)		0.930	10.414	<0.001
s(C211)		2.284	111.426	<0.001
s(C213)		1.020	43.689	<0.001
s(C221)		0.769	3.183	0.041
s(C222)		0.840	5.496	0.010
s(C223)		0.319	0.426	0.247
s(C224)		0.833	5.063	0.013
s(C231)		0.001	0.000	0.496
s(C311)		2.807	173.444	<0.001
s(C312)		0.902	7.310	0.004
s(C313)		2.352	64.723	<0.001
s(C320)		0.005	0.002	0.560
s(C321)		0.961	14.896	<0.001
s(C330)		0.733	2.559	0.061
s(C410)		0.731	2.906	0.046
s(C511)		0.002	0.003	0.200

Eurasian Blue Tit (*Cyanistes caeruleus*) — Model nC-ZIP-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.418	0.038	−37.220	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.972	1564.800	<0.001
s(Urb_{2500})		2.874	167.800	<0.001
s(For_{2500})		2.955	1000.300	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.264	0.158	−7.988	<0.001
Year 1995	0.041	0.213	0.192	0.848
Year 1996	0.555	0.187	2.961	0.003
Year 1999	0.447	0.173	2.585	0.010
Year 2000	0.580	0.169	3.443	<0.001
Year 2001	0.923	0.175	5.282	<0.001
Year 2002	0.703	0.183	3.847	<0.001
Year 2003	0.884	0.181	4.881	<0.001
Year 2004	0.247	0.219	1.128	0.259
Year 2005	0.450	0.182	2.474	0.013
Year 2006	0.605	0.174	3.474	<0.001
Year 2007	0.551	0.183	3.006	0.003
Year 2008	0.790	0.181	4.373	<0.001
Year 2009	0.665	0.183	3.637	<0.001
Year 2010	0.772	0.181	4.259	<0.001
Year 2011	0.929	0.172	5.400	<0.001
Year 2012	0.646	0.180	3.582	<0.001
Year 2013	0.544	0.182	2.993	0.003
Year 2014	0.632	0.180	3.519	<0.001
Year 2015	0.392	0.188	2.084	0.037
Year 2016	0.521	0.185	2.808	0.005
Year 2017	0.644	0.187	3.434	<0.001
Year 2018	0.467	0.195	2.395	0.017
Year 2019	0.431	0.195	2.205	0.027
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.986	176.400	<0.001

Eurasian Blue Tit (*Cyanistes caeruleus*) — Model nC-ZINB-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.460	0.037	−39.550	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.965	1521.800	<0.001
s(Urb$_{2500}$)		2.896	213.100	<0.001
s(For$_{2500}$)		2.954	1039.600	<0.001

Count component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.268	0.158	−8.008	<0.001
Year 1995	0.031	0.213	0.144	0.886
Year 1996	0.584	0.187	3.118	0.002
Year 1999	0.443	0.173	2.561	0.010
Year 2000	0.574	0.169	3.402	<0.001
Year 2001	0.948	0.175	5.422	<0.001
Year 2002	0.680	0.183	3.718	<0.001
Year 2003	0.886	0.181	4.883	<0.001
Year 2004	0.268	0.219	1.224	0.221
Year 2005	0.458	0.182	2.517	0.012
Year 2006	0.595	0.174	3.411	<0.001
Year 2007	0.605	0.183	3.301	<0.001
Year 2008	0.816	0.181	4.510	<0.001
Year 2009	0.691	0.183	3.772	<0.001
Year 2010	0.775	0.182	4.268	<0.001
Year 2011	0.897	0.172	5.212	<0.001
Year 2012	0.654	0.181	3.625	<0.001
Year 2013	0.603	0.182	3.317	<0.001
Year 2014	0.663	0.180	3.690	<0.001
Year 2015	0.427	0.188	2.266	0.023
Year 2016	0.529	0.186	2.849	0.004
Year 2017	0.683	0.188	3.641	<0.001
Year 2018	0.483	0.195	2.477	0.013
Year 2019	0.453	0.196	2.318	0.020
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.956	103.000	<0.001

Eurasian Blue Tit (*Cyanistes caeruleus*) — Model nC-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.252	0.158	−14.234	<0.001
Year 1995	−0.352	0.213	−1.650	0.099
Year 1996	0.307	0.187	1.643	0.100
Year 1999	0.490	0.173	2.835	0.005
Year 2000	0.628	0.168	3.727	<0.001
Year 2001	0.516	0.174	2.957	0.003
Year 2002	0.556	0.183	3.043	0.002
Year 2003	0.688	0.181	3.795	<0.001
Year 2004	−0.035	0.219	−0.160	0.873
Year 2005	0.070	0.182	0.387	0.698
Year 2006	0.470	0.174	2.701	0.007
Year 2007	0.388	0.183	2.116	0.034
Year 2008	0.546	0.181	3.020	0.003
Year 2009	0.359	0.183	1.961	0.050
Year 2010	0.402	0.181	2.214	0.027
Year 2011	0.824	0.172	4.792	<0.001
Year 2012	0.473	0.180	2.622	0.009
Year 2013	0.376	0.182	2.071	0.038
Year 2014	0.335	0.180	1.865	0.062
Year 2015	0.137	0.188	0.729	0.466
Year 2016	0.224	0.185	1.209	0.227
Year 2017	0.514	0.187	2.742	0.006
Year 2018	0.270	0.195	1.385	0.166
Year 2019	0.249	0.195	1.275	0.202
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.906	229.700	<0.001

Eurasian Blue Tit (*Cyanistes caeruleus*) — Model nC-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.287	0.180	−12.739	<0.001
Year 1995	−0.326	0.238	−1.371	0.170
Year 1996	0.328	0.214	1.534	0.125
Year 1999	0.511	0.198	2.578	0.010
Year 2000	0.660	0.193	3.422	<0.001
Year 2001	0.567	0.200	2.838	0.005
Year 2002	0.567	0.212	2.683	0.007
Year 2003	0.710	0.210	3.377	<0.001
Year 2004	−0.003	0.247	−0.011	0.991
Year 2005	0.088	0.207	0.428	0.669
Year 2006	0.488	0.200	2.444	0.015
Year 2007	0.445	0.209	2.122	0.034
Year 2008	0.602	0.208	2.902	0.004
Year 2009	0.392	0.210	1.868	0.062
Year 2010	0.439	0.208	2.112	0.035
Year 2011	0.857	0.198	4.318	<0.001
Year 2012	0.513	0.207	2.480	0.013
Year 2013	0.431	0.208	2.075	0.038
Year 2014	0.375	0.205	1.829	0.067
Year 2015	0.169	0.214	0.791	0.429
Year 2016	0.263	0.211	1.244	0.214
Year 2017	0.595	0.215	2.764	0.006
Year 2018	0.311	0.223	1.394	0.163
Year 2019	0.284	0.223	1.270	0.204
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.983	165.900	<0.001

Italian Sparrow (*Passer italiae*) — Model C-ZIP-GAM

Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	6.307	0.180	35.120	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.150	1884.500	<0.001
s(Urb$_{2500}$)		0.999	729.900	<0.001
s(For$_{2500}$)		0.000	0.000	0.552
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.322	0.052	−6.163	<0.001
Year 1995	−0.351	0.058	−6.045	<0.001
Year 1996	−0.534	0.056	−9.451	<0.001
Year 1999	−0.073	0.055	−1.333	0.183
Year 2000	−0.268	0.052	−5.182	<0.001
Year 2001	−0.560	0.056	−10.082	<0.001
Year 2002	−0.393	0.064	−6.179	<0.001
Year 2003	−0.593	0.068	−8.675	<0.001
Year 2004	−0.621	0.077	−8.047	<0.001
Year 2005	−0.643	0.055	−11.637	<0.001
Year 2006	−0.791	0.057	−13.808	<0.001
Year 2007	−0.916	0.064	−14.283	<0.001
Year 2008	−0.916	0.064	−14.220	<0.001
Year 2009	−1.003	0.063	−15.837	<0.001
Year 2010	−0.998	0.064	−15.556	<0.001
Year 2011	−1.119	0.063	−17.764	<0.001
Year 2012	−1.157	0.068	−17.088	<0.001
Year 2013	−1.245	0.067	−18.446	<0.001
Year 2014	−1.388	0.067	−20.794	<0.001
Year 2015	−1.177	0.065	−18.127	<0.001
Year 2016	−1.355	0.071	−19.011	<0.001
Year 2017	−1.145	0.078	−14.722	<0.001
Year 2018	−0.977	0.073	−13.454	<0.001
Year 2019	−1.017	0.073	−13.869	<0.001
Sin	0.000	0.014	−0.034	0.973
Cos	0.000	0.022	0.010	0.992
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.964	194.297	<0.001
s(Elev)		1.377	127.582	<0.001
S(Slope)		1.065	25.331	<0.001
s(C110)		2.300	179.201	<0.001
s(C112)		2.965	655.634	<0.001
s(C211)		1.323	33.441	<0.001
s(C213)		2.153	54.436	<0.001
s(C221)		2.490	17.050	<0.001
s(C222)		0.758	3.026	0.044
s(C223)		0.931	9.306	0.001
s(C224)		1.584	3.588	0.093
s(C231)		1.845	71.784	<0.001
s(C311)		2.905	171.857	<0.001
s(C312)		1.000	66.285	<0.001
s(C313)		2.198	94.083	<0.001
s(C320)		0.959	29.269	<0.001
s(C321)		1.836	3.547	0.129
s(C330)		1.635	8.853	0.005
s(C410)		0.897	13.400	<0.001
s(C511)		2.695	6.356	0.068

Italian Sparrow (*Passer italiae*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	6.218	0.186	33.480	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		1.452	1766.300	<0.001
s(Urb$_{2500}$)		1.003	787.700	<0.001
s(For$_{2500}$)		0.000	0.000	0.778
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.363	0.055	−6.574	<0.001
Year 1995	−0.370	0.061	−6.101	<0.001
Year 1996	−0.540	0.059	−9.154	<0.001
Year 1999	−0.109	0.057	−1.908	0.056
Year 2000	−0.282	0.054	−5.205	<0.001
Year 2001	−0.563	0.058	−9.713	<0.001
Year 2002	−0.409	0.066	−6.163	<0.001
Year 2003	−0.620	0.071	−8.769	<0.001
Year 2004	−0.659	0.080	−8.250	<0.001
Year 2005	−0.667	0.058	−11.570	<0.001
Year 2006	−0.821	0.060	−13.771	<0.001
Year 2007	−0.931	0.067	−13.989	<0.001
Year 2008	−0.935	0.067	−13.984	<0.001
Year 2009	−1.028	0.066	−15.637	<0.001
Year 2010	−1.018	0.066	−15.309	<0.001
Year 2011	−1.134	0.065	−17.378	<0.001
Year 2012	−1.178	0.070	−16.832	<0.001
Year 2013	−1.275	0.070	−18.292	<0.001
Year 2014	−1.411	0.069	−20.481	<0.001
Year 2015	−1.202	0.067	−17.874	<0.001
Year 2016	−1.374	0.073	−18.698	<0.001
Year 2017	−1.170	0.080	−14.603	<0.001
Year 2018	−0.998	0.075	−13.287	<0.001
Year 2019	−1.038	0.076	−13.694	<0.001
Sin	0.002	0.015	0.156	0.876
Cos	−0.011	0.022	−0.495	0.621
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.010	137.810	<0.001
s(Elev)		2.129	180.581	<0.001
S(Slope)		1.141	23.523	<0.001
s(C110)		2.429	232.464	<0.001
s(C112)		2.949	743.942	<0.001
s(C211)		1.750	48.787	<0.001
s(C213)		1.148	50.023	<0.001
s(C221)		0.926	11.781	<0.001
s(C222)		0.660	2.003	0.079
s(C223)		0.911	10.431	<0.001
s(C224)		0.499	0.992	0.149
s(C231)		1.929	92.324	<0.001
s(C311)		2.828	195.868	<0.001
s(C312)		1.111	68.668	<0.001
s(C313)		2.011	104.251	<0.001
s(C320)		0.987	30.758	<0.001
s(C321)		0.003	0.003	0.368
s(C330)		0.905	8.845	0.002
s(C410)		0.939	14.596	<0.001
s(C511)		0.429	0.752	0.180

Italian Sparrow (*Passer italiae*) — Model C-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.634	0.054	−11.726	<0.001
Year 1995	−0.344	0.058	−5.937	<0.001
Year 1996	−0.526	0.056	−9.337	<0.001
Year 1999	−0.080	0.055	−1.460	0.144
Year 2000	−0.263	0.052	−5.095	<0.001
Year 2001	−0.548	0.056	−9.878	<0.001
Year 2002	−0.381	0.064	−5.990	<0.001
Year 2003	−0.575	0.068	−8.428	<0.001
Year 2004	−0.619	0.077	−8.026	<0.001
Year 2005	−0.632	0.055	−11.444	<0.001
Year 2006	−0.784	0.057	−13.684	<0.001
Year 2007	−0.909	0.064	−14.169	<0.001
Year 2008	−0.909	0.064	−14.106	<0.001
Year 2009	−0.996	0.063	−15.738	<0.001
Year 2010	−0.987	0.064	−15.405	<0.001
Year 2011	−1.111	0.063	−17.646	<0.001
Year 2012	−1.146	0.068	−16.927	<0.001
Year 2013	−1.238	0.067	−18.366	<0.001
Year 2014	−1.377	0.067	−20.633	<0.001
Year 2015	−1.170	0.065	−18.028	<0.001
Year 2016	−1.342	0.071	−18.833	<0.001
Year 2017	−1.134	0.078	−14.582	<0.001
Year 2018	−0.969	0.073	−13.355	<0.001
Year 2019	−1.007	0.073	−13.734	<0.001
Sin	0.000	0.014	0.028	0.977
Cos	0.004	0.022	0.190	0.849
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.965	193.815	<0.001
s(Elev)		2.561	370.089	<0.001
s(Slope)		1.077	28.214	<0.001
s(C110)		2.294	228.001	<0.001
s(C112)		2.965	782.139	<0.001
s(C211)		1.272	48.313	<0.001
s(C213)		2.173	69.473	<0.001
s(C221)		2.438	18.820	<0.001
s(C222)		0.783	3.762	0.027
s(C223)		0.935	10.024	<0.001
s(C224)		1.572	4.743	0.045
s(C231)		1.848	94.233	<0.001
s(C311)		2.920	177.120	<0.001
s(C312)		1.014	72.480	<0.001
s(C313)		2.206	96.962	<0.001
s(C320)		0.954	31.515	<0.001
s(C321)		0.001	0.000	0.882
s(C330)		0.872	10.759	<0.001
s(C410)		0.903	12.975	<0.001
s(C511)		0.019	0.020	0.311

Italian Sparrow (*Passer italiae*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.634	0.057	−11.215	<0.001
Year 1995	−0.355	0.061	−5.839	<0.001
Year 1996	−0.527	0.059	−8.895	<0.001
Year 1999	−0.109	0.058	−1.890	0.059
Year 2000	−0.273	0.055	−5.014	<0.001
Year 2001	−0.548	0.058	−9.408	<0.001
Year 2002	−0.391	0.067	−5.865	<0.001
Year 2003	−0.595	0.071	−8.382	<0.001
Year 2004	−0.651	0.080	−8.123	<0.001
Year 2005	−0.651	0.058	−11.252	<0.001
Year 2006	−0.805	0.060	−13.458	<0.001
Year 2007	−0.921	0.067	−13.781	<0.001
Year 2008	−0.924	0.067	−13.759	<0.001
Year 2009	−1.017	0.066	−15.424	<0.001
Year 2010	−1.002	0.067	−15.022	<0.001
Year 2011	−1.123	0.066	−17.141	<0.001
Year 2012	−1.164	0.070	−16.574	<0.001
Year 2013	−1.263	0.070	−18.068	<0.001
Year 2014	−1.397	0.069	−20.203	<0.001
Year 2015	−1.192	0.067	−17.662	<0.001
Year 2016	−1.357	0.074	−18.420	<0.001
Year 2017	−1.154	0.080	−14.365	<0.001
Year 2018	−0.986	0.075	−13.091	<0.001
Year 2019	−1.025	0.076	−13.482	<0.001
Sin	0.003	0.015	0.220	0.826
Cos	−0.008	0.022	−0.337	0.736
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.014	151.670	<0.001
s(Elev)		2.693	394.501	<0.001
s(Slope)		1.170	29.700	<0.001
s(C110)		2.432	242.641	<0.001
s(C112)		2.949	771.239	<0.001
s(C211)		1.746	54.822	<0.001
s(C213)		1.492	57.154	<0.001
s(C221)		0.936	13.427	<0.001
s(C222)		0.716	2.595	0.055
s(C223)		0.914	10.808	<0.001
s(C224)		0.651	1.864	0.085
s(C231)		1.938	98.477	<0.001
s(C311)		2.829	184.876	<0.001
s(C312)		1.116	72.296	<0.001
s(C313)		1.984	103.648	<0.001
s(C320)		0.990	31.930	<0.001
s(C321)		0.006	0.001	0.762
s(C330)		0.922	10.820	<0.001
s(C410)		0.935	13.748	<0.001
s(C511)		0.115	0.131	0.280

Italian Sparrow (*Passer italiae*) — Model nC-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	1.063	0.046	22.910	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.004	1220.500	<0.001
s(Urb$_{2500}$)		2.973	673.200	<0.001
s(For$_{2500}$)		2.918	304.100	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.836	0.042	19.858	<0.001
Year 1995	−0.521	0.058	−9.056	<0.001
Year 1996	−0.489	0.056	−8.752	<0.001
Year 1999	−0.359	0.053	−6.725	<0.001
Year 2000	−0.415	0.051	−8.143	<0.001
Year 2001	−0.627	0.055	−11.390	<0.001
Year 2002	−0.558	0.063	−8.857	<0.001
Year 2003	−0.795	0.067	−11.788	<0.001
Year 2004	−0.708	0.076	−9.292	<0.001
Year 2005	−0.740	0.055	−13.505	<0.001
Year 2006	−0.959	0.057	−16.873	<0.001
Year 2007	−0.897	0.064	−14.091	<0.001
Year 2008	−0.883	0.064	−13.810	<0.001
Year 2009	−0.947	0.063	−15.080	<0.001
Year 2010	−0.987	0.064	−15.495	<0.001
Year 2011	−1.088	0.063	−17.375	<0.001
Year 2012	−1.151	0.067	−17.176	<0.001
Year 2013	−1.166	0.067	−17.406	<0.001
Year 2014	−1.288	0.066	−19.505	<0.001
Year 2015	−1.043	0.064	−16.172	<0.001
Year 2016	−1.304	0.071	−18.396	<0.001
Year 2017	−1.145	0.077	−14.792	<0.001
Year 2018	−0.949	0.072	−13.120	<0.001
Year 2019	−0.990	0.073	−13.555	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.304	5.608	0.014

Italian Sparrow (*Passer italiae*) — Model nC-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	1.493	0.057	26.330	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elev)		2.601	1393.500	<0.001
s(Urb$_{2500}$)		2.963	563.200	<0.001
s(For$_{2500}$)		2.933	274.800	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.796	0.048	16.548	<0.001
Year 1995	−0.503	0.064	−7.828	<0.001
Year 1996	−0.469	0.063	−7.502	<0.001
Year 1999	−0.381	0.060	−6.345	<0.001
Year 2000	−0.412	0.057	−7.165	<0.001
Year 2001	−0.605	0.061	−9.855	<0.001
Year 2002	−0.543	0.070	−7.769	<0.001
Year 2003	−0.782	0.074	−10.581	<0.001
Year 2004	−0.690	0.083	−8.273	<0.001
Year 2005	−0.724	0.061	−11.865	<0.001
Year 2006	−0.945	0.063	−15.048	<0.001
Year 2007	−0.885	0.070	−12.671	<0.001
Year 2008	−0.867	0.070	−12.359	<0.001
Year 2009	−0.934	0.069	−13.577	<0.001
Year 2010	−0.971	0.070	−13.934	<0.001
Year 2011	−1.076	0.068	−15.735	<0.001
Year 2012	−1.138	0.073	−15.647	<0.001
Year 2013	−1.153	0.073	−15.851	<0.001
Year 2014	−1.268	0.072	−17.716	<0.001
Year 2015	−1.029	0.070	−14.621	<0.001
Year 2016	−1.292	0.076	−16.918	<0.001
Year 2017	−1.135	0.083	−13.628	<0.001
Year 2018	−0.936	0.079	−11.910	<0.001
Year 2019	−0.977	0.079	−12.338	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.612	10.070	0.002

Italian Sparrow (*Passer italiae*) — Model nC-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.131	0.043	3.060	0.002
Year 1995	−0.372	0.058	−6.468	<0.001
Year 1996	−0.372	0.056	−6.655	<0.001
Year 1999	−0.360	0.053	−6.739	<0.001
Year 2000	−0.450	0.051	−8.801	<0.001
Year 2001	−0.617	0.055	−11.218	<0.001
Year 2002	−0.656	0.063	−10.410	<0.001
Year 2003	−0.788	0.067	−11.681	<0.001
Year 2004	−0.684	0.076	−8.973	<0.001
Year 2005	−0.630	0.055	−11.500	<0.001
Year 2006	−0.774	0.057	−13.597	<0.001
Year 2007	−0.872	0.064	−13.704	<0.001
Year 2008	−0.818	0.064	−12.785	<0.001
Year 2009	−0.832	0.063	−13.255	<0.001
Year 2010	−0.882	0.064	−13.850	<0.001
Year 2011	−1.020	0.063	−16.283	<0.001
Year 2012	−1.062	0.067	−15.853	<0.001
Year 2013	−1.085	0.067	−16.180	<0.001
Year 2014	−1.161	0.066	−17.573	<0.001
Year 2015	−0.953	0.064	−14.772	<0.001
Year 2016	−1.272	0.071	−17.944	<0.001
Year 2017	−1.116	0.077	−14.413	<0.001
Year 2018	−0.915	0.072	−12.651	<0.001
Year 2019	−0.953	0.073	−13.055	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.997	2579.000	<0.001

Italian Sparrow (*Passer italiae*) — Model nC-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.124	0.054	2.278	0.023
Year 1995	−0.352	0.072	−4.912	<0.001
Year 1996	−0.354	0.070	−5.066	<0.001
Year 1999	−0.368	0.067	−5.514	<0.001
Year 2000	−0.470	0.064	−7.349	<0.001
Year 2001	−0.628	0.068	−9.189	<0.001
Year 2002	−0.661	0.077	−8.627	<0.001
Year 2003	−0.790	0.081	−9.793	<0.001
Year 2004	−0.707	0.091	−7.773	<0.001
Year 2005	−0.628	0.068	−9.280	<0.001
Year 2006	−0.763	0.069	−11.023	<0.001
Year 2007	−0.867	0.076	−11.356	<0.001
Year 2008	−0.822	0.077	−10.702	<0.001
Year 2009	−0.831	0.075	−11.008	<0.001
Year 2010	−0.879	0.076	−11.516	<0.001
Year 2011	−1.015	0.075	−13.599	<0.001
Year 2012	−1.054	0.079	−13.354	<0.001
Year 2013	−1.078	0.079	−13.671	<0.001
Year 2014	−1.149	0.078	−14.811	<0.001
Year 2015	−0.934	0.077	−12.198	<0.001
Year 2016	−1.269	0.082	−15.430	<0.001
Year 2017	−1.115	0.090	−12.458	<0.001
Year 2018	−0.914	0.085	−10.731	<0.001
Year 2019	−0.954	0.086	−11.124	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.997	2225.000	<0.001

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Chapter 3

Species traits drive long-term population trends of common breeding birds in northern Italy

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Abstract

Long-term population trends are considerable sources of information to set wildlife conservation priorities and to evaluate the performance of management actions. In addition, trends observed in functional groups (e.g. trophic guilds) can provide the foundation to test specific hypotheses about the drivers of the observed population dynamics. The aims of this study were to assess population trends of common breeding birds in Lombardy (N Italy) from 1992 to 2019 and to explore the relationship between trends and species sharing similar ecological and life-history traits. Trends were quantified and tested for significance by weighted linear regression models and using yearly population indices (median and 95% confidence interval) predicted through generalised additive models. Results showed that 45% of the species increased, 24% decreased, and 31% showed non-significant trends. Among declining species, 12 showed a decrease greater than 50%, and 6 of them underwent a worrying population reduction greater than 80%. Findings on life-history traits revealed a general decrease of migrants, of species with short incubation period and of species with high annual fecundity. Results on ecological traits showed that plant-eaters and species feeding on invertebrates, farmland birds, and ground-nesters declined, while woodland birds increased. Further studies should focus on investigation of the relationship between long-term trends and species traits at large spatial scales, and on quantifying the effects of specific drivers across multiple functional groups.

3.1. Introduction

Wildlife monitoring programs are fundamental to implement species conservation strategies and to verify to what extent they are effective (Donald et al., 2007; Stanton et al., 2018; Rosenberg et al., 2019). Population trends represent one of the most informative proxies of the status of populations' health, from local to continental spatial scales. One of the most monitored taxa worldwide are birds (Di Marco et al., 2017; Callaghan et al., 2021), an animal group of large conservation interest, target of several conservation policies in different countries, as well as at a continental scale (e.g. Birds Directive 2009/147/EC in European Union). Since the past century, many bird monitoring programs have been started in many countries worldwide, both at continental scale (e.g. the Pan-European Common Bird Monitoring Scheme [PECBMS] in Europe [PECBMS, 2021]; the North American Breeding Bird Survey [Sauer et al., 2017]) and national scale (e.g. in Finland [Fraixedas et al., 2015a, 2015b], the Breeding Bird Survey in UK [Harris et al., 2019]). In other cases, many data are available, although these have often been collected within projects with a specific purpose other than long-term monitoring (Massimino et al., 2008). Historical data collected in different years by different projects are surely a valuable but often overlooked source of information, available for the evaluation of the conservation status of species, communities, and ecosystems [Bani et al., 2019; Sibilia et al., 2019; Bani et al., 2020; Stefani et al., 2020). Beyond the assessment of population dynamics of each bird species, which is essential to define species-specific conservation priorities and actions, birds represent valuable ecological indicators that can potentially provide useful information about the overall biodiversity and ecosystem processes (Burger & Gochfeld, 2004; Dondina et al., 2015; Natsukawa, 2021; Oettel & Lapin, 2021; Santangeli & Girardello, 2021). Changes in species assemblages can be driven by species-specific responses to environmental perturbations (either natural or anthropic), and identifying which factors cause the observed changes is crucial to mitigate the impact of these perturbations. Although species population trends are not directly informative on drivers of population changes (Krebs, 1991), observing a common trend among species with similar ecological or life-history traits can provide the foundation to test specific hypotheses about the drivers of the observed population dynamics (Kamp et al., 2021). Despite the arising attention of a trait-based approach in community ecology (Villéger et al., 2008; Gagig et al., 2015; Jokimäki et al., 2016; Dondina et al., 2017; Jacoboski & Hartz, 2020; Stefani et al., 2020; Betancurt-Grisales et al., 2021; Leveau, 2021) and population ecology (Pocock, 2011; Sullivan et al., 2015; Rocchia et al., 2018; Hanzelka et al., 2019; Vergara-Tabares et al., 2020), only in the last few years researchers have started to explore the link between traits and population trends in avifauna over long time periods, highlighting the existence of different patterns among distinct functional groups (Flousek et al., 2015; Soykan et al., 2016; Bowler et al., 2019; Garcia-R & Di Marco, 2020; Vavylis et al., 2020; Morelli et al., 2020; Dumandan et al., 2021; Kamp et al., 2021).

In Europe, the decline of long-distance migrants wintering in Sub-Saharan Africa compared to short-distance migrants or sedentary species has been emphasised in several studies (e.g. Sanderson et al., 2006; Flousek et al., 2015; Kamp et al., 2021), as well as the general decline of farmland birds, as underlined by the tendency of the Common Farmland Birds Indicator (PECBMS, 2021). Gregory et al. (2019) highlighted the existence, in the period from 1980 to 2015 across 28 European countries, of different trends among farmland species and generalist forest species, with the first ones decreasing and the second ones stable. However, some contrasting trends were found for old forest species due to forest management (Fraixedas et al., 2015b). Insectivorous birds are declining in Europe (Bowler et al., 2019). In Germany, however, this trend has not been confirmed for the entire guild, since differences emerged between trends of farmland insectivorous birds and forest insectivorous birds, with the former decreasing and the latter stable (Kamp et al., 2021). Moreover, species with narrow niche breadth (i.e. specialist species) may suffer more from human-driven environmental alterations than species with broad niche breadth (i.e. generalist species), resulting in contrasting trends between the two groups (Morelli et al., 2020; Liordos et al., 2021). Nesting location can influence the breeding success by affecting the exposure of the nest to predation (e.g. birds or mammals; see Roos et al., 2018). For example, ground-nesting bird populations have decreased during recent decades in Europe (Chamberlain et al., 2000a; Isaksson et al., 2007) with most dramatic declines reported for larger species such as waders and bustards inhabiting agricultural landscape (MacDonald & Bolton, 2008; Kaasiku et al., 2019) or forest grouses (Tetraonidae; see Jahren et al., 2016; Warren et al., 2019). In addition, many others less explored life-history traits (e.g. incubation and fledging period, body mass, fecundity, species' mobility) can provide useful insights about the relationship between population trends and groups of species sharing similar traits.

In Italy, where a long-term monitoring program at national scale is available only from 2000 (MITO2000 projects, see Fornasari et al., 2002, 2004), no studies explored this relationship over long time series. However, in Lombardy (a region in the north of Italy), bird data from different projects have been collected for almost 30 years (1992-ongoing). They can be merged to assess long-term population trends in the region, while accounting for different sources of data heterogeneity (i.e. environmental bias, overdispersion and zero inflation [Tirozzi et al., 2022 and *Chapter 2*], see Section

3.2.3). In this study, we aimed at estimating trends for common breeding birds in Lombardy from 1992 to 2019, and at investigating how species traits are linked to population trends, in order to identify species that need major conservation attention, and which functional groups are experiencing the most considerable demographic changes.

3.2. Materials and Methods

3.2.1. Study area

The study was carried out in Lombardy, a region of 23,861 km2 in Northern Italy (45° N, 9° E). The northern part of the area is characterised by mountains Alps and Prealps, separated from each other by the wide glacial valley of Valtellina. The southwestern corner is characterised by the hilly landscape of northern Apennines. The rest of the region hosts a large portion of the alluvial plain of the Po River (the widest plain in Italy) extending from west to east for more than 12,000 km2. The average elevation of the whole region is 610 m above sea level (a.s.l.), but it shows a large variation across different areas, ranging from 2 m a.s.l. of the plain to roughly 4,000 m a.s.l. of the Alps. Land use is characterised by urban areas (14.7%), agricultural lands (42.2%), and natural and semi-natural lands (39.6%, of which 61.4% are forests). Alps and Prealps are mainly characterised by coniferous forests, meadows and grasslands at higher elevations, and deciduous forest at lower ones. The Apennine area is characterised by vineyards, extensive farming and deciduous and mixed forests. The Po Plain is heavily men-modified, with intensive cereal cultivations (mainly maize) in the central and eastern part, and dense urban areas and paddy fields in the west (Figure 3.1).

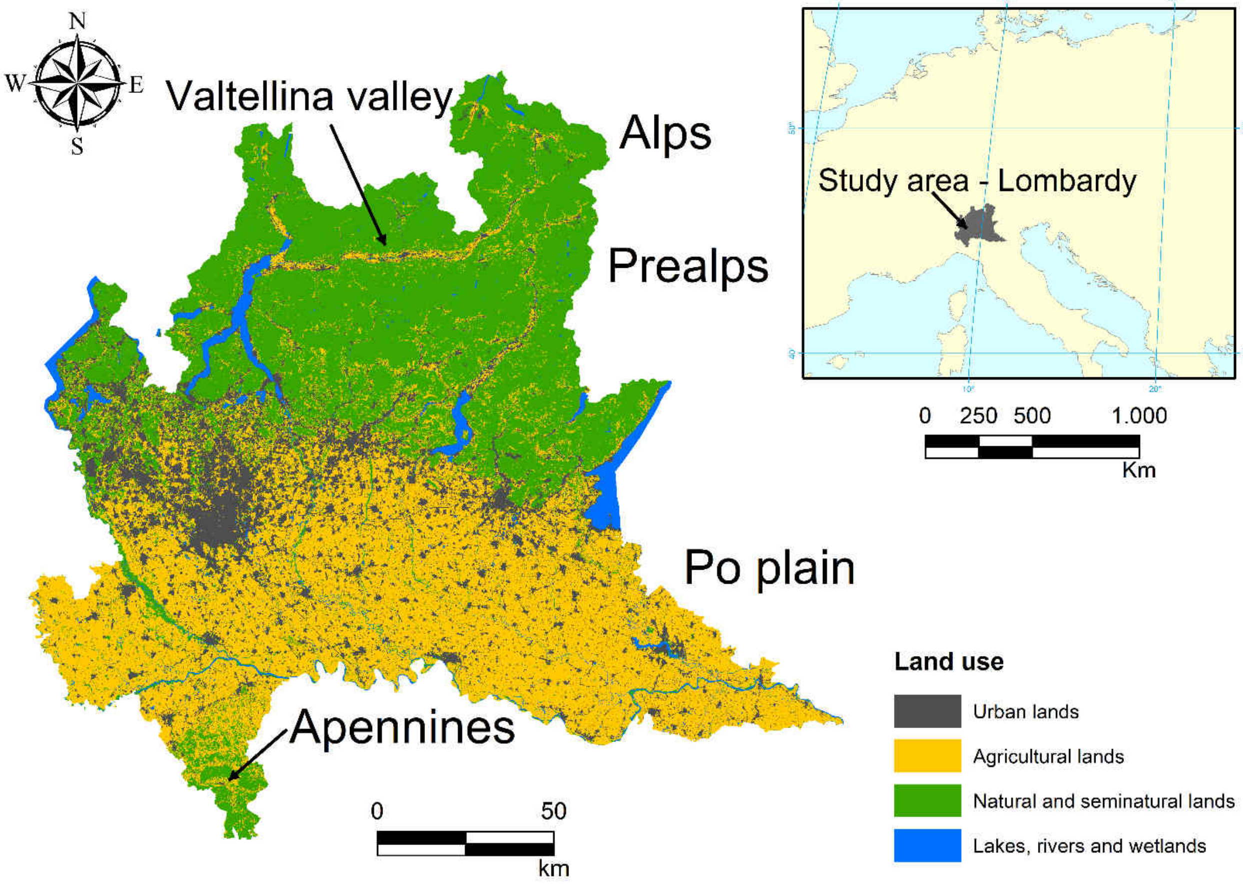


Figure 3.1. Study area. Land use refers to DUSAF 2018 digital map, level 1 of classification (ERSAF, 2018).

3.2.2. Survey design and bird data

Data were collected from five different projects on breeding bird surveys in Lombardy carried out from 1992 to 2019. Overall, the dataset consists of 18,505 point counts, with an average of 771 point counts per year (range 373 - 1,443; SD = 244). No data are available for years 1993, 1994, 1997, and 1998 (S3.1 in Supplementary materials). The first project was the “Long-term Monitoring Program”, launched in 1992 and covering 18 years. It consisted in a stratified sampling design, where seven primary sampling units were defined based on the main landscapes present in the Region. Within each primary sampling units, secondary sampling units, corresponding to about 10 km × 10 km squares (“Tavolette IGMI”, 1:25,000 maps) were extracted proportionally to the representativeness of each landscape, and yearly renewed to guarantee complete coverage of the Region in the long-term. Point counts were randomly located within secondary sampling units, according to territory accessibility. From 2007 to 2016, fixed secondary sampling units (20 in 2007, 21 in 2008, 23 in 2009 - 2010, 24 in 2011 - 2016) were added to the random ones. Finally, starting from 2017, all sampling units became fixed (34 units per year, including all of them previously performed). The "Regional Fauna Database" project was carried out from 2000 to 2006, using a systematic stratified sampling design. Finally, other three projects ("Forest Biodiversity Survey", "Lowland Biodiversity Survey", and "Greenway Project") were performed in restricted sub-areas of the region during a limited period (few years) with the aims of surveying breeding birds living in forests, in agricultural lands and in the Apennines, respectively (S3.2 in Supplementary materials and see *Chapter 2*). In all projects, data were collected using a single-visit point-count method with unlimited distance (Blondel et al., 1981). The minimum distance between sampling locations was 500 m within each year. All birds heard or seen in 10 min were recorded (Fornasari et al., 1998). Bird surveys were performed during the breeding season (10 May to 20 June) to minimise the count of migrants (birds not breeding in the study area) and to survey territorial birds. Surveys were conducted from sunrise to 11.00 a.m., only in good weather conditions, sunny to cloudy, without rain or strong wind (Bani et al., 2009). This technique provides a measure of relative bird abundance (Blondel et al., 1970; Bibby et al., 2000). The technique is effective in detecting bird species belonging to the orders Columbiformes, Cuculiformes, Apodiformes, Coraciiformes, Piciformes, and Passeriformes (Bani et al., 2009), but can also be used to survey some other common species, such as the Common Buzzard (*Buteo buteo*) and the Common Kestrel (*Falco tinnunculus*). All counts were expressed in number of breeding pairs according to Blondel et al. (1981). For early-breeding sedentary species (e.g. tits) that in our study area might start to breed in February-March, the sampling period might not entirely fit. Actually, this may represent a weakness in the detection of such species. However, since the early-breeding sedentary species can be detected in groups composed by parents and offspring during the late spring, each family group was converted into one breeding pairs in order to not overestimate the counts. Although some limitations can arise for some species starting to breed in the early spring (e.g. woodpeckers), the survey window we set (10 May to 20 June) can be considered suitable for most of species that can be detected by point counts technique in our study area. Additionally, even if an underestimate of detected individuals whose territorially behaviour peak precedes the beginning of the survey period, this source of bias remain constant over years. This way, counts of early-breeding sedentary species do not affect the trend estimates. In the case of large-scale monitoring programs, it is essential to obtain an optimal trade-off between costs (i.e. within-season multiple surveys effective to detect early- and late-breeders) and benefits (i.e. large representative sample). Thus, we prefer to obtain a large representative

sample, relying on single-visit survey, accepting an underestimation of early-breeders that do not jeopardise the trend estimates.

Since data did not rely on within-season multiple surveys, it was impossible to account for species detection probability. However, although the detection probability might represent an issue to be addressed in trend analysis relying on density estimates (Kéry et al., 2009), when using relative abundance data coming from a large dataset, where the effect of stochasticity on species detection is limited (Dondina et al., 2017), accounting for the detection probability can be considered superfluous (see S3.3 in Supplemetary materials). Among the 204 species detected in the whole period, we modelled trends for those with an overall relative frequency higher than 2%.

To avoid an overestimation of the number of breeding pairs for gregarious species during the breeding season, whose groups are composed of parental pairs and fledglings, we used the following conversion factor (CF) (i.e. the number of individuals considered as one breeding pair, see Bani, 1995): Feral Pigeon (*Columba livia*), CF = 8; Long-tailed Tit (*Aegithalos caudatus*), CF = 14; Common Starling (*Sturnus vulgaris*), CF = 11; Italian Sparrow (*Passer italiae*) and House Sparrow (*Passer domesticus*), CF = 14; Eurasian Tree Sparrow (*Passer montanus*), CF = 16. For instance, in the case of the Common Starling, the detection from one to 11 individuals has been converted into one breeding pairs, from 12 to 22 individuals into two breeding pairs, and so on.

3.2.3. Population trend assessment

Our dataset is affected by environmental bias inherited from spatial bias (i.e. the inadequate representation of the variability of environmental covariates in the study area; Phillips et al., 2009; Kramer-Schadt et al., 2013), due to differences in the sampling design of the five projects merged to obtain the final dataset. This issue prevents the trend assessment by using original data (Tirozzi et al., 2022 and *Chapter 2*). Furthermore, overdispersion, i.e. the variance is larger than the mean, and zero inflation, i.e. a particular type of overdispersion due to an excess of zero counts, could be present in count data (Martin et al., 2005; Zuur et al., 2009; Denes et al., 2015), and ignoring them can lead to serious errors in the interpretation of results from an ecological perspective (Blasco-Moreno et al., 2019). To handle environmental bias, overdispersion and zero inflation, we adopted the modelling procedure described in Tirozzi et al. (2022) (see *Chapter 2*), which is summarised in the following part of the Section and to which the reader can refer for a more detailed explanation. In their work, authors assessed long-term population trends for six bird species adopting a full-factorial design to account for environmental bias, overdispersion and zero inflation. Since environmental bias resulted the most relevant factor to determine the magnitude of trend estimates, in our analyses we excluded models not accounting for that. Following the aforementioned approach, we performed, starting from the original count data, four generalised additive models (GAMs; Hastie & Tibshirani, 1986, 1990; Wood 2017), namely C-ZIP-GAM, C-ZINB-GAM, C-P-GAM, C-NB-GAM (C: model with covariates dealing with environmental bias; ZIP: zero-inflated Poisson; ZINB: zero-inflated negative binomial; P: Poisson; NB: negative binomial). GAMs allow for relaxing parametric assumptions of generalised linear models (GLMs, McCullagh & Nelder, 1982), replacing some, or all, of the parametric terms by smooth functions of the covariates. We used the year of survey as a parametric factor; 17 land cover variables (continue urban matrix and infrastructures, discontinue urban matrix, arable lands, paddy fields, vineyards, orchards, olive groves, wood plantations, meadows and pastures, broadleaved forests, mixed forests, coniferous forests, grasslands, shrub lands, areas with sparse or absent vegetation, wetland vegetation, rivers and streams) recorded as percentage cover within a 250 m circular buffer around each survey site and four topographic variables (average values within a 250 m circular buffer around each survey site of elevation, sine and cosine of the aspect, slope) as covariates to account for environmental bias; and the spatial trend (interactions between X and Y coordinates [UTM 32N, WGS84 Datum]) to account for spatial pattern in the data (Dormann et al., 2007) and potential spatial autocorrelation (Dondina et al., 2017; Bani et al., 2019). For the zero-inflated GAMs, elevation and the percentage cover of urban and forest area within a 2500 m circular buffer designed around the survey site were used as predictors to explain the zero-inflation process. All covariates were modelled as smooth function (maximum degree of freedom set at four), except for the sine and cosine of the aspect which were modelled as linear effect. Based on the AIC (Burnham & Anderson, 2002), for each species, the best of the four models was picked out. Thus, it was used to predict yearly population indices through a parametric bootstrap with 1,000 simulations (Nelson, 2008). We used the median of the distribution of bootstrapped predictions as population index estimator for each year, and calculated the 95% confidence intervals by the percentile method (Davison & Hinkley, 2006). Land cover values in the prediction matrix were predicted from GAMs wherein the yearly average values for each covariate, derived from the six-digital land-use vector map DUSAF available from 1980 to 2019 (DUSAF 1980, 1999, 2007, 2012, 2015, and 2018, downloadable from http://www.geoportale.regione.lombardia.it/, accessed on 21 September 2021) were fitted as smooth function of year. In addition, since topographic variables and coordinates are time-invariant, they were fixed at the overall mean and the centroid of the area, respectively. Since some species could have clustered or geographically restricted distribution (e.g. alpine species), we used point counts in which the species was present in the period 1992-2019 to determine the species distribution area (km^2) across the region (Minimum Convex Hull method: MCH). For species that had a ratio between the MCH and the regional area less than 0.80, we used the MCH as polygon to extract values for all covariates; otherwise, the entire Region was used.

To assess the long-term population trends, a weighted least square linear regression (WLS) was performed, using the median of the yearly population index as response variable (estimated number of breeding pairs per sampling site), the year as continuous explanatory variable, and the reciprocal of the width of the confidence interval associated to the yearly estimate as weight. We acknowledge that yearly indices are not temporally independent, but since our aim was to assess long-term trends, a linear regression can be considered adequate for the purpose (Byrkjedal et al., 2012; Lockerbie et al., 2016). The model can be summarised as $I_t = \beta * Year + \varepsilon_i, w = 1/CI$, whereby we tested whether the trend was significantly different from zero (p(β) ≤ 0.05). The variation in population dimension from 1992 to 2019 (T%) was quantified as $T\% = [(I_{2019} - I_{1992})/I_{1992}] * 100$.

Geospatial analyses were performed in ESRI ArcMap version 10.7.1 (ESRI, 2019), while trend analyses in R software (R Core Development Team, 2020) using the packages *mcgv* (Wood, 2021) and *zigam* (Wotherspoon & Burch, 2016). Since these last analyses were particularly resource-consuming, they were performed on the supercomputer Marconi-A3 HPC (CINECA, 2020).

3.2.4. Trait-based analysis

3.2.4.1. Bird traits

To explore whether species sharing similar life-history and ecological traits showed a similar demographic signal in responding to specific drivers, we selected a set of 12 traits (see S3.4 in Supplementay materials). After evaluating the association among each pair of traits (categorical variables) through the Cramer's V coefficient (Cramér, 1946) using R package *vcd* (Meyer et al., 2020), we retained those traits not significantly associated with the others (Chi-Square test of independence or Fisher's exact test if the expected frequencies were less than five). In case of significant relationships, we retained the traits with a weak or moderate degree of association (Cramer's V < 0.5; Cohen, 1988; Gejdoŝ et al., 2021; see S3.5 in Supplementary materials). After this check, four life-history and four ecological traits were selected for the following analyses. Life-history traits encompassed the migration strategy, dispersal ratio, annual fecundity, and incubation period. Migration strategy was derived from Vigorita & Cucé (2008), which reports detailed information about phenology of populations in the study area. We classified species into three groups: “sedentary species” (non-migrants), “short-distance migrants” (wintering in Europe or North Africa), and “long-distance migrants” (wintering in Sub-Saharan Africa). Dispersal ratio (mean wing length [mm]/cube root of mean body mass [g]) was used as index of species’ mobility (Li et al., 2018). Annual fecundity was calculated as the product of average clutch size and average number of broods per year (Jiguet et al., 2007), and incubation period was the mean duration of eggs’ incubation (days). We derived this information from Storchová & Hořák (2018). For the Common Cuckoo (*Cuculus canorus*), we set to one the number of average broods per year. We transformed dispersal ratio, annual fecundity and incubation period from numerical to categorical variables, following the approach suggested by Kamp et al. (2021). We used the first quartile of the variable values of all species considered in the analyses (Dispersal ratio: values ≤ 28.278, Annual fecundity: values ≤ 5, Incubation period: values ≤ 13) to identify the groups “low dispersal ratio”, “low annual fecundity”, and “short incubation period”. The upper quartile (Dispersal ratio: values ≥ 33.737, Annual fecundity: values ≥ 10.625, Incubation period: values ≥ 17.25) was used to define the levels “high dispersal ratio”, “high annual fecundity”, and “long incubation period”. Finally, the values in-between were considered to represent species with intermediate characteristics. Ecological traits included diet, nest type, landscape type, and degree of specialisation. Diet represents the main source of food on which the species feeds on. It was derived from information collected in Wilman et al. (2014), where the percentage of food items used by the species is reported. We assigned species to the level “vertebrates” if it feeds on at least 70% of vertebrates, to “plant-eaters” if it feeds on at least 70% of vegetal material (seeds, nectar, fruits, other part of plants), and to “invertebrates” if it eats at least 70% of invertebrates (arthropods, mollusks, annelids). We assigned species to “omnivores” whether none of the foregoing categories individually exceeded the threshold of 70%. The Black Kite (*Milvus migrans*), resulting as scavenger for at least 70%, was classified as “vertebrates”. Nest type represents the nest location and it was derived from Storchová & Hořák (2018). We reclassified the original categories “open-arboreal” and “closed-arboreal” into the group “elevated-nesters”; “ground” and “ground-closer” into “ground-nesters”, and “hole-nesters” were retained as in the original study. Common Cuckoo was assigned to “elevated-nesters” (Pearman et al., 2014). Landscape type represents the habitat preference of the species at landscape scale. To derive this trait, we used our dataset that, being of large dimension and temporal coverage, can be considered a reliable source of information on habitat usage by the species. We calculated, for each level (urban, agricultural, forest, natural-open habitat, wetlands-rivers-lakes) classified according to DUSAF map (ERSAF, 2018), the median of percentage cover within a radius of 2500 m around the point counts where the species was present. Point counts of each year were related to the temporally closest available DUSAF or CORINE (CORINE Land Cover, 2021) digital map. Whether the median of the percentage cover of a specific level was greater than 50% we assigned that level as landscape type, namely “farmland”, “woodland”, and “natural-open habitat” (such as shrubs, grasslands, rocks). Whether the median did not exceed 50% for any levels we assigned the category “several”. To calculate the degree of specialisation we started from information collected in Pearman et al. (2014). We calculated single-species specialisation indices (Julliard et al., 2006) for each of the five following traits: food type, acquisition behavior, substrate from which food is acquired, foraging habitats, nesting habitats. Subsequently, we derived an overall specialisation index (SI) by computing the mean of the five indices. Hence, the higher the SI, the greater the species specialisation. In foraging habitats, we added “urban” and “garden” as habitats used by the Feral Pigeon, and “dry grassland”, “urban” and “garden” as habitats used by the Eurasian Magpie (*Pica pica*). Moreover, in the category “substrate from which food is acquired”, we grouped the levels “watersurface”, “underwater” and “water” into a single level.

3.2.4.2. Relationship between population trends and species traits

To test whether species belonging to the same functional group showed similar responses in terms of population trends, and if differences among trends of different groups were significant, we used a distinct weighted linear regression model for each trait. The median of the yearly population index was considered as response variable, and “year”, the trait and their interaction as explanatory variables. The reciprocal of the width of the confidence interval associated to each median yearly index was used as weight. The interaction term represents the trend for the specific group. In order to test whether the coefficient for each interaction term was significantly different from zero and from the other levels, we carried out additional statistic tests using the finite-sample F statistic by the function *linearHypothesis* of the R package *car* (Fox et al., 2020).

As the absolute value of the population index is not directly comparable among different species since it depends on the regional species abundance, we divided, within each species, the median of the yearly index by the median value of the index in the first year of the time series (i.e. I_{1992}). Exceptions were made for the Great Cormorant (*Phalacrocorax carbo*) (I_{2005}), Northern Lapwing (*Vanellus vanellus*), Short-toed Treecreeper (*Certhia brachydactyla*) and Common Linnet (*Linaria* *cannabina*) (I_{1995}) since they were not recorded in 1992. To obtain comparable confidence intervals (used as weights in the model), we adopted the identical procedure for the 2.5th and the 97.5th percentiles. This way, we assigned the value one at the median population index in the first year, and all the others indices (median, 2.5th and 97.5th percentiles) were expressed as variation in relation to the median of the first year.

3.3. Results

3.3.1. Single-species population trends

We assessed population indices and trends for 76 breeding bird species. According to AIC ranking, C-P-GAM (i.e. Poisson GAM with covariates dealing with environmental bias) was picked out as best model for 12 species, C-NB-GAM (i.e. negative binomial GAM with covariates dealing with environmental bias) for nine, C-ZIP-GAM (i.e. zero-inflated Poisson GAM with covariates dealing with environmental bias) for 40, and C-ZINB-GAM (i.e. zero-inflated negative binomial GAM with covariates dealing with environmental bias) for 15 (see S3.6 in Supplementary materials). In the selected models (see S3.7 in Supplementary materials for models' summary), the explained deviance ranged between 10.90% and 77.80% (mean = 38.61%) in the non-zero-inflated GAMs, while it ranged between 52.90% and 97.20% (mean = 82.62%) and between 7.30% and 66.60% (mean = 30.27%) in the binomial (i.e. zero-inflated part) and count component of the zero-inflated GAMs, respectively (see S3.6). Long-term trend analyses resulting from the weighted least square linear regression (WLS), highlighted a significant positive trend (T%) for 34 species (ranging from +12,060% for the Great Cormorant to +14.45% for the Eurasian Blackcap *Sylvia atricapilla*), negative for 18 species, 12 of which experienced a population decrease larger than 50%, while 24 species did not show a significant trend (p-value > 0.05; Table 3.1 and S3.8 in Supplementary materials).

Table 3.1. Summary of weighted least square linear regression models (WLS) for each species. Column "WLS model" indicates the best model selected by the AIC, used to perform the linear regression. C = model with covariates dealing with environmental bias; ZIP = zero-inflated Poisson; ZINB, zero-inflated negative binomial; P = Poisson; NB = negative binomial; GAM = generalised additive model. Β = estimate of regression coefficient for the explanatory variable "Year"; SE = standard error of β; t-value = t statistic; T% 1992 - 2019 = percentage of change in the population size from 1992 to 2019 according to the WLS model (significant trends are marked in bold); Adj-R^2 = adjusted R-square (in case of negative value it was round to zero). Estimates and standard errors for the intercept are not showed. The common names of the species are presented according to the nomenclature suggested by Gill et al. (2021).

Species	WLS model	β^1	SE^1	t-value	p-value	T% 1992 - 2019	Adj-R^2
Great Cormorant *Phalacrocorax carbo*	C-NB-GAM	0.050	0.007	–7.046	<0.001	**+12,060**	0.78
Black-crowned Night Heron (*Nycticorax nycticorax*)	C-NB-GAM	–0.112	0.068	–1.661	0.111	–47.86	0.07
Little Egret (*Egretta garzetta*)	C-NB-GAM	0.366	0.134	2.745	0.012	**+100.59**	0.22
Grey Heron (*Ardea cinerea*)	C-NB-GAM	0.022	0.008	2.719	0.013	**+54.76**	0.22
Mallard (*Anas platyrhynchos*)	C-ZINB-GAM	0.019	0.003	6.776	<0.001	**+525.19**	0.66
Black Kite (*Milvus migrans*)	C-ZINB-GAM	–0.053	0.022	–2.459	0.022	**–54.96**	0.18
Common Buzzard (*Buteo buteo*)	C-P-GAM	0.074	0.052	1.416	0.171	+50.42	0.04
Common Kestrel (*Falcon tinnunculus*)	C-P-GAM	0.083	0.018	4.760	<0.001	**+239.37**	0.49
Common Quail (*Coturnix coturnix*)	C-ZIP-GAM	–0.044	0.030	–1.471	0.155	**–46.83**	0.05
Common Pheasant (*Phasianus colchicus*)	C-NB-GAM	0.121	0.016	7.596	<0.001	**+591.31**	0.71
Common Moohren (*Gallinula chloropus*)	C-NB-GAM	–0.008	0.009	–0.819	0.421	–13.83	0
Northern Lapwing (*Vanellus vanellus*)	C-NB-GAM	0.218	0.033	6.514	<0.001	**+1,653.42**	0.65

Table 3.1 (cont.)

Feral Pigeon (*Columba livia*)	C-ZINB-GAM	0.062	0.079	0.779	0.444	+30.28	0
Common Wood Pigeon (*Columba palumbus*)	C-ZIP-GAM	1.213	0.175	6.945	<0.001	**+1,727.33**	0.67
Eurasian Collared Dove (*Streptopelia decaocto*)	C-ZINB-GAM	0.415	0.060	6.876	<0.001	**+196.25**	0.67
European Turtle Dove (*Streptopelia turtur*)	C-ZIP-GAM	0.253	0.279	0.907	0.374	+22.53	0
Common Cuckoo (*Cuculus canorus*)	C-ZIP-GAM	0.104	0.227	0.458	0.651	+5.81	0
Common Swift (*Apus apus*)	C-ZINB-GAM	–1.857	0.583	–3.187	0.004	**–50.01**	0.29
European Bee-eater (*Merops apiaster*)	C-NB-GAM	0.287	0.045	6.367	<0.001	**+1,325.78**	0.63
Eurasian Wryneck (*Jinx torquilla*)	C-ZIP-GAM	–0.484	0.074	–6.557	<0.001	**–81.59**	0.65
European Green Woodpecker (*Picus viridis*)	C-P-GAM	0.316	0.043	7.314	<0.001	**+418.48**	0.70
Great Spotted Woodpecker (*Dendrocopos major*)	C-P-GAM	0.425	0.034	12.448	<0.001	**+1,530.25**	0.87
Eurasian Skylark (*Alauda arvensis*)	C-ZIP-GAM	–0.744	0.087	–8.521	<0.001	**–99.65**	0.76
Eurasian Crag Martin (*Ptyonoprogne rupestris*)	C-NB-GAM	0.078	0.052	1.498	0.148	+64.74	0.05
Barn Swallow (*Hirundo rustica*)	C-ZINB-GAM	–1.788	0.288	–6.209	<0.001	**–67.41**	0.62
Common House Martin (*Delichon urbicum*)	C-ZINB-GAM	–0.864	0.276	–3.127	0.005	**—45.55**	0.28
Tree Pipit (*Anthus trivialis*)	C-ZIP-GAM	0.134	0.176	0.761	0.455	+14.41	0
Water Pipit (*Anthus spinoletta*)	C-ZINB-GAM	0.019	0.025	0.746	0.463	+15.12	0
Western Yellow Wagtail (*Motacilla flava*)	C-ZIP-GAM	–1.057	0.149	–7.073	<0.001	**–64.79**	0.68
Grey Wagtail (*Motacilla cinerea*)	C-P-GAM	0.003	0.034	0.088	0.931	+1.36	0
White Wagtail (*Motacilla alba*)	C-P-GAM	–0.338	0.126	–2.693	0.013	**–33.56**	0.21

Table 3.1 (cont.)

Eurasian Wren (*Troglodytes troglodytes*)	C-ZIP-GAM	–0.054	0.087	–0.626	0.538	–8.91	0
Dunnock (*Prunella modularis*)	C-P-GAM	0.597	0.101	5.923	<0.001	**+309.03**	0.60
European Robin (*Erithacus rubecula*)	C-ZIP-GAM	0.140	0.053	2.640	0.015	**+35.51**	0.21
Common Nigthingale (*Luscinia megarhynchos*)	C-ZIP-GAM	–0.356	0.116	–3.055	0.006	**–35.32**	0.27
Black Redstart (*Phoenicurus ochruros*)	C-ZIP-GAM	0.161	0.021	7.523	<0.001	**+135.77**	0.71
Common Redstart (*Phoenicurus Phoenicurus*)	C-ZIP-GAM	0.569	0.121	4.682	<0.001	**+126.60**	0.48
European Stonechat (*Saxicola rubicola*)	C-ZIP-GAM	–0.687	0.143	–4.793	<0.001	**–87.83**	0.49
Northern Wheatear (*Oenanthe oenanthe*)	C-P-GAM	–0.001	0.006	–0.136	0.893	–3.67	0
Common Blackbird (*Turdus merula*)	C-ZIP-GAM	1.291	0.682	1.894	0.072	+25.15	0.10
Song Thrush (*Turdus philomelos*)	C-ZIP-GAM	0.561	0.051	11.026	<0.001	**+2,869.64**	0.84
Mistle Trush (*Turdus viscivorus*)	C-ZIP-GAM	0.439	0.078	5.608	<0.001	**+468.08**	0.57
Cetti’s Warbler (*Cettia cetti*)	C-ZIP-GAM	–0.096	0.031	–3.049	0.006	**–62.35**	0.27
Melodius Warbler (*Hippolais polyglotta*)	C-ZIP-GAM	0.273	0.044	6.154	<0.001	**+346.07**	0.62
Lesser Whitethroat (*Curruca curruca*)	C-ZIP-GAM	0.141	0.042	3.320	0.003	**+153.05**	0.30
Eurasian Blackcap (*Sylvia atricapilla*)	C-ZIP-GAM	0.848	0.387	2.192	0.039	**+14.50**	0.14
Western Bonelli’s Warbler (*Phylloscopus bonelli*)	C-ZINB-GAM	0.355	0.110	3.214	0.004	**+79.62**	0.29
Common Chiffchaff (*Phylloscopus collybita*)	C-ZIP-GAM	–0.154	0.053	–2.919	0.008	**–40.64**	0.25
Goldcrest (*Regulus regulus*)	C-ZIP-GAM	–0.102	0.047	–2.184	0.040	**–41.42**	0.14
Common Firecrest (*Regulus ignicapilla*)	C-ZIP-GAM	0.363	0.084	4.349	<0.001	**+309.79**	0.44

Table 3.1 (cont.)

Spotted Flycatcher (*Muscicapa striata*)	C-P-GAM	1.477	0.209	7.080	<0.001	**+490.70**	0.68
Long-tailed Tit (*Aegithalos caudatus*)	C-P-GAM	0.186	0.049	3.781	0.001	**+114.79**	0.37
Marsh Tit (*Poecile palustris*)	C-ZIP-GAM	0.295	0.049	6.006	<0.001	**+340.76**	0.60
Willow Tit (*Poecile montanus*)	C-ZIP-GAM	0.155	0.068	2.289	0.032	**+116.63**	0.16
European Crested Tit (*Lophophanes cristatus*)	C-ZIP-GAM	0.072	0.020	3.640	0.001	**+141.11**	0.35
Coal Tit (*Periparus ater*)	C-ZIP-GAM	0.046	0.040	1.155	0.261	+20.66	0.01
Eurasian Blue Tit (*Cyanistes caeruleus*	C-ZIP-GAM	0.179	0.071	2.538	0.019	**+48.78**	0.19
Great Tit (*Parus major*)	C-ZIP-GAM	1.615	0.248	6.502	<0.001	**+104.37**	0.64
Eurasian Nuthatch (*Sitta europea*)	C-ZIP-GAM	0.015	0.009	1.788	0.088	+81.84	0.09
Short-toed Treecreeper (*Certhia brachydactyla*)	C-ZIP-GAM	0.160	0.022	7.155	<0.001	**+998.50**	0.70
Eurasian Golden Oriole (*Oriolus oriolus*)	C-ZIP-GAM	0.229	0.067	3.404	0.003	**+75.75**	0.32
Red-backed Shrike (*Lanius collurio*)	C-P-GAM	–0.576	0.112	–5.128	<0.001	**–80.13**	0.52
Eurasian Jay (*Garrulus glandarius*)	C-P-GAM	0.146	0.020	7.218	<0.001	**+174.93**	0.69
Eurasian Magpie (*Pica pica*)	C-ZIP-GAM	0.279	0.029	9.541	<0.001	**+753.86**	0.80
Carrion Crow (*Corvus corone*)	C-ZIP-GAM	–0.008	0.044	–0.192	0.850	–6.24	0
Hooded Crow (*Corvus cornix*)	C-ZINB-GAM	0.395	0.301	1.309	0.204	+13.31	0.03
Common Starling (*Sturnus vulgaris*)	C-ZINB-GAM	–0.261	0.177	–1.473	0.155	–18.55	0.05
Italian Sparrow (*Passer italiae*)	C-ZIP-GAM	–1.902	0.235	–8.077	<0.001	**–71.06**	0.74
Eurasian Tree Sparrow (*Passer montanus*)	C-ZIP-GAM	–0.272	0.064	–4.253	<0.001	**–41.31**	0.43

Table 3.1 (cont.)

Common Chaffinch (*Fringilla coelebs*)	C-ZIP-GAM	–0.333	0.286	–1.161	0.258	–5.45	0.02
European Serin (*Serinus serinus*)	C-ZIP-GAM	–0.111	0.345	–0.322	0.751	–4.49	0
European Greenfinch (*Chloris chloris*)	C-ZINB-GAM	–2.590	0.338	–7.657	<0.001	**–82.00**	0.72
European Goldfinch (*Carduelis carduelis*)	C-ZINB-GAM	–2.477	0.297	–8.329	<0.001	**–86.89**	0.75
Common Linnet (*Linaria cannabina*)	C-ZINB-GAM	0.034	0.044	0.767	0.452	+20.60	0
Common Redpoll (*Acanthis flammea*)	C-ZINB-GAM	–0.427	0.247	–1.727	0.098	–42.55	0.08
Eurasian Bullfinch (*Pyrrhula pyrrhula*)	C-ZIP-GAM	0.099	0.063	1.561	0.133	+73.22	0.06

[1] Values are multiplied for 10^2 to ease comparisons

3.3.2. Relationship between population trends and species traits

3.3.2.1. Life-history traits

Results for life-history traits were summarised in Table 3.2A-D. Sedentary species showed an increasing but not significant trend, while short and long-distance migrants significantly decreased (Figure 3.2A), but the magnitude of decline did not differ significantly between these two groups (Table 3.2A, p-value = 0.517). Species with intermediate dispersal ratio showed a significant decreasing trend (Figure 3.2B), even if it was not significantly different from the trend estimated for species with high and low dispersal ratio (Table 3.2B, p-value = 0.194 and p-value = 0.295, respectively). Analyses for the annual fecundity showed that species with high annual fecundity decreased (Figure 3.2C), and their decline was significantly different from the trends of the other two groups (Table 3.2C). Finally, concerning the incubation period, only species with low incubation period showed a significant trend, which was negative (Table 3.2D and Figure 3.2D).

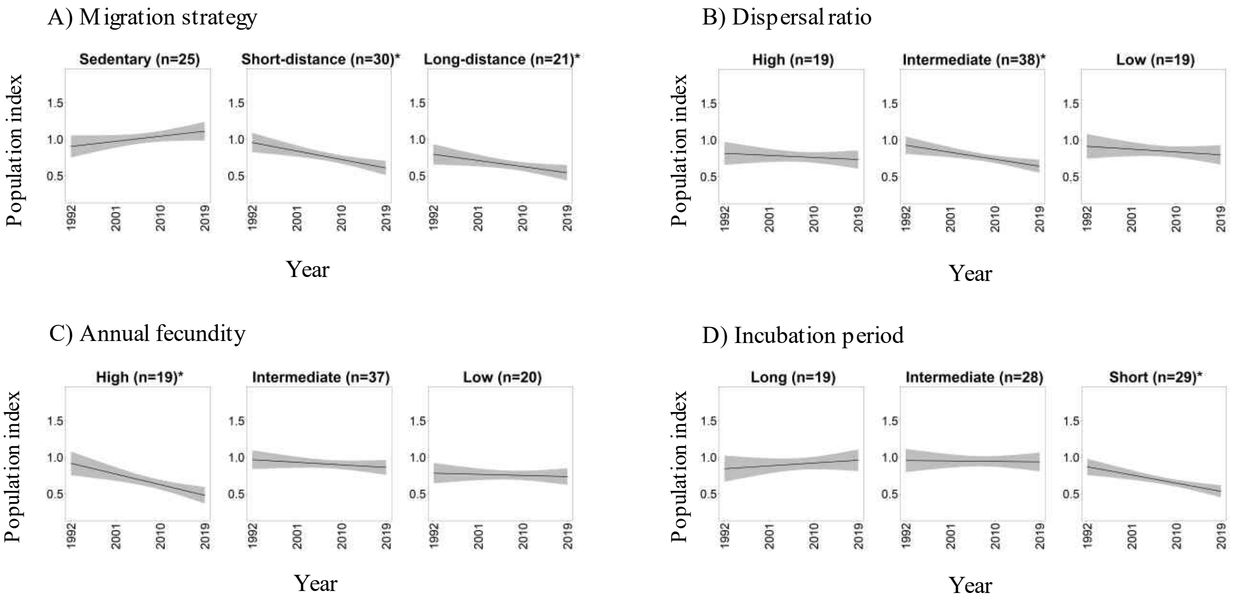


Figure 3.2. Population trends for bird species grouped according to the life-history traits. A) Migration strategy; B) dispersal ratio; C) annual fecundity; D) incubation period. Y-axis represents the population index of the species (see Section 3.2.4.2 for details). The shaded area represents the 95% confidence interval of the regression line. The number of species in each group is shown in parenthesis. Asterisks indicate the significance of the trends in relation to non-zero slope.

Table 3.2. Weighted linear regression models showing the response of avian functional groups in relation to life-history traits. In "model output" are shown model statistics (estimate = estimated coefficient; SE = standard error; t value = t-statistic) and the significance of each coefficient (p-value). The term "Intercept" and "Year" represent the reference group. The number of species included in each group is shown in parenthesis. In "Additional tests", hypotheses of non-zero slope and of equivalence for the coefficients of the interaction terms different from the reference level were tested (F value: F statistic). Significant p-values (≤ 0.05) for the interaction terms are marked in bold. A) Migration strategy. Groups: sedentary (reference level), short distance migrants (SDM), long distance migrants (LDM); adj-R^2= 0.05. B) Dispersal ratio: Groups: high dispersal ratio (reference level), intermediate dispersal ratio (IDR), limited dispersal ratio (LDR); adj-R^2 = 0.01. C) Annual fecundity. Groups: high annual fecundity (reference level), intermediate annual fecundity (IAF), low annual fecundity (LAF); adj-R^2 = 0.02. D) Incubation period. Groups: short incubation period (reference level), intermediate incubation period (IIP), long incubation period (LIP); adj-R^2 = 0.04.

A) Migration Strategy

Model output

Term	Estimate	SE	t-value	p-value
Intercept (25)	−14.441	9.176	−1.574	0.116
SDM (30)	40.904	11.808	3.464	<0.001
LDM (21)	33.821	12.351	2.738	0.006
Year	0.008	0.005	1.683	0.093
Year : SDM	−0.021	0.006	−3.486	**<0.001**
Year : LDM	−0.017	0.006	−2.769	**0.006**

Additional tests

Null hypothesis	F-value	p-value
Year : SDM = 0	11.966	**<0.001**
Year : LDM = 0	5.143	**0.023**
Year : SDM = Year : LDM	0.391	0.532

Table 3.2 (cont.)

B) Dispersal ratio

Model output

Term	Estimate	SE	t-value	p-value
Intercept (19)	7.039	9.335	0.754	0.451
IDR (38)	15.051	11.582	1.300	0.194
LDR (19)	2.484	13.642	0.182	0.856
Year	−0.003	0.005	−0.672	0.502
Year : IDR	−0.008	0.006	−1.300	0.194
Year : LDR	−0.001	0.007	−0.176	0.860

Additional tests

Null hypothesis	F-value	p-value
Year: IDR = 0	9.683	**0.002**
Year : LDR = 0	0.761	0.383
Year : IDR= Year : LDR	1.097	0.295

C) Annual fecundity

Model output

Term	Estimate	SE	t-value	p-value
Intercept (19)	33.284	9.141	3.641	<0.001
IAF (37)	−24.554	11.909	−2.062	0.039
LAF (20)	−29.050	12.367	−2.349	0.019
Year	−0.016	0.005	−3.570	**<0.001**
Year : IAF	0.012	0.006	2.083	**0.037**
Year : LAF	0.015	0.006	2.357	**0.019**

Additional tests

Null hypothesis	F-value	p-value
Year : IAF = 0	1.051	0.305
Year : LAF = 0	0.174	0.676
Year : IAF = Year : LAF	0.148	0.701

Table 3.2 (cont.)

D) Incubation period

Model output

Term	Estimate	SE	t-value	p-value
Intercept (29)	25.684	6.411	4.006	<0.001
IIP (28)	−23.327	11.436	−2.040	0.042
LIP (19)	−33.426	12.549	−2.664	0.008
Year	−0.012	0.003	−3.902	**<0.001**
Year : IIP	0.012	0.006	2.063	**0.039**
Year : LIP	0.017	0.006	2.682	**0.007**

Additional tests

Null hypothesis	F-value	p-value
Year : IIP = 0	0.022	0.881
Year : LIP = 0	0.643	0.423
Year : IIP = Year : LIP	0.492	0.483

3.3.2.2. Ecological traits

Results for ecological traits were summarised in Table 3.3A-D. As regards the diet, pairwise comparison among groups did not show significant differences. However, tests for non-zero slope within each group revealed a significant decline for plant-eaters and species feeding on invertebrates, while omnivores and species eating vertebrates did not exhibit any significant trend (Table 3.3A and Figure 3.3A). Ground-nesters showed a decreasing trend, while neither elevated-nesters nor hole-nesters resulted to have significant population changes (Table 3.3B and Figure 3.3B). Species inhabiting farmland landscapes showed a clear decrease, while species preferring woodland landscapes were on increase (Figure 3.3C). Although species of natural-open habitat showed a raising tendency, the trend was not significant, maybe due to the limited sample dimension for this group (nine species). Finally, for the group of species classified as “several” (i.e. those not having a prevalent habitat preference) the regression coefficient for the interaction term was roughly equal to zero (Table 3.3C). In relation to the overall specialisation index, the model highlighted a significant negative trend for species with a medium degree of specialisation, while both specialists and generalists did not show significant population changes over the period (Figure 3.3D). However, no differences were detected among trends of the three groups, probably due to the weak dissimilarity among the coefficients (Table 3.3D).

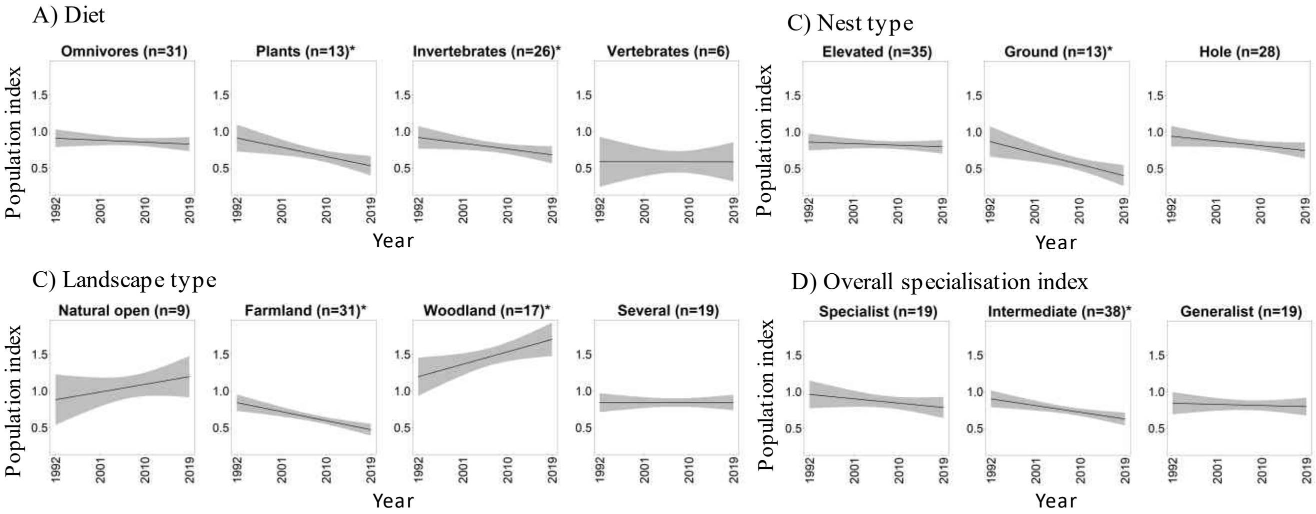


Figure 3.3. Population trends for bird species grouped according to ecological traits. A) Diet; B) nest type; C) landscape type; D) overall specialisation index. Y-axis represents the population index of the species (see Section 3.2.4.2 for details). The number of species in each group is shown in parenthesis. Asterisks indicate the significance of the trends in relation to non-zero slope.

Table 3.3. Weighted linear regression models showing the response of avian functional groups in relation to ecological traits. In "model output" are shown model statistics (Estimate, estimated coefficient; SE, standard error; t value, t-statistic) and the significance of each coefficient (p-value). The term "Intercept" and "Year" represent the reference group. The number of species included in each group is shown in parenthesis. In "Additional tests", hypotheses of non-zero slope and of equivalence for the coefficients of the interaction terms different from the reference level were tested (F value: F statistic). Significant p-values (≤0.05) for the interaction terms are marked in bold. A) Diet. Groups: omnivores (references level), plant-eaters (PLA), invertebrates (INV), vertebrates (VER); adj-R^2 = 0.01. B) Nest type. Groups: elevated-nesters (reference level), ground-nesters (GR), hole-nesters (HL); adj-R^2 = 0.02. C) Landscape type. Groups: natural-open habitat (reference level), farmland (FAR), woodland (WOO), several (SEV); adj-R^2 = 0.11. D) SI. Groups: generalist species (reference level), intermediate species (INT), specialist species (SPE); adj-R^2 = 0.02.

A) Diet

Model output

Term	Estimate	SE	t-value	p-value
Intercept (31)	6.242	7.250	0.861	0.389
PLA (13)	22.686	12.764	1.777	0.076
INV (26)	12.264	11.541	1.063	0.288
VER (6)	−0.662	20.755	−0.032	0.975
Year	−0.003	0.004	−0.743	0.458
Year : PLA	−0.011	0.006	−1.791	0.074
Year : INV	−0.006	0.006	−1.069	0.285
Year : VER	0.000	0.010	0.021	0.983

Additional tests

Null hypothesis	F-value	p-value
Year: PLA = 0	7.232	**0.007**
Year : INV = 0	3.898	**0.048**
Year : VER = 0	0.065	0.799
Year : PLA = Year :INV	0.579	0.446
Year : PLA = Year : VER	1.111	0.292
Year : INV = Year : VER	0.356	0.551

Table 3.3 (cont.)

B) Nest type

Model output

Term	Estimate	SE	t-value	p-value
Intercept (35)	5.627	6.834	0.823	0.410
GR (13)	29.582	13.532	2.186	0.029
HL (28)	9.696	10.731	0.904	0.366
Year	−0.002	0.003	−0.703	0.482
Year : GR	−0.015	0.007	−2.203	**0.028**
Year : HL	−0.005	0.005	−0.903	0.367

Additional tests

Null hypothesis	F-value	p-value
Year : GR = 0	8.790	**0.003**
Year : HL= 0	3.070	0.080
Year : GR = Year : HL	1.976	0.160

C) Landscape type

Model output

Term	Estimate	SE	t-value	p-value
Intercept (9)	−22.340	20.764	−1.076	0.282
FAR (31)	50.341	21.718	2.318	0.021
WOO (17)	−14.078	26.297	−0.535	0.593
SEV (19)	22.952	22.164	1.036	0.301
Year	0.012	0.010	1.127	0.260
Year : FAR	−0.025	0.011	−2.338	**0.020**
Year : WOO	0.007	0.013	0.551	0.581
Year : SEV	−0.012	0.011	−1.045	0.296

Additional tests

Null hypothesis	F-value	p-value
Year : FAR = 0	18.505	**<0.001**
Year : WOO = 0	5.513	**0.019**
Year : SEV = 0	<0.001	0.977
Year : FAR = Year : WOO	14.153	**<0.001**
Year : FAR = Year : SEV	7.572	**0.006**
Year : WOO = Year : SEV	4.426	**0.036**

D) Overall specialisation index

Model output

Term	Estimate	SE	t-value	p-value
Intercept (19)	4.256	9.046	0.471	0.638
INT (38)	16.896	11.230	1.505	0.133
SPE (19)	9.934	14.312	0.694	0.488
Year	−0.002	0.005	−0.381	0.704
Year : INT	−0.008	0.006	−1.511	0.131
Year : SPE	−0.005	0.007	−0.691	0.490

Additional tests

Null hypothesis	F-value	p-value
Year : INT = 0	9.411	**0.002**
Year : SPE = 0	1.446	0.230
Year : INT = Year : SPE	0.300	0.584

3.4. Discussion

3.4.1. Modelling approach

The use of adequate models to obtain reliable estimates of yearly population indices is fundamental to assess non-distorted population trends, whose evaluation is of extreme importance in wildlife conservation. In this context, our results showed that zero-inflated models should be used more than they are. Specifically, for 72% of the 76 species, zero-inflated GAMs were the most suitable models for predicting yearly population indices. Unexpectedly, zero-inflated models are often overlooked in population trend analysis without an objective reason, but their use should be always tested in case of a high number of zero counts in the data. Overdispersion, which is often detected in count data deriving from multi-species surveys (Bani et al., 2009; Wagh & Kamalja, 2018), can actually disappear or decrease if zero-inflated models are used (see S3.6). The management of zero counts and the error structure for the response variable can strongly affect trend estimations (Tirozzi et al., 2022 and *Chapter 2*), and it should not be carried out a priori but after a modelling selection procedure, which compares multiple candidate models.

3.4.2. Species population trends

The long-term trend analyses allowed obtaining an updated portrait of the conservation status of 76 common breeding birds in Lombardy. Although roughly three-quarters of them showed non-significant or increasing population trends, 24% of the studied species resulted on decline. The Eurasian Skylark (*Alauda arvensis*) showed a worrying trend: its population was reduced by 99.65% since 1992, pointing out the extremely critical situation that the breeding populations of the species are experiencing in the Region. In a previous work, Bani et al. (2009) found a reduction of 75% of the species regional population for the period from 1992 to 2009; after 2009, the population indices estimated by our analyses revealed a further decrease until 2015 (S3.8), resulting in a stronger population decline, overall. However, at national and continental scale, the species exhibits a minor accentuated decrease (PECBMS, 2021; Rete Rurale Nazionale & Lipu, 2020). In farmland, this species is very sensitive to the intensive agricultural management (with the use of pesticides, fertilisers, and excessive mowing) as well as to the decrease in crop diversity, both leading to unsuitable conditions for nesting (Chamberlain & Siriwardena, 2000; Chamberlain et al., 2000b; Eraud & Boutin, 2002; Koleček et al., 2015). Urbanisation around arable land negatively affect the occurrence of the species (Loretto et al., 2019), as well as the anthropic alterations in natural and semi-natural grassland in mountains areas (Brambilla et al., 2020). In the Alpine area of Lombardy, the distribution of the Eurasian Skylark might be adversely affected by shrubs and forest expansion, as shown for other alpine species (Bani et al., 2019), but this pattern needs to be confirmed. Other five species (the European Stonechat *Saxicola rubicola*, the European Goldfinch *Carduelis carduelis*, the European Greenfinch *Chloris chloris*, the Eurasian Wryneck *Jynx torquilla*, and the Red-backed Shrike *Lanius collurio*) showed very strong negative trend, with population declines greater than 80%. The European Stonechat experienced a sharp drop from 2006 (S3.8). The decline was greater than reported at national scale in Italy, where a decrease of 68.5% was detected from 2000 to 2020 (Rete Rurale Nazionale & Lipu, 2020). However, in the close Switzerland, a region environmentally and climatically similar to the Alpine area of Lombardy, the species appeared to be on increase (Knaus et al., 2021), and in Europe it seemed to be stable (PECBMS, 2021). These contrasting trends can derive from local factors (e.g. land management) that, acting at smaller spatial scale, can produce different effects in breeding areas (Rocchia et al., 2018). For this species, land consolidation of arable fields, leading to the degradation of rural landscape structure, might act as ecological traps (Denac & Kmecl, 2021). Trends for the European Goldfinch and the European Greenfinch showed a more drastic situation compared to the known status at national scale in the last twenty years (Rete Rurale Nazionale & Lipu, 2020). The decline found by Bani et al. (2009) in Lombardy seems to be continued over the last decade. However, in Europe these two finches did not decline over long period (PECBMS, 2021), or showed fluctuant dynamics, suggesting the existence of different drivers, such as seeds availability or epidemics, acting at local spatial scale (Lehikoinen et al., 2013). In addition, both the Eurasian Wryneck and the Red-backed Shrike highlighted a more marked decline than that shown at national (Rete Rurale Nazionale & Lipu, 2020) and European (PECBMS, 2021) level. In the study area, the two species mainly inhabit semi-open environments, especially extensively managed farmland. Agricultural intensification, leading to loss of suitable foraging and nesting sites, as well as to a reduction of preys (mainly represented by insects) availability and detectability, may have played a key role in their decline (Coudrain et al., 2010; Weisshaupt et al., 2011; Le Roux et al., 2016; Bakx et al., 2020; Denac & Kmecl, 2021). We noted that other five species, the Barn Swallow (*Hirundo rustica*), the Western Yellow Wagtail (*Motacilla flava*), the Italian Sparrow, the Cetti's Warbler (*Cettia cetti*), and the Common Swift (*Apus apus*) experienced a significant decline ranging from 50% to 80%, higher than the known situation at national scale (Rete Rurale Nazionale & Lipu, 2020; MITO2000, 2021). The Barn Swallow, in our study area, showed a population decline of rough 50% during 1990s and 2000s (Bani et al., 2009; Ambrosini et al., 2012; Sicurella et al., 2014), and the negative trend continued over the last decade. Causes can be linked to both changes in agricultural practices as well as cattle farming (Ambrosini et al., 2011a). The Western Yellow Wagtail, which in Lombardy is associated to farmlands, may have suffered from the intensification and changes in agricultural practices, in particular from loss of late mown areas (Broyer et al., 2016). The Italian Sparrow, in agricultural breeding areas, could be negatively affected by the progressive shift of cereal cultivations from wheat to maize, other than changes in livestock farming practices (Brlík et al., 2021). In urban settlements, the food shortage (e.g. caused by a more efficient street cleaning and by a reduction in "weedy" areas), the reduction of suitable breeding sites, predation and competition had likely contributed to the species decline (Wilkinson, 2006; Dinetti, 208; Brlík et al., 2021). Both the Common Swift and the declining Common House Martin (−45.55%) might have suffered from climatic factors acting in wintering and breeding grounds, but also along migration flyways (Rajchard et al., 2006; Ambrosini et al., 2011b). Moreover, such species living in urban areas may suffer from different kinds of pollutants, as shown by Miniero et al. (2008). Less clear remain the drivers of the negative long-term trend of the Black Kite (−54.96%), although some study highlighted the possible effect of electrocution and road casualty (De Pascalis et al., 2020). As for many other long-migrants species, we do not exclude that other factors might act in sub-Saharan wintering areas (see Section 3.4.3).

Among the species resulting on increase, the Great Cormorant exhibited a remarkable positive trend (+12,060 %) in the last fourteen years. This finding suggests the need of further and specific investigations in order to assess in detail the absolute dimension of the population, considering the impact that the species may have on herons (Giammarino et al., 2021), fish species (Delmastro et al., 2015) and economic activities as fisheries (Veneranta et al., 2020). All tits (included the Long-tail Tit) resulted significantly on increase, except the Coal Tit (*Periparus ater*) that showed a positive but non-significant trend. These findings are largely in accordance with trends observed in Switzerland during the same period (Knaus et al., 2021), while in Europe, during the last forty years, the Marsh Tit (*Poecile palustris*), the Willow Tit (*Poecile montanus*) and the European Crested Tit (*Lophophanes cristatus*) declined (PECBMS, 2021). Also in Finland, these last two species declined due to intensive forestry (Laaksonen & Lehikoinen, 2013), and the Willow Tit has been added in the National Red List (Tiainen et al., 2016). We found a considerable increase of the population of the Northern Lapwing (+1653%), a result quite in contrast with the negative trend observed in Europe (PECBMS, 2021), especially in arable land (Thorup, 2018; Lislevand et al., 2021), which is the type of habitat where the species mainly occurs in Lombardy. However, the first case of breeding of the Northern Lapwing in our study area is reported in 1960s, and from 1980s to the first decade of the twenty-first century the population has grown from a few hundreds of individuals to about two thousands of breeding pairs, probably supported by the water management of paddy fields, which represent the favorite breeding habitat for the species in Lombardy (Brichetti & Fracasso, 2004; Longoni et al., 2011; Orioli et al., 2021). However, changes in agricultural practices for this kind of crops (in particular the delay of the flooding period) occurred in the last years, can negatively affect the reproductive success of the species, pointing out the importance to carry on specific demographic studies. Eurasian Magpie showed a strong increasing trend (+754%). It resulted greater than the average increment at national scale (Rete Rurale Nazionale & Lipu, 2020), and in contrast with the European situation, where the species from the early 1990s exhibited a clear decrease (PECBMS, 2021). In our region, where the urbanised areas increased during the last decades (ERSAF, 2018), the positive tendency of the Eurasian Magpie can be linked to its capacity of adapting to highly urbanised habitats. In this type of environment, the density of pairs can reach higher values than in non-urbanised habitats (Ciebiera et al., 2021), maybe favored by high food availability. We have not evidence that the species increase is linked to a reduction of human persecution, as occurred in other areas (e.g. see Jokimäki et al., 2017). Song Thrush (*Turdus philomelos*), Common Wood Pigeon (*Columba palumbus*), Great Spotted Woodpecker (*Dendrocopos major*) and Short-toed Treecreeper showed strong positive trends, with regional population increased tenfold or more from the beginning of the time series. These findings confirmed the trends of the species in Europe, where from the early 1990s remarkable increments of the continental population were detected (PECBMS, 2021).

Population trends are one of the most important criteria for the conservation status assessment of species (e.g. IUCN, 2012). Looking at the IUCN Italian Red List (Rondinini et al., 2013), we found that six of the 18 declining species are listed as “vulnerable”, and one of them, the Eurasian Wryneck, as “engendered”. The European Goldfinch and the European Greenfinch, which showed strong decreasing trends, are listed as “near threatened”. Although our results are at regional scale, they can provide valuable information for updating local, national and continental Red Lists (Vavylis et al., 2020).

3.4.3. Relationship between population trends and species traits

The trait-based approach proved to be very useful to infer on general drivers acting on wildlife populations, laying the foundations for more specific studies with the aim of identifying the proximal causes shaping bird population dynamic. Our analyses detected a general decline of migrant species, and a positive but non-significant trend for sedentary species. The decline of long-distance migrants has been extensively outlined for European breeding birds (Sanderson et al., 2006; Vickery et al., 2014; Bowler et al., 2021), with some exceptions (e.g. in Estonia, Kuresoo et al., 2011), and several explanations have been proposed (e.g. drought of Sahel areas, habitat loss and degradation, hunting, phenological mismatch; see Sanderson et al., 2006; Cresswell et al., 2007; Ambrosini et al., 2011c; Ockendon et al., 2012; Morrison et al., 2013; Vickery et al., 2014; Howard et al., 2020; Telenský et al., 2020). Moreover, long-distance migrants were proved to decline faster than short-distance migrants in Europe (Sanderson et al., 2006; Flousek et al., 2015; Kamp et al., 2021), but we did not detect such a difference between the two groups, corroborating the idea that geographic variation in trends may occur (Bowler et al., 2021).

The link between dispersal ratio, as surrogate of species’ mobility, and the population trend did not highlight a clear gradient for this trait. In a previous study, Crawford et al. (2014) found that a lesser species’ mobility was associated with a high rate of adult mortality. Although our results did not confirm this finding, and differences among the three groups did not emerge, a signal that long-term population dynamic can vary in relation to species’ mobility was found for species with intermediate mobility. Further studies should focus on this life-history trait that is very poorly investigated in trend analysis.

Species with high annual fecundity exhibited a clear negative trend. This finding was in accordance with results underlined by Jiguet et al. (2007) for common breeding birds in France. Annual fecundity strongly influences variations in population size in short-lived species (Sæther & Bakke, 2000), and it is possible that individuals of such species will have too short a lifespan to learn and adapt to directional environmental changes. Moreover, density-dependent effects might also explain the observed pattern: high fecundity could lead to an increase in juvenile mortality, due to increased intraspecific competition (Arcese et al., 1992; Jiguet et al., 2007).

Results for the incubation period highlighted that species with shorter incubation period decline, while those with longer incubation period showed a positive tendency, although it was not significant. On one hand, species with longer incubation period might be longer exposed to anthropogenic and ecological pressures during a critical stage of their life cycle. However, Liu et al. (2021) highlighted that the incubation period is strongly and positively associated with nest concealment. Species that can hide their nests more efficiently, may be less exposed to predation risk, with positive effects on fitness in the long period. Additionally, shorter incubation periods are often found in species that face higher levels of nest predation (Martin, 2002; Li & Lu, 2012). However, predation risk may also be a habitat-dependent process (Butler & Gillings, 2004). Moreover, human activities can contribute to enhance this risk, as well as they can directly affect hatching success (Faria et al., 2016; Ponce et al., 2018). Further studies to investigate the effects of anthropogenic pressures on hatching success across different types of habitats can provide novel insights for planning ad hoc conservation strategies.

Analyses of ecological traits showed a decline of plant-eaters and species feeding on invertebrates. The decrease in insect populations has been largely recognised (Laether, 2018) and reported in several countries in Europe (see Hallmann et al., 2017; Valtonen et al., 2017), as well as worldwide (Sánchez-Bayo & Wyckhuys, 2019), but can only partially explain the general decrease of insectivore birds in Europe in the period 1990-2015 (Bowler et al., 2019). In our study, several species that eat invertebrates, such as the Northern Lapwing, the European Bee-eater (*Merops apiaster*), the Short-toed Treecreeper, the European Green Woodpecker (*Picus viridis*), the Spotted Flycatcher (*Muscicapa striata*), the Common Firecrest (*Regulus ignicapilla*) and the Melodius Warbler (*Hippolais polyglotta*) exhibited strong increasing trends (> 300%), highlighting that other component (e.g. habitat preferences) can interact with food habits in shaping population dynamic (Bowler et al., 2019; Reif & Hanzelka, 2020; Kamp et al., 2021). The decline of plant-eater species (in our work mainly represented by species feeding on seeds) emerged in our study was in accordance with results in Europe (Bowler et al., 2019). In particular, plant-eaters linked with urban settlements and farmland, such as the Italian Sparrow, the European Goldfinch and the European Greenfinch, showed stronger negative trends. The use of herbicide and the disappearance of spring-sown cereals at the cost of winter-sown grains represent one of the major threats for the guild in farmland (Newton, 2004). Additionally, the use of pesticides can have sub-lethal effects, such as impairing migratory ability in seed-eating species (Eng et al., 2017).

As regards nest type, the general decrease of ground-nesters (largely farmland birds) can be associated with their higher predation risk (Söderström et al., 1998; Roos et al., 2018; Liu et al., 2021), which might also be linked to agricultural practices that reduce the concealment of nests by modifying the habitat structure (Wittingham & Evans, 2004).

Farmland species showed a strong decline (roughly equal to that of short-distance migrants, see Table 3.2A and Table 3.3C for comparison between regression coefficients). This finding is not surprising, since the decrease of farmland avifauna in Europe is well known (Gregory et al., 2019; PECBMS, 2021), as well as documented in Italy in the last 20 years (with a stronger negative trend in Lombardy compared to the situation at national scale (Rete Rurale Nazionale & Lipu, 2020). Causes of this decline are ascribed to agricultural intensification (Newton, 2004), which lead to simplification and homogenization of agricultural landscapes (land consolidation, loss of fallows), reduction of crop diversity and massive use of pesticides. Moreover, changes in agricultural management, such as increasing number of cuts, dense swards and reseeding with high-yielding grass crops, can lead to an increase of human disturbance and to a decrease of habitat suitability for many species. It is probably that all or a part of these processes have played, and still play, an important role in our study area, where intensive agriculture is widely spread. For example, in Lombardy the average harvest for maize and autumn-sown grains per hectare, thought to be a good indicator of agricultural intensity (Donald et al., 2006), was 9.3 ton/ha in the period 2006-2019, while the national average in the same period was 5.3 ton/ha (ISTAT, 2021). However, 13 of the 31 farmland species showed significant positive trends, highlighting that species-specific drivers can occur and determine different demographic responses. For instance, some thermophilic farmland species, such as the European Bee-eater, showed strong positive trends, probably favored by temperature increasing (Gregory et al., 2009; Reif et al., 2010; Stiels et al., 2021). Woodland birds, which appear stable or increasing in Europe (Ram et al., 2017; Gregory et al., 2019; Kamp et al., 2021), confirmed this pattern in our study area. The increase in wood extension occurred in Lombardy over the last 40 years (ERSAF, 2018), due to both natural processes linked to the abandonment of mountain meadows and pastures, and human-made reforestations of bare grounds, may have increased the amount of suitable and available habitats for this group of species. This can have led to the establishment of new sub-populations and to the reduction of intraspecific and interspecific competition. Additionally, it is not to exclude that possible changes in forest management, resulting in an increase of forest quality, may have favored the positive trend of forest birds (Griesser & Lagemberg, 2012; Wade et al., 2013; Eggers & Low, 2014; Vatka et al., 2014), but see Fraixedas et al. (2015b). Among woodland species, only two of them showed a negative trend: the Common Chiffchaff (*Phylloscopus collybita*), with a population reduction of 40.64%, and the Goldcrest (*Regulus regulus*), with a decrease of 41.42%. The Common Chiffchaff was also detected on decline by Bani et al. (2009), but its trend is quite different compared to the observed trends in Europe (PECBMS, 2021), in Italy from 2000 to 2014 (MITO2000, 2021) and in other European countries (e.g. Germany, Kamp et al., 2022; Switzerland, Knaus et al., 2021; Sweden, Lindström et al., 2007). The species has many traits (long-distance migrant, intermediate dispersal ratio, ground-nester, high annual fecundity, feeding on invertebrates) linked to negative trends, and it is probably that one or more of these species-specific characteristics are responsible of the observed negative trend in our study area. The Goldcrest experienced a general decline in Europe (PECBMS, 2021) as well as in Italy (MITO2000, 2021). It is a cold adapted and forest specialist species, and the combination of these two factors may be the cause of the decline (Lehikoinen et al., 2016; Gregory et al., 2019). Species of natural-open habitat, which represent nine of the 11 species living in high mountain areas, did not show a significant trend. The finding is in accordance with that reported in some European mountains during the period 2002-2014 (i.e. Alps, Apennines), although in other mountain areas, such as Fennoscandia and Iberia, bird species declined significantly (Lehikoinen et al., 2014, 2019). Indeed, mountain birds can differently respond to ecological drivers (e.g. climate change and land use changes), affecting local population trends and distribution (Bani et al., 2019; Lehikoinen et al., 2019).

Finally, we did not find a strong relationship between trends and the overall specialisation index. This result did not fully support findings highlighted in previous studies. For example, Morelli et al. (2020) underlined a negative relationship between the degree of specialisation and population trends for 139 species in Europe, especially in relation to nesting site specialisation. Similarly, Kamp et al. (2021) found a decline of specialist birds in relation to habitat breadth and diet breadth (note that categorisation of these traits differs from the approach adopted in this study). Bird communities are moving to assemblages composed by more generalist species that are nonrandomly replacing specialist ones (Le Viol et al., 2012), probably due to anthropogenic drivers such as habitat fragmentation that can more negatively affect specialists than generalists (Dondina et al., 2017). In our study, a signal that non-generalist species respond more adversely than generalist ones has been noted (Table 3.3D and Figure 3.3D).

3.4. Conclusions

The study provided an updating of long-term populations trends (1992-2019) for 76 common breeding birds in Lombardy using a statistical approach that allowed taking into account environmental bias, overdispersion and zero inflation. Zero-inflated models largely resulted the best modelling choice in order to predict yearly population indices, and we encourage a broader application in population trend analysis than their current employment. Overall, the bird conservation status in the region highlighted a favorable situation, with roughly three-quarters of the species showing positive or non-significant trends over the period. However, among the remnant species, 12 showed a decline greater than 50%, and 6 experienced a worrying population reduction greater than 80%, with the extreme drop of the Eurasian Skylark population (−99.65%). Identifying the causes of the observed trends, especially when dramatically negative, is the foundation of any management plan and conservation action. In this context, a functional approach linking the species traits with the population trends allowed us to identify the most threatened groups. We found a decrease of migrant birds, species with high annual fecundity and short incubation period. Plant-eaters, species feeding on invertebrates and ground-nesters also decreased. Farmland birds showed a negative trend, while woodland species resulted on increase. A weaker signal was found in relation to the species' mobility and the degree of specialisation. A trait-based approach should represent the starting point from which implementing studies that test specific hypotheses aimed at identifying the direct causes responsible of the observed population dynamics. Further studies should focus on investigation of the relationship between long-term trends and species traits at large spatial scales, and on quantifying the effects of specific drivers across multiple species sharing similar functional characteristics.

Supplementary materials

List of Contents

S3.1

Number of point counts surveyed per year.

Year of survey	N of point counts
1992	373
1993	-
1994	-
1995	650
1996	696
1997	-
1998	-
1999	1,103
2000	1,443
2001	993
2002	593
2003	603
2004	401
2005	1,092
2006	1,051
2007	730
2008	704
2009	758
2010	744
2011	898
2012	766
2013	795
2014	886
2015	805
2016	799
2017	542
2018	538
2019	542

S3.2

Monitoring programs from which bird data were derived.

Project name	Project goal	Years	Sampling design	Number of point counts
Long-term Monitoring Program	Long-term survey at regional scale	1992, 1995-1996, 2005-2006	Stratified random sampling according to the different landscapes in the Region.	2,756
		2007-2016	Stratified random sampling with random and fixed sampling units according to the different landscapes in the Region.	7,885
		2017-2019	Stratified random sampling with fixed sampling units according to the different landscapes in the Region.	1,622
Forest Biodiversity Survey	Survey of forest habitats	1999-2004	Random sampling in woodlands.	1,903
Lowland Biodiversity Survey	Survey of agricultural habitats	2000-2002	Random sampling in agricultural lands.	952
Regional Fauna Database	Survey at regional scale	2000-2006	Systematic stratified sampling at regional scale.	3,240
Greenway Project	Survey of Lombard Apennines to draw a greenway	2002-2003	Random sampling along river corridors in the Apennine zone.	147

S3.3

Consideration on detection bias issue in population trend analysis.

The detection bias (i.e. the distortion due to factors that affect the species detection probability) represents an important issue in several studies (e.g. see Dorazio, 2014; Guillera-Arroita, 2017; Fink et al., 2020). However, at times, it is an overrated aspect, used unnecessarily at the expense of simplicity and cheapness. Detection bias can depend on species extrinsic or intrinsic factors. Extrinsic factors do not depend on the species behavior, and they include the surveyor ability, meteorological conditions (e.g. wind direction), environmental noises (e.g. vehicle traffic, waterfalls). Another important extrinsic factor to be considered is the variation of the detection probability according to the distance of the individual from the observer (each species has its specific detection probability function, that describes the relationship between the individual-observer distance and the probability to detect an individual in a specific habitat). Intrinsic factors rely on species behavior that directly affect the detection probability at the sampling site. They depend on the conspicuousness of a species but can also be affected by extrinsic factors that can alter the species behavior. Accounting for all these potential sources of bias is crucial when the goal of a study is the assessment of the population density or an absolute magnitude, such as the population size, of a given species. To cope with such detection bias, multiple surveys of the same site along the same season or years are required (Royle & Dorazio, 2008).

When the goal of the study is the assessment of population trends (i.e. the relative variation of population size over time), the relative abundance is an adequate information, provided that it is estimated using data coming from a standardised sampling scheme. In this case, the sampling allows collecting representative information, comparable over time, since the survey technique does not change, and the same amount (or even proportion) of each habitat is taken into account in each year. This way, remaining the sampling design constant over time, the bias that would be produced by the differences in the species habitat-specific detection function, does not affect the trend estimation, since the relative abundance of a species is affected by the same detection bias over time.

However, when trend analysis relies on datasets deriving from many long-term monitoring programs, wherein the sampling design experienced some changes over time, or built using opportunistic data, the problem of obtaining a standardised-like dataset arise. The modelling approach applied in this research allows incorporating the detection bias arising from the species habitat-specific detection function, as well as the environmental bias among years (see Section

3.2.3; Tirozzi et al., 2022 and *Chapter 2*). Moreover, the effect of detection bias arising from the above-mentioned extrinsic factors, out of the detection probability function, could be difficult to manage (but see N-mixture models; Royle, 2004; Royle & Dorazio, 2008), but it can be considered negligible when statistical inferences are applied on large datasets (Dondina et al., 2017).

Finally, in the case of monitoring programs performed at large spatial scale, the use of the unlimited distance technique (Blondel et al., 1981), prevent from the introduction of further source of bias. Indeed, when several surveyors are involved in data collection, a rough estimate by eye of detection distance on the field (e.g. fixed radius) could differ among observers, leading to a bias that would be difficult to deal with. Therefore, in our opinion, it would be helpful to promote studies aimed at estimating the species habitat-specific detection function, along with the collection of data without distance limits. This is a crucial point to obtain population density or size.

S3.4

Life-history and ecological traits for the studied species. For the definition of levels and tresholds of each trait, see Section 3.2.4.1 in the main text. For traits not used in trait-based analysis: Fledging period (Short: ≤ 14, Intermediate: > 14 and < 26, Long: ≥ 26) and body mass (Low: ≤ 15.64, Intermediate: > 15.64 and < 149.10, High: ≥ 149.10) were derived from Storchová & Hořák (2018). Nesting habitat was derived from Pearman et al. (2014) and expert-based revised in relation to preferences of the species in the study area.

Species	Dispersal ratio	Annual fecundity	Incubation period	Fledging period	Migration strategy	Diet	Nest type	Altitudinal range (meters a.s.l.)	Landscape type	Nesting habitat	Overall specialisation index	Body mass
Great Cormorant (*Phalacrocorax carbo*)	Low	Low	Long	Long	Sedentary	Vertebrates	Elevated	Plain (≤200)	Farmland	Water	High	High
Black-crowned Night Heron (*Nycticorax nycticorax*)	High	Low	Long	Long	Long-distance	Vertebrates	Elevated	Plain (≤200)	Farmland	Water	Intermediate	High
Little Egret (*Egretta garzetta*)	High	Low	Long	Long	Short-distance	Omnivores	Elevated	Plain (≤200)	Farmland	Water	Intermediate	High
Grey Heron (*Ardea cinerea*)	High	Low	Long	Long	Short-distance	Vertebrates	Elevated	Plain (≤200)	Farmland	Water	Intermediate	High
Mallard (*Anas platyrhynchos*)	Low	High	Long	Long	Short-distance	Omnivores	Ground	Plain (≤200)	Farmland	Several	Low	High
Black Kite (*Milvus migrans*)	High	Low	Long	Long	Long-distance	Vertebrates	Elevated	Hill (201-700)	Several	Forest	Intermediate	High
Common Buzzard (*Buteo buteo*)	High	Low	Long	Long	Short-distance	Vertebrates	Elevated	Hill (201-700)	Several	Forest	Intermediate	High
Common Kestrel (*Falcon tinnunculus*)	High	Low	Long	Long	Short-distance	Vertebrates	Hole	Plain (≤200)	Farmland	Several	Low	High

S3.4 (cont.)

Common Quail (*Coturnix coturnix*)	Low	Intermediate	Long	Intermediate	Long-distance	Plant-eaters	Ground	Plain (≤200)	Farmland	Open	High	Intermediate
Common Pheasant (*Phasianus colchicus*)	Low	High	Long	Short	Sedentary	Plant-eaters	Ground	Plain (≤200)	Farmland	Forest	High	High
Common Moohren (*Gallinula chloropus*)	Low	High	Long	Long	Short-distance	Omnivores	Ground	Plain (≤200)	Farmland	Water	Intermediate	High
Northern Lapwing (*Vanellus vanellus*)	High	Low	Long	Long	Short-distance	Invertebrates	Ground	Plain (≤200)	Farmland	Open	High	High
Feral Pigeon (*Columba livia*)	Intermediate	Intermediate	Long	Long	Sedentary	Plant-eaters	Hole	Plain (≤200)	Farmland	Several	High	High
Common Wood Pigeon (*Columba palumbus*)	Intermediate	Low	Intermediate	Long	Short-distance	Plant-eaters	Elevated	Plain (≤200)	Farmland	Several	Intermediate	High
Eurasian Collared Dove (*Streptopelia decaocto*)	Intermediate	Intermediate	Intermediate	Intermediate	Sedentary	Plant-eaters	Elevated	Plain (≤200)	Farmland	Urban	High	High
European Turtle Dove (*Streptopelia turtur*)	Intermediate	Low	Intermediate	Intermediate	Long-distance	Plant-eaters	Elevated	Plain (≤200)	Farmland	Shrubs	High	Intermediate
Common Cuckoo (*Cuculus canorus*)	High	Intermediate	Short	Intermediate	Long-distance	Invertebrates	Elevated	Hill (201-700)	Several	Several	Intermediate	Intermediate
Common Swift (*Apus apus*)	High	Low	Long	Long	Long-distance	Invertebrates	Hole	Plain (≤200)	Several	Urban	High	Intermediate
European Bee-eater (*Merops apiaster*)	High	Intermediate	Long	Long	Long-distance	Invertebrates	Hole	Plain (≤200)	Farmland	Water	High	Intermediate

S3.4 (cont.)

Eurasian Wryneck (*Jinx torquilla*)	Low	Intermediate	Short	Intermediate	Long-distance	Invertebrates	Hole	Hill (201-700)	Farmland	Open	High	Intermediate
European Green Woodpecker (*Picus viridis*)	Low	Intermediate	Long	Intermediate	Sedentary	Invertebrates	Hole	Hill (201-700)	Several	Forest	Intermediate	High
Great Spotted Woodpecker (*Dendrocopos major*)	Intermediate	Intermediate	Short	Intermediate	Sedentary	Omnivores	Hole	Hill (201-700)	Several	Forest	Intermediate	Intermediate
Eurasian Skylark (*Alauda arvensis*)	Intermediate	High	Short	Intermediate	Short-distance	Omnivores	Ground	Plain (≤200)	Farmland	Open	Intermediate	Intermediate
Eurasian Crag Martin (*Ptyonoprogne rupestris*)	High	Intermediate	Intermediate	Long	Sedentary	Invertebrates	Hole	Low Mountain (701-1500)	Woodland	Urban	High	Intermediate
Barn Swallow (*Hirundo rustica*)	High	High	Intermediate	Intermediate	Long-distance	Invertebrates	Hole	Plain (≤200)	Farmland	Open	High	Intermediate
Common House Martin (*Delichon urbicum*)	High	Intermediate	Intermediate	Long	Long-distance	Invertebrates	Hole	Plain (≤200)	Several	Urban	High	Intermediate
Tree Pipit (*Anthus trivialis*)	Intermediate	Intermediate	Short	Short	Long-distance	Omnivores	Ground	High Mountain (>1500)	Several	Shrubs	Low	Intermediate
Water Pipit (*Anthus spinoletta*)	Intermediate	Intermediate	Intermediate	Intermediate	Short-distance	Invertebrates	Ground	High Mountain (>1500)	Natural-open habitat	Open	High	Intermediate
Western Yellow Wagtail (*Motacilla flava*)	Intermediate	Low	Short	Intermediate	Long-distance	Invertebrates	Ground	Plain (≤200)	Farmland	Open	Intermediate	Intermediate
Grey Wagtail (*Motacilla cinerea*)	Intermediate	Intermediate	Short	Short	Short-distance	Invertebrates	Hole	Low Mountain (701-1500)	Several	Water	Intermediate	Intermediate

S3.4 (cont.)

White Wagtail (*Motacilla alba*)	Intermediate	High	Short	Short	Short-distance	Invertebrates	Hole	Hill (201-700)	Several	Several	Low	Intermediate
Eurasian Wren (*Troglodytes troglodytes*)	Low	High	Intermediate	Intermediate	Short-distance	Omnivores	Hole	Low Mountain (701-1500)	Woodland	Forest	Intermediate	Low
Dunnock (*Prunella modularis*)	Low	Intermediate	Short	Short	Short-distance	Omnivores	Elevated	High Mountain (>1500)	Natural-open habitat	Shrubs	Intermediate	Intermediate
European Robin (*Erithacus rubecula*)	Low	Intermediate	Intermediate	Short	Short-distance	Omnivores	Hole	Low Mountain (701-1500)	Woodland	Forest	Low	Intermediate
Common Nigthingale (*Luscinia megarhynchos*)	Intermediate	Intermediate	Short	Short	Long-distance	Invertebrates	Ground	Plain (≤200)	Farmland	Shrubs	Low	Intermediate
Black Redstart (*Phoenicurus ochruros*)	High	Intermediate	Intermediate	Intermediate	Short-distance	Omnivores	Hole	High Mountain (>1500)	Natural-open habitat	Open	High	Intermediate
Common Redstart (*Phoenicurus Phoenicurus*)	Intermediate	High	Short	Intermediate	Long-distance	Invertebrates	Hole	Hill (201-700)	Woodland	Several	Low	Intermediate
European Stonechat (*Saxicola rubicola*)	Low	High	Intermediate	Short	Short-distance	Invertebrates	Ground	Plain (≤200)	Farmland	Open	High	Low
Northern Wheatear (*Oenanthe oenanthe*)	High	Intermediate	Short	Intermediate	Long-distance	Invertebrates	Hole	High Mountain (>1500)	Natural-open habitat	Open	Intermediate	Intermediate
Common Blackbird (*Turdus merula*)	Low	Intermediate	Short	Short	Sedentary	Omnivores	Elevated	Hill (201-700)	Several	Several	Low	Intermediate
Song Thrush (*Turdus philomelos*)	Low	Intermediate	Short	Short	Short-distance	Omnivores	Elevated	Low Mountain (701-1500)	Woodland	Forest	Intermediate	Intermediate

S3.4 (cont.)

Mistle Trush (*Turdus viscivorus*)	Intermediate	Intermediate	Intermediate	Short	Short-distance	Omnivores	Elevated	High Mountain (>1500)	Several	Shrubs	Intermediate	Intermediate
Cetti’s Warbler (*Cettia cetti*)	Low	Intermediate	Intermediate	Intermediate	Sedentary	Invertebrates	Elevated	Plain (≤200)	Farmland	Shrubs	Intermediate	Low
Melodius Warbler (*Hippolais polyglotta*)	Intermediate	Low	Short	Short	Long-distance	Invertebrates	Elevated	Plain (≤200)	Farmland	Shrubs	Low	Low
Lesser Whitethroat (*Curruca curruca*)	Intermediate	Low	Short	Short	Long-distance	Omnivores	Elevated	High Mountain (>1500)	Natural-open habitat	Shrubs	Low	Low
Eurasian Blackcap (*Sylvia atricapilla*)	Low	Low	Short	Short	Short-distance	Omnivores	Elevated	Hill (201-700)	Several	Several	Intermediate	Intermediate
Western Bonelli’s Warbler (*Phylloscopus bonelli*)	Intermediate	Intermediate	Short	Short	Long-distance	Invertebrates	Ground	Low Mountain (701-1500)	Woodland	Shrubs	Intermediate	Low
Common Chiffchaff (*Phylloscopus collybita*)	Intermediate	High	Intermediate	Intermediate	Short-distance	Invertebrates	Ground	Low Mountain (701-1500)	Woodland	Forest	Intermediate	Low
Goldcrest (*Regulus regulus*)	Intermediate	High	Intermediate	Intermediate	Short-distance	Invertebrates	Elevated	Low Mountain (701-1500)	Woodland	Forest	High	Low
Common Firecrest (*Regulus ignicapilla*)	Intermediate	High	Intermediate	Intermediate	Short-distance	Invertebrates	Elevated	Low Mountain (701-1500)	Woodland	Forest	Intermediate	Low
Spotted Flycatcher (*Muscicapa striata*)	High	Intermediate	Short	Short	Long-distance	Invertebrates	Elevated	Hill (201-700)	Several	Several	Intermediate	Intermediate
Long-tailed Tit (*Aegithalos caudatus*)	Intermediate	Intermediate	Intermediate	Intermediate	Sedentary	Omnivores	Elevated	Hill (201-700)	Several	Forest	Intermediate	Low
Marsh Tit (*Poecile palustris*)	Intermediate	Intermediate	Intermediate	Intermediate	Sedentary	Omnivores	Hole	Hill (201-700)	Woodland	Forest	Intermediate	Low

S3.4 (cont.)

Willow Tit (*Poecile montanus*)	Low	Intermediate	Intermediate	Intermediate	Sedentary	Omnivores	Hole	High Mountain (>1500)	Natural-open habitat	Shrubs	Intermediate	Low
European Crested Tit (*Lophophanes cristatus*)	Intermediate	Intermediate	Intermediate	Intermediate	Sedentary	Omnivores	Hole	Low Mountain (701-1500)	Woodland	Forest	High	Low
Coal Tit (*Periparus ater*)	Intermediate	High	Intermediate	Intermediate	Sedentary	Omnivores	Hole	Low Mountain (701-1500)	Woodland	Forest	Intermediate	Low
Eurasian Blue Tit (*Cyanistes caeruleus*	Intermediate	High	Intermediate	Intermediate	Sedentary	Omnivores	Hole	Hill (201-700)	Woodland	Forest	Intermediate	Low
Great Tit (*Parus major*)	Intermediate	High	Intermediate	Intermediate	Sedentary	Omnivores	Hole	Hill (201-700)	Several	Several	Intermediate	Intermediate
Eurasian Nuthatch (*Sitta europea*)	Intermediate	Intermediate	Intermediate	Intermediate	Sedentary	Invertebrates	Hole	Hill (201-700)	Woodland	Forest	Intermediate	Intermediate
Short-toed Treecreeper (*Certhia brachydactyla*)	Intermediate	High	Intermediate	Intermediate	Sedentary	Invertebrates	Hole	Hill (201-700)	Woodland	Forest	Intermediate	Low
Eurasian Golden Oriole (*Oriolus oriolus*)	High	Low	Intermediate	Intermediate	Long-distance	Omnivores	Elevated	Plain (≤200)	Farmland	Forest	Low	Intermediate
Red-backed Shrike (*Lanius collurio*)	Intermediate	Low	Intermediate	Intermediate	Long-distance	Omnivores	Elevated	Hill (201-700)	Several	Shrubs	Intermediate	Intermediate
Eurasian Jay (*Garrulus glandarius*)	Intermediate	Intermediate	Intermediate	Long	Sedentary	Omnivores	Elevated	Hill (201-700)	Woodland	Forest	Low	High
Eurasian Magpie (*Pica pica*)	Intermediate	Intermediate	Long	Long	Sedentary	Omnivores	Elevated	Plain (≤200)	Farmland	Several	Low	High
Carrion Crow (*Corvus corone*)	High	Low	Long	Long	Sedentary	Omnivores	Elevated	High Mountain (>1500)	Natural-open habitat	Several	Low	High

S3.4 (cont.)

Hooded Crow (*Corvus cornix*)	High	Low	Long	Long	Sedentary	Omnivores	Elevated	Plain (≤200)	Farmland	Several	Low	High
Common Starling (*Sturnus vulgaris*)	Intermediate	Intermediate	Short	Intermediate	Short-distance	Omnivores	Hole	Plain (≤200)	Farmland	Several	Intermediate	Intermediate
Italian Sparrow (*Passer italiae*)	Low	High	Short	Short	Sedentary	Plant-eaters	Hole	Plain (≤200)	Farmland	Urban	Low	Intermediate
Eurasian Tree Sparrow (*Passer montanus*)	Low	High	Short	Intermediate	Short-distance	Omnivores	Hole	Plain (≤200)	Farmland	Shrubs	Intermediate	Intermediate
Common Chaffinch (*Fringilla coelebs*)	Intermediate	Low	Short	Short	Short-distance	Omnivores	Elevated	Hill (201-700)	Several	Several	Low	Intermediate
European Serin (*Serinus serinus*)	Intermediate	Intermediate	Short	Intermediate	Short-distance	Plant-eaters	Elevated	Hill (201-700)	Several	Urban	Intermediate	Low
European Greenfinch (*Chloris chloris*)	Intermediate	Intermediate	Short	Short	Short-distance	Plant-eaters	Elevated	Plain (≤200)	Farmland	Urban	Intermediate	Intermediate
European Goldfinch (*Carduelis carduelis*)	Intermediate	Intermediate	Short	Intermediate	Short-distance	Plant-eaters	Elevated	Plain (≤200)	Farmland	Several	Intermediate	Low
Common Linnet (*Linaria cannabina*)	Intermediate	High	Short	Short	Sedentary	Plant-eaters	Elevated	High Mountain (>1500)	Natural-open habitat	Shrubs	High	Intermediate
Common Redpoll (*Acanthis flammea*)	Intermediate	Intermediate	Short	Short	Sedentary	Plant-eaters	Elevated	High Mountain (>1500)	Natural-open habitat	Shrubs	Low	Low
Eurasian Bullfinch (*Pyrrhula pyrrhula*)	Low	Intermediate	Short	Intermediate	Short-distance	Plant-eaters	Elevated	Low Mountain (701-1500)	Woodland	Forest	Low	Intermediate

S3.5

Cramer's V coefficients for the traits originally considered in the analyses. Statistically significant correlations (Chi-square test or Fisher's exact test) are in bold.

	Dispersal ratio	Annual fecundity	Incubation period	Fledging period	Migration strategy	Diet	Nest type	Altitudinal range	Landscape type	Nesting habitat	Overall specialisation index	Body mass
Dispersal ratio	1											
Annual fecundity	**0.31**	1										
Incubation period	**0.36**	**0.31**	1									
Fledging period	**0.41**	**0.33**	**0.63**	1								
Migration strategy	**0.26**	0.23	0.20	0.10	1							
Diet	**0.36**	**0.36**	**0.38**	**0.35**	**0.35**	1						
Nest type	0.15	**0.34**	0.17	0.21	0.21	0.29	1					
Altitudinal	0.19	0.24	**0.34**	**0.32**	0.23	0.23	0.24	1				
Landscape type	0.21	**0.31**	**0.39**	0.28	0.18	0.23	0.25	**0.81**	1			
Nesting habitat	0.31	0.25	**0.47**	**0.50**	**0.33**	**0.38**	**0.40**	**0.50**	**0.50**	1		
Overall specialisation index	0.13	0.10	**0.27**	**0.30**	0.16	**0.29**	0.18	0.26	0.21	**0.44**	1	
Body mass	**0.31**	**0.33**	**0.61**	**0.55**	**0.27**	**0.39**	0.19	**0.34**	**0.39**	**0.44**	0.16	1

S3.6

Explained deviance (%) and the Akaike Information Criterion (AIC) of the models performed for the 76 species under study. For zero-inflated GAMs are shown the deviance explained by the two components of the model. C = model with covariates dealing with environmental bias; ZIP = zero-inflated Poisson; ZINB = zero-inflated negative binomial; P = Poisson; NB = negative binomial; GAM = generalised additive model. For negative binomial models, values of the estimated dispersion parameter θ (the smaller θ, the larger overdispersion) are indicated in parentheses. High values of θ indicates the absence of overdispersion.

Species	Model	AIC	Explained deviance (%)	
Great Cormorant (*Phalacrocorax carbo*)	C-NB-GAM (0.284)	3,029.39		57.60
	C-ZINB-GAM (0.736)	3,076.70	Binomial	77.90
			Count	54.80
	C-ZIP-GAM	3,231.56	Binomial	61.80
			Count	59.70
	C-P-GAM	3,395.69		54.70
Black-crowned Night Heron (*Nycticorax nycticorax*)	C-NB-GAM (0.608)	6,480.73		54.80
	C-ZINB-GAM (1.179)	6,537.11	Binomial	89.00
			Count	42.40
	C-ZIP-GAM	6,730.28	Binomial	78.00
			Count	45.40
	C-P-GAM	6,921.94		49.60
Little Egret (*Egretta garzetta*)	C-NB-GAM (0.754)	9,928.53		57.60
	C-ZINB-GAM (1.092)	9,939.50	Binomial	92.40
			Count	42.20
	C-ZIP-GAM	10,388.91	Binomial	73.30
			Count	47.10
	C-P-GAM	10,690.01		52.30
Grey Heron (*Ardea cinerea*)	C-NB-GAM (1.668)	13,735.41		43.20
	C-ZINB-GAM (2.020)	13,754.99	Binomial	93.00
			Count	24.20
	C-ZIP-GAM	14,081.95	Binomial	84.30
			Count	25.30
	C-P-GAM	14,134.81		40.30
Mallard (*Anas platyrhynchos*)	C-ZINB-GAM (0.334)	11,911.70	Binomial	83.00
			Count	27.30
	C-NB-GAM (0.184)	11,951.06		45.00
	C-P-GAM	16,149.18		34.40
	C-ZIP-GAM			Not converged
Black Kite (*Milvus migrans*)	C-ZINB-GAM (1.595)	3,533.71	Binomial	60.30
			Count	21.80
	C-ZIP-GAM	3,554.90	Binomial	49.60
			Count	27.30
	C-NB-GAM (0.236)	3,563.95		25.50
	C-P-GAM	3,708.34		22.40

S3.6 (cont.)

Common Buzzard (*Buteo buteo*)	C-P-GAM	6,141.11		10.90
	C-ZIP-GAM	6,155.44	Binomial	50.70
			Count	9.10
	C-NB-GAM (1,144)	6,173.12		9.98
	C-ZINB-GAM (92,409)	6,173.28	Binomial	54.80
			Count	7.74
Common Kestrel (*Falcon tinnunculus*)	C-P-GAM	6,927.50		12.80
	C-NB-GAM (299,509)	6,929.30		12.70
	C-ZIP-GAM	7,031.40	Binomial	46.20
			Count	10.90
	C-ZINB-GAM (295,104)	7,045.20	Binomial	48.80
			Count	10.40
Common Quail (*Coturnix coturnix*)	C-ZIP-GAM	4,384.35	Binomial	62.40
			Count	30.90
	C-NB-GAM (0.805)	4,406.25		30.70
	C-ZINB-GAM (71,374)	4,407.33	Binomial	61.90
			Count	29.90
	C-P-GAM	4,432.33		28.10
Common Pheasant (*Phasianus colchicus*)	C-NB-GAM (1.884)	11,672.84		38.90
	C-ZIP-GAM	11,699.55	Binomial	73.20
			Count	29.50
	C-ZINB-GAM (9.601)	11,719.96	Binomial	74.50
			Count	28.70
	C-P-GAM	11,768.93		37.50
Common Moohren (*Gallinula chloropus*)	C-NB-GAM (3.303)	8,059.16		42.00
	C-P-GAM	8,069.28		40.90
	C-ZIP-GAM	8,082.19	Binomial	88.80
			Count	29.90
	C-ZINB-GAM (18.068)	8,096.48	Binomial	89.30
			Count	29.70
Northern Lapwing (*Vanellus vanellus*)	C-NB-GAM (0.315)	3,496.99		68.80
	C-ZINB-GAM (0.675)	3,514.25	Binomial	92.20
			Count	57.10
	C-ZIP-GAM	3,602.08	Binomial	81.80
			Count	63.30
	C-P-GAM	3,968.96		61.00
Feral Pigeon (*Columba livia*)	C-ZINB-GAM (0.473)	26,373.81	Binomial	89.30
			Count	24.50
	C-NB-GAM (0.380)	26,547.21		47.00
	C-ZIP-GAM	33,086.27	Binomial	29.00
			Count	36.70
	C-P-GAM	39,737.77		36.90
Common Wood Pigeon (*Columba palumbus*)	C-ZIP-GAM	16,727.40	Binomial	73.30
			Count	23.30
	C-ZINB-GAM (15.744)	16,751.67	Binomial	75.00
			Count	22.60
	C-NB-GAM	16,791.70		29.70
	C-P-GAM	16,829.58		29.10

S3.6 (cont.)

Eurasian Collared Dove (*Streptopelia decaocto*)	C-ZINB-GAM (4.220)	23,900.66	Binomial	85.50
			Count	37.80
	C-NB-GAM (2.668)	24,021.06		47.70
	C-ZIP-GAM	24,057.30	Binomial	74.60
			Count	38.50
	C-P-GAM	24,405.06		46.00
European Turtle Dove (*Streptopelia turtur*)	C-ZIP-GAM	12,102.23	Binomial	70.10
			Count	28.60
	C-ZINB-GAM (9.848)	12,110.22	Binomial	71.50
			Count	28.20
	C-NB-GAM (1.318)	12,185.88		33.60
	C-P-GAM	12,326.01		31.70
Common Cuckoo (*Cuculus canorus*)	C-ZIP-GAM	25,792.68	Binomial	80.70
			Count	14.70
	C-ZINB-GAM (336,562)	25,863.40	Binomial	80.10
			Count	14.10
	C-P-GAM	26,140.75		19.00
	C-NB-GAM (305,9509)	26,180.97		18.70
Common Swift (*Apus apus*)	C-ZINB-GAM (0.295)	40,080.10	Binomial	54.80
			Count	9.61
	C-NB-GAM (0.178)	40,556.48		14.40
	C-ZIP-GAM	55,397.13	Binomial	7.87
			Count	8.44
	C-P-GAM	79,149.04		14.80
European Bee-eater (*Merops apiaster*)	C-NB-GAM (0.073)	4,230.85		48.40
	C-ZINB-GAM (0.376)	4,286.48	Binomial	45.70
			Count	42.30
	C-ZIP-GAM	4,475.40	Binomial	14.30
			Count	55.90
	C-P-GAM	5,468.65		37.30
Eurasian Wryneck (*Jynx torquilla*)	C-ZIP-GAM	3,713.88	Binomial	63.40
			Count	28.00
	C-ZINB-GAM (66,017)	3,753.80	Binomial	64.10
			Count	26.60
	C-P-GAM	3,754.60		26.10
	C-NB-GAM (0.346)	4,277.52		26.30
European Green Woodpecker (*Picus viridis*)	C-P-GAM	7,913.30		17.60
	C-ZIP-GAM	7,931.24	Binomial	64.30
			Count	15.90
	C-NB-GAM (15,411)	7,997.53		16.10
	C-ZINB-GAM (905,764)	8,011.81	Binomial	63.80
			Count	13.50
Great Spotted Woodpecker (*Dendrocopos major*)	C-P-GAM	11,958.44		20.90
	C-NB-GAM (92,666)	12,021.31		20.20
	C-ZIP-GAM	12,023.01	Binomial	79.10
			Count	18.20
	C-ZINB-GAM (207,106)	12,076.00	Binomial	79.60
			Count	17.40

S3.6 (cont.)

Eurasian Skylark (*Alauda arvensis*)	C-ZIP-GAM	13,476.92	Binomial	77.60
			Count	45.00
	C-ZINB-GAM (14.493)	13,504.58	Binomial	78.70
			Count	44.50
	C-NB-GAM (2.362)	13,667.07		48.30
	C-P-GAM	13,742.54		47.00
Eurasian Crag Martin (*Ptyonoprogne rupestris*)	C-NB-GAM (0.159)	3,798.65		47.10
	C-ZINB-GAM (1.021)	3,833.38	Binomial	62.40
			Count	43.60
	C-ZIP-GAM	3,844.65	Binomial	40.00
			Count	49.90
	C-P-GAM	4,178.56		39.60
Barn Swallow (*Hirundo rustica*)	C-ZINB-GAM (0.802)	40,303.37	Binomial	87.20
			Count	25.20
	C-NB-GAM (0.708)	40,464.14		41.00
	C-ZIP-GAM	47,492.13	Binomial	31.40
			Count	26.10
	C-P-GAM	51,918.72		35.00
Common House Martin (*Delichon urbicum*)	C-ZINB-GAM (0.291)	23,845.97	Binomial	60.60
			Count	12.20
	C-NB-GAM (0.154)	24,040.40		18.30
	C-ZIP-GAM	27,742.22	Binomial	8.39
			Count	16.70
	C-P-GAM	36,579.74		17.00
Tree Pipit (*Anthus trivialis*)	C-ZIP-GAM	5,021.72	Binomial	93.80
			Count	47.20
	C-ZINB-GAM (259,222)	5,050.91	Binomial	93.60
			Count	46.50
	C-P-GAM	5,177.49		65.90
	C-NB-GAM (4.512)	5,224.74		66.50
Water Pipit (*Anthus spinoletta*)	C-ZINB-GAM (177,199)	3,707.63	Binomial	95.50
			Count	66.60
	C-P-GAM	3,715.80		84.60
	C-NB-GAM (11.8)	3,742.13		84.90
	C-ZIP-GAM			Not converged
Western Yellow Wagtail (*Motacilla flava*)	C-ZIP-GAM	11,274.22	Binomial	87.00
			Count	35.60
	C-ZINB-GAM (8.354)	11,290.24	Binomial	89.40
			Count	35.00
	C-NB-GAM (2.546)	11,421.31		54.40
	C-P-GAM	11,501.58		52.10
Grey Wagtail (*Motacilla cinerea*)	C-P-GAM	4,879.06		30.40
	C-ZIP-GAM	4,896.97	Binomial	87.20
			Count	24.40
	C-NB-GAM (32.599)	4,935.47		29.00
	C-ZINB-GAM (119,200)	4,960.33	Binomial	86.90
			Count	22.30

S3.6 (cont.)

White Wagtail (*Motacilla alba*)	C-P-GAM	11,209.53		20.40
	C-NB-GAM (34,911)	11,225.74		20.20
	C-ZIP-GAM	11,234.61	Binomial	75.80
			Count	19.90
	C-ZINB-GAM (125,329)	11,264.26	Binomial	75.30
			Count	19.50
Eurasian Wren (*Troglodytes troglodytes*)	C-ZIP-GAM	17,495.73	Binomial	90.50
			Count	18.30
	C-ZINB-GAM (96,764)	17,517.74	Binomial	90.10
			Count	18.10
	C-P-GAM	17,682.89		39.60
	C-NB-GAM (10.698)	17,943.17		38.30
Dunnock (*Prunella modularis*)	C-P-GAM	4,894.66		69.90
	C-ZIP-GAM	4,902.03	Binomial	96.50
			Count	40.50
	C-NB-GAM (90,289)	4,908.35		69.70
	C-ZINB-GAM (290,852)	4,923.56	Binomial	96.30
			Count	40.00
European Robin (*Erithacus rubecula*)	C-ZIP-GAM	16,251.34	Binomial	93.40
			Count	33.30
	C-ZINB-GAM (93,303)	16,273.17	Binomial	93.30
			Count	33.30
	C-P-GAM	16,634.23		52.80
	C-NB-GAM (87.877)	16,645.47		52.80
Common Nigthingale (*Luscinia megarhynchos*)	C-ZIP-GAM	25,515.68	Binomial	89.60
			Count	33.50
	C-ZINB-GAM (213,716)	25,573.05	Binomial	89.20
			Count	33.70
	C-P-GAM	26,089.01		52.70
	C-NB-GAM (690,471)	26,114.85		52.50
Black Redstart (*Phoenicurus ochruros*)	C-ZIP-GAM	7,593.68	Binomial	88.70
			Count	41.10
	C-ZINB-GAM (387,811)	7,603.81	Binomial	89.00
			Count	40.80
	C-P-GAM	7,635.01		56.00
	C-NB-GAM (141,339)	7,636.27		56.00
Common Redstart (*Phoenicurus Phoenicurus*)	C-ZIP-GAM	11,928.43	Binomial	88.20
			Count	23.10
	C-ZINB-GAM (38,5821)	11,948.16	Binomial	88.10
			Count	22.90
	C-P-GAM	12,013.63		34.20
	C-NB-GAM (229,589)	12,021.75		34.10
European Stonechat (*Saxicola rubicola*)	C-ZIP-GAM	5,151.91	Binomial	54.40
			Count	33.40
	C-ZINB-GAM (32,713)	5,180.57	Binomial	53.50
			Count	32.40
	C-NB-GAM (0.629)	5,181.02		29.10
	C-P-GAM	5,224.84		26.50

S3.6 (cont.)

Northern Wheatear (*Oenanthe oenanthe*)	C-P-GAM	2,515.16		77.80
	C-ZIP-GAM	2,519.88	Binomial	97.90
			Count	55.00
	C-NB-GAM (41,460)	2,526.04		77.30
	C-ZINB-GAM (762,946)	2,536.48	Binomial	97.90
			Count	54.30
Common Blackbird (*Turdus merula*)	C-ZIP-GAM	45,864.32	Binomial	81.20
			Count	22.20
	C-ZINB-GAM (1,720,556)	45,714.74	Binomial	81.00
			Count	22.00
	C-P-GAM	45,832.06		28.00
	C-NB-GAM (2,692,926)	45,851.83		27.80
Song Thrush (*Turdus philomelos*)	C-ZIP-GAM	6,540.94	Binomial	92.90
			Count	23.60
	C-ZINB-GAM (129,475)	6,648.63	Binomial	91.90
			Count	20.00
	C-P-GAM	6,674.23		44.40
	C-NB-GAM (3.090)	6,806.35		43.70
Mistle Thrush (*Turdus viscivorus*)	C-ZIP-GAM	2,902.87	Binomial	88.20
			Count	24.30
	C-ZINB-GAM (1,001,115)	2,925.33	Binomial	89.50
			Count	19.10
	C-P-GAM	2,932.33		46.30
	C-NB-GAM (1.580)	2,934.39		48.10
Cetti's Warbler (*Cettia cetti*)	C-ZIP-GAM	6,450.23	Binomial	84.50
			Count	37.30
	C-ZINB-GAM (8.695)	6,468.52	Binomial	84.60
			Count	37.00
	C-NB-GAM (0.996)	6,486.37		46.30
	C-P-GAM	6,565.63		43.30
Melodius Warbler (*Hippolais polyglotta*)	C-ZIP-GAM	4,529.84	Binomial	65.30
			Count	31.10
	C-NB-GAM (0.435)	4,534.72		31.40
	C-ZINB-GAM (17.146)	4,555.42	Binomial	64.90
			Count	29.30
	C-P-GAM	4,585.81		28.70
Lesser Whitethroat (*Curruca curruca*)	C-ZIP-GAM	3,000.43	Binomial	91.80
			Count	31.80
	C-ZINB-GAM (66,638)	3,014.07	Binomial	91.10
			Count	32.20
	C-P-GAM	3,020.25		61.30
	C-NB-GAM (1.63)	3,042.61		63.10
Eurasian Blackcap (*Sylvia atricapilla*)	C-ZIP-GAM	48,060.23	Binomial	88.60
			Count	21.50
	C-ZINB-GAM (595,897)	48,132.52	Binomial	87.20
			Count	20.80
	C-P-GAM	48,209.62		29.30
	C-NB-GAM (566,535)	48,282.73		28.80

S3.6 (cont.)

Western Bonelli’s Warbler (*Phylloscopus bonelli*)	C-ZINB-GAM (3.52)	6,627.47	Binomial	71.00
			Count	41.40
	C-NB-GAM (0.405)	6,726.72		57.80
	C-P-GAM	7,211.36		51.50
	C-ZIP-GAM			Not converged
Common Chiffchaff (*Phylloscopus collybita*)	C-ZIP-GAM	13,150.88	Binomial	91.90
			Count	27.70
	C-ZINB-GAM (58,861)	13,172.84	Binomial	91.50
			Count	28.30
	C-P-GAM	13,329.43		50.40
	C-NB-GAM (17,966)	13,330.12		50.40
Goldcrest (*Regulus regulus*)	C-ZIP-GAM	5,562.70	Binomial	91.80
			Count	47.30
	C-P-GAM	5,640.06		59.70
	C-ZINB-GAM (25.475)	5,643.97	Binomial	91.30
			Count	45.40
	C-NB-GAM (2.305)	5,674.59		60.90
Common Firecrest (*Regulus ignicapilla*)	C-ZIP-GAM	4,838.47	Binomial	72.80
			Count	40.30
	C-ZINB-GAM (21,117)	4,900.82	Binomial	67.80
			Count	40.30
	C-NB-GAM (0.671)	4,902.20		45.40
	C-P-GAM	4,916.71		42.10
Spotted Flycatcher (*Muscicapa striata*)	C-P-GAM	13,412.03		21.40
	C-ZIP-GAM	13,427.06	Binomial	79.10
			Count	15.80
	C-NB-GAM	13,429.56		21.10
	C-ZINB-GAM (1,537,699)	13,502.62	Binomial	81.80
			Count	14.20
Long-tailed Tit (*Aegithalos caudatus*)	C-P-GAM	8,768.01		17.80
	C-NB-GAM (2,531,114)	8,771.23		17.80
	C-ZIP-GAM	8,855.56	Binomial	71.00
			Count	12.60
	C-ZINB-GAM (88,403)	8,861.84	Binomial	71.30
			Count	12.40
Marsh Tit (*Poecile palustris*)	C-ZIP-GAM	6,839.02	Binomial	86.00
			Count	31.90
	C-ZINB-GAM (30.045)	6,877.20	Binomial	86.00
			Count	30.70
	C-NB-GAM (1.056)	7,001.02		45.80
	C-P-GAM	7,057.28		42.80
Willow Tit (*Poecile montanus*)	C-ZIP-GAM	2,750.03	Binomial	89.80
			Count	32.40
	C-ZINB-GAM (255,855)	2,760.22	Binomial	90.00
			Count	30.70
	C-NB-GAM (1.532)	2,810.90		58.80
	C-P-GAM	2,827.38		55.90

S3.6 (cont.)

European Crested Tit (*Lophophanes cristatus*)	C-ZIP-GAM	4,225.32	Binomial	86.30
			Count	46.30
	C-ZINB-GAM (28.989)	4,240.97	Binomial	86.30
			Count	46.00
	C-NB-GAM	4,298.49		58.00
	C-P-GAM	4,372.76		54.00
Coal Tit (*Periparus ater*)	C-ZIP-GAM	13,899.30	Binomial	89.50
			Count	42.20
	C-ZINB-GAM (26.712)	13,939.49	Binomial	90.30
			Count	41.80
	C-NB-GAM (5.177)	14,211.60		67.50
	C-P-GAM	14,249.30		66.40
Eurasian Blue Tit (*Cyanistes caeruleus*)	C-ZIP-GAM	13,764.00	Binomial	79.50
			Count	19.70
	C-ZINB-GAM (166.830)	13,844.32	Binomial	78.30
			Count	18.70
	C-P-GAM	13,997.30		32.90
	C-NB-GAM ((2.661)	14,038.47		33.20
Great Tit (*Parus major*)	C-ZIP-GAM	32,209.26	Binomial	81.10
			Count	13.50
	C-ZINB-GAM (122,665)	32,248.47	Binomial	80.50
			Count	13.30
	C-P-GAM	32,296.40		21.80
	C-NB-GAM (56,747)	32,317.42		21.60
Eurasian Nuthatch (*Sitta europaea*)	C-ZIP-GAM	4,736.48	Binomial	85.30
			Count	32.00
	C-ZINB-GAM (2,673)	4,833.81	Binomial	84.30
			Count	28.60
	C-P-GAM	4,887.27		38.50
	C-NB-GAM (0.821)	4,914.27		40.40
Short-toed Treecreeper (*Certhia brachydactyla*)	C-ZIP-GAM	2,952.57	Binomial	91.30
			Count	36.70
	C-P-GAM	2,956.61		45.60
	C-NB-GAM (4.807)	2,965.82		46.00
	C-ZINB-GAM (67,079)	2,973.61	Binomial	91.00
			Count	35.70
Eurasian Golden Oriole (*Oriolus oriolus*)	C-ZIP-GAM	9,430.02	Binomial	85.30
			Count	30.50
	C-ZINB-GAM (94,932)	9,466.67	Binomial	83.50
			Count	31.40
	C-P-GAM	9,514.51		40.40
	C-NB-GAM	9,533.47		41.10
Red-backed Shrike (*Lanius collurio*)	C-P-GAM	6,147.40		23.20
	C-NB-GAM (7.766)	6,153.75		23.20
	C-ZIP-GAM	6,172.55	Binomial	69.70
			Count	25.40
	C-ZINB-GAM (131,338)	6,189.26	Binomial	70.30
			Count	25.10

S3.6 (cont.)

Eurasian Jay (*Garrulus glandarius*)	C-P-GAM	9,552.70		29.40
	C-NB-GAM (453,507)	9,578.89		28.90
	C-ZIP-GAM	9,589.78	Binomial	85.80
			Count	20.40
	C-ZINB-GAM (132,878)	9,836.27	Binomial	84.30
			Count	16.00
Eurasian Magpie (*Pica pica*)	C-ZIP-GAM	12,836.52	Binomial	89.50
			Count	27.70
	C-ZINB-GAM (16.487)	12,858.11	Binomial	89.80
			Count	27.40
	C-NB-GAM (4.266)	12,882.85		39.50
	C-P-GAM	12,897.32		28.70
Carrion Crow (*Corvus corone*)	C-ZIP-GAM	3,261.47	Binomial	86.70
			Count	45.70
	C-ZINB-GAM (2.416)	3,264.04	Binomial	89.60
			Count	41.50
	C-NB-GAM (0.732)	3,348.44		55.00
	C-P-GAM	3,391.32		53.00
Hooded Crow (*Corvus cornix*)	C-ZINB-GAM (2.221)	47,078.79	Binomial	91.40
			Count	32.30
	C-NB-GAM (2.184)	47,142.09		39.20
	C-ZIP-GAM	51,689.46	Binomial	75.30
			Count	29.90
	C-P-GAM	51,896.28		36.60
Common Starling (*Sturnus vulgaris*)	C-ZINB-GAM (3.064)	32,012.92	Binomial	97.10
			Count	32.40
	C-NB-GAM (3.011)	32,013.45		48.00
	C-ZIP-GAM	33,407.99	Binomial	94.80
			Count	29.90
	C-P-GAM	33,442.58		43.70
Italian Sparrow (*Passer italiae*)	C-ZIP-GAM	30,881.22	Binomial	97.20
			Count	39.00
	C-ZINB-GAM (21.534)	30,913.60	Binomial	96.90
			Count	39.80
	C-P-GAM	30,937.87		48.90
	C-NB-GAM (19.285)	30,944.07		49.20
Eurasian Tree Sparrow (*Passer montanus*)	C-ZIP-GAM	17,891.27	Binomial	94.90
			Count	21.90
	C-P-GAM	17,912.57		33.90
	C-ZINB-GAM (658,979)	17,934.73	Binomial	94.50
			Count	21.40
	C-NB-GAM (353,604)	17,953.29		33.50
Common Chaffinch (*Fringilla coelebs*)	C-ZIP-GAM	41,633.72	Binomial	79.60
			Count	24.20
	C-ZINB-GAM (3,555,510)	41,665.93	Binomial	79.80
			Count	24.00
	C-P-GAM	43,408.70		41.10
	C-NB-GAM (785,815)	43,430.87		40.90

S3.6 (cont.)

European Serin (*Serinus serinus*)	C-ZIP-GAM	15,368.22	Binomial	87.80
			Count	26.30
	C-ZINB-GAM (63.969)	15,437.27	Binomial	87.50
			Count	25.90
	C-NB-GAM	15,962.71		35.20
	C-P-GAM	16,008.36		34.40
European Greenfinch (*Chloris chloris*)	C-ZINB-GAM (2.639)	16,415.30	Binomial	68.10
			Count	23.10
	C-NB-GAM (0.902)	16,485.18		30.10
	C-ZIP-GAM	16,532.33	Binomial	57.40
			Count	25.00
	C-P-GAM	17,042.48		27.50
European Goldfinch (*Carduelis carduelis*)	C-ZINB-GAM (1.775)	19,064.10	Binomial	52.90
			Count	19.00
	C-NB-GAM (0.623)	19,084.07		21.50
	C-ZIP-GAM	19,157.66	Binomial	34.40
			Count	23.40
	C-P-GAM	19,939.70		20.10
Common Linnet (*Linaria cannabina*)	C-ZINB-GAM (1.336)	3,209.39	Binomial	92.10
			Count	39.90
	C-ZIP-GAM	3,253.82	Binomial	82.90
			Count	45.90
	C-NB-GAM (0.473)	3,275.33		65.90
	C-P-GAM	3,458.20		59.20
Common Redpoll (*Acanthis flammea*)	C-ZINB-GAM (1.190)	3,421.109	Binomial	94.20
			Count	29.10
	C-ZIP-GAM	3,466.635	Binomial	81.70
			Count	41.00
	C-NB-GAM (0.592)	3,515.496		69.00
	C-P-GAM	3,699.918		62.20
Eurasian Bullfinch (*Pyrrhula pyrrhula*)	C-ZIP-GAM	3,601.80	Binomial	89.30
			Count	29.30
	C-P-GAM	3,617.81		49.20
	C-NB-GAM (2.084)	3,627.82		50.60
	C-ZINB-GAM (87,108)	3,631.22	Binomial	87.60
			Count	28.70

S3.7

Summary of models performed for each species. In each table the common and scientific name of the species, the type of model and summary statistics for both parametric and smooth terms are shown. Edf = estimated degree of freedom.

Great Cormorant (*Phalacrocorax carbo*) — Model C-NB-GAM				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−7.963	1.052	−7.568	<0.001
Year 2005	0.459	0.390	1.178	0.239
Year 2006	−0.583	0.620	−0.941	0.347
Year 2007	0.709	0.441	1.607	0.108
Year 2008	0.954	0.403	2.369	0.018
Year 2009	1.698	0.365	4.655	<0.001
Year 2010	1.540	0.387	3.978	<0.001
Year 2011	1.899	0.371	5.120	<0.001
Year 2012	1.453	0.383	3.797	<0.001
Year 2013	1.709	0.374	4.575	<0.001
Year 2014	2.574	0.349	7.374	<0.001
Year 2015	2.743	0.348	7.888	<0.001
Year 2016	2.240	0.382	5.872	<0.001
Year 2017	2.208	0.378	5.839	<0.001
Year 2018	2.382	0.374	6.370	<0.001
Year 2019	−0.126	0.092	−1.364	0.172
Sin	0.232	0.140	1.661	0.097
Cos	−7.963	1.052	−7.568	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		2.015	242.782	<0.001
s(Elevation)		2.488	168.363	<0.001
s(Slope)		0.756	2.814	0.051
s(C110)		2.062	76.111	<0.001
s(C112)		1.024	28.223	<0.001
s(C211)		1.502	65.433	<0.001
s(C213)		1.020	30.178	<0.001
s(C221)		0.606	1.369	0.129
s(C222)		0	0	0.645
s(C223)		0	0	0.369
s(C224)		0.924	11.020	<0.001
s(C231)		1.095	33.632	<0.001
s(C311)		2.332	34.278	<0.001
s(C312)		0.693	1.728	0.114
s(C313)		0.910	8.012	0.002
s(C320)		0	0	0.747
s(C321)		0.358	0.451	0.259
s(C330)		0	0	0.396
s(C410)		0.987	43.675	<0.001
s(C511)		0.622	1.477	0.118

Black-crowned Night Heron (*Nycticorax nycticorax*) — Model C-NB-GAM				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−7.401	1.021	−7.247	<0.001
Year 1995	−2.113	0.289	−7.302	<0.001
Year 1996	−1.349	0.226	−5.956	<0.001
Year 1999	−1.293	0.223	−5.810	<0.001
Year 2000	−0.766	0.195	−3.923	<0.001
Year 2001	−1.083	0.201	−5.375	<0.001
Year 2002	−1.883	0.272	−6.922	<0.001
Year 2003	−2.128	0.320	−6.640	<0.001
Year 2004	−1.573	0.331	−4.745	<0.001
Year 2005	−1.655	0.216	−7.646	<0.001
Year 2006	−1.557	0.228	−6.814	<0.001
Year 2007	−1.486	0.240	−6.187	<0.001
Year 2008	−1.230	0.230	−5.353	<0.001
Year 2009	−1.734	0.237	−7.304	<0.001
Year 2010	−0.921	0.210	−4.376	<0.001
Year 2011	−1.282	0.225	−5.700	<0.001
Year 2012	−2.048	0.272	−7.539	<0.001
Year 2013	−1.329	0.232	−5.729	<0.001
Year 2014	−1.261	0.232	−5.440	<0.001
Year 2015	−1.250	0.226	−5.540	<0.001
Year 2016	−1.703	0.249	−6.836	<0.001
Year 2017	−1.621	0.305	−5.323	<0.001
Year 2018	−1.914	0.296	−6.457	<0.001
Year 2019	−2.487	0.378	−6.573	<0.001
Sin	0.091	0.056	1.610	0.107
Cos	−0.076	0.086	−0.880	0.379
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		1.954	114.550	<0.001
s(Elevation)		1.017	58.680	<0.001
s(Slope)		0.284	0.355	0.257
s(C110)		1.016	19.906	<0.001
s(C112)		0.122	0.143	0.275
s(C211)		0.992	7.735	0.003
s(C213)		2.681	216.444	<0.001
s(C221)		0.798	3.332	0.040
s(C222)		0.865	5.404	0.012
s(C223)		0.688	0.418	0.436
s(C224)		0.011	0.009	0.351
s(C231)		0.914	7.470	0.003
s(C311)		0.001	0.001	0.166
s(C312)		0	0	0.696
s(C313)		0	0	0.577
s(C320)		0.002	0.001	0.392
s(C321)		0.631	1.035	0.200
s(C330)		0.501	0.865	0.187
s(C410)		1.007	132.680	<0.001
s(C511)		0	0	0.423

Little Egret (*Egretta garzetta*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−11.318	1.510	−7.497	<0.001
Year 1995	−0.667	0.272	−2.452	0.014
Year 1996	−0.386	0.253	−1.526	0.127
Year 1999	0.282	0.234	1.204	0.229
Year 2000	0.722	0.220	3.276	0.001
Year 2001	0.211	0.225	0.938	0.348
Year 2002	0.399	0.244	1.635	0.102
Year 2003	−0.416	0.278	−1.497	0.134
Year 2004	−0.391	0.325	−1.201	0.230
Year 2005	0.087	0.228	0.381	0.703
Year 2006	0.245	0.231	1.061	0.289
Year 2007	0.064	0.247	0.259	0.795
Year 2008	0.228	0.243	0.939	0.348
Year 2009	0.302	0.233	1.296	0.195
Year 2010	0.574	0.230	2.490	0.013
Year 2011	0.479	0.234	2.046	0.041
Year 2012	−0.126	0.252	−0.498	0.618
Year 2013	0.758	0.231	3.282	0.001
Year 2014	0.671	0.235	2.857	0.004
Year 2015	0.595	0.234	2.546	0.011
Year 2016	0.735	0.232	3.173	0.002
Year 2017	0.598	0.258	2.319	0.020
Year 2018	0.326	0.258	1.264	0.206
Year 2019	0.375	0.260	1.442	0.149
Sin	0.013	0.043	0.296	0.767
Cos	−0.055	0.067	−0.828	0.408
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		1.857	98.662	<0.001
s(Elevation)		1.005	102.320	<0.001
s(Slope)		0.942	10.682	<0.001
s(C110)		1.171	71.180	<0.001
s(C112)		0.985	20.906	0
s(C211)		0.001	0	0.795
s(C213)		2.815	521.595	<0.001
s(C221)		0.768	2.776	0.057
s(C222)		0.783	3.110	0.046
s(C223)		0	0	0.579
s(C224)		0.001	0	0.593
s(C231)		0.943	9.713	0.001
s(C311)		0	0	0.893
s(C312)		0.001	0	0.462
s(C313)		0.831	3.812	0.032
s(C320)		0	0	0.522
s(C321)		0.759	2.934	0.049
s(C330)		0.988	38.116	<0.001
s(C410)		0.424	0.775	0.176
s(C511)		1.014	111.684	<0.001

Grey Heron (*Ardea cinerea*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−9.742	1.568	−6.213	<0.001
Year 1995	0.046	0.221	0.207	0.836
Year 1996	0.269	0.211	1.278	0.201
Year 1999	0.814	0.199	4.091	<0.001
Year 2000	0.886	0.193	4.593	<0.001
Year 2001	0.947	0.193	4.910	<0.001
Year 2002	0.637	0.214	2.973	0.003
Year 2003	0.776	0.213	3.646	<0.001
Year 2004	0.700	0.236	2.968	0.003
Year 2005	0.855	0.192	4.446	<0.001
Year 2006	0.762	0.196	3.895	<0.001
Year 2007	0.452	0.211	2.147	0.032
Year 2008	0.538	0.209	2.577	0.010
Year 2009	0.628	0.202	3.110	0.002
Year 2010	0.590	0.204	2.890	0.004
Year 2011	0.810	0.200	4.050	<0.001
Year 2012	0.635	0.206	3.085	0.002
Year 2013	0.910	0.199	4.571	<0.001
Year 2014	0.909	0.201	4.525	<0.001
Year 2015	0.743	0.202	3.669	<0.001
Year 2016	0.847	0.202	4.196	<0.001
Year 2017	0.793	0.217	3.661	<0.001
Year 2018	0.505	0.221	2.287	0.022
Year 2019	0.621	0.219	2.838	0.005
Sin	0.003	0.031	0.105	0.916
Cos	0.015	0.047	0.326	0.744
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		2.935	76.038	<0.001
s(Elevation)		2.867	225.553	<0.001
s(Slope)		2.795	31.002	<0.001
s(C110)		1.235	93.546	<0.001
s(C112)		1.021	28.564	<0.001
s(C211)		0.821	3.683	0.025
s(C213)		2.738	162.063	<0.001
s(C221)		0.640	1.695	0.102
s(C222)		0.877	6.600	0.006
s(C223)		0.006	0.004	0.393
s(C224)		2.408	28.354	<0.001
s(C231)		0.019	0.013	0.343
s(C311)		2.739	27.867	<0.001
s(C312)		0.829	3.816	0.031
s(C313)		0.416	0.676	0.200
s(C320)		0.746	2.794	0.052
s(C321)		0.538	1.386	0.108
s(C330)		0	0	0.472
s(C410)		0.980	38.584	<0.001
s(C511)		0.911	9.891	<0.001

Mallard (*Anas platyrhynchos*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.811	0.022	−36.330	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.991	2248.900	<0.001
s(Urb$_{2500}$)		2.949	322.900	<0.001
s(For$_{2500}$)		2.979	330.900	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−4.313	0.399	−10.820	<0.001
Year 1995	0.847	0.388	2.183	0.029
Year 1996	0.758	0.394	1.926	0.054
Year 1999	1.381	0.370	3.728	<0.001
Year 2000	1.628	0.363	4.481	<0.001
Year 2001	1.985	0.361	5.491	<0.001
Year 2002	1.766	0.388	4.549	<0.001
Year 2003	1.581	0.386	4.093	<0.001
Year 2004	0.485	0.468	1.035	0.301
Year 2005	1.558	0.364	4.275	<0.001
Year 2006	1.724	0.364	4.738	<0.001
Year 2007	1.533	0.380	4.037	<0.001
Year 2008	1.464	0.382	3.837	<0.001
Year 2009	2.148	0.368	5.845	<0.001
Year 2010	1.987	0.369	5.385	<0.001
Year 2011	2.040	0.369	5.533	<0.001
Year 2012	2.166	0.370	5.848	<0.001
Year 2013	2.034	0.368	5.529	<0.001
Year 2014	1.764	0.374	4.714	<0.001
Year 2015	2.478	0.366	6.766	<0.001
Year 2016	2.020	0.372	5.435	<0.001
Year 2017	1.934	0.387	4.999	<0.001
Year 2018	1.900	0.385	4.930	<0.001
Year 2019	2.269	0.380	5.970	<0.001
Sin	0.026	0.048	0.537	0.591
Cos	0.052	0.073	0.705	0.481
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.937	58.503	<0.001
s(Elevation)		1.458	45.520	<0.001
s(Slope)		2.373	22.097	<0.001
s(C110)		2.791	186.880	<0.001
s(C112)		2.119	96.149	<0.001
s(C211)		2.036	158.817	<0.001
s(C213)		2.211	28.997	<0.001
s(C221)		0.988	39.576	<0.001
s(C222)		0.001	0.000	0.840
s(C223)		0.897	8.025	0.003
s(C224)		0.980	26.780	<0.001
s(C231)		1.952	118.316	<0.001
s(C311)		2.188	163.735	<0.001
s(C312)		0.910	7.923	0.003
s(C313)		1.071	40.083	<0.001
s(C320)		0.984	29.452	<0.001
s(C321)		0.720	1.930	0.099
s(C330)		0.620	1.292	0.147
s(C410)		0.918	9.850	0.001
s(C511)		2.783	64.860	<0.001

Black Kite (*Milvus migrans*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.105	0.027	−77.000	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.210	656.520	<0.001
s(Urb$_{2500}$)		1.040	47.190	<0.001
s(For$_{2500}$)		2.992	1,251.260	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.701	0.394	−6.858	<0.001
Year 1995	1.539	0.420	3.667	<0.001
Year 1996	0.360	0.466	0.771	0.441
Year 1999	0.591	0.416	1.422	0.155
Year 2000	0.626	0.409	1.529	0.126
Year 2001	0.281	0.448	0.627	0.530
Year 2002	0.037	0.545	0.067	0.946
Year 2003	0.210	0.493	0.427	0.669
Year 2004	0.860	0.494	1.741	0.082
Year 2005	0.099	0.457	0.216	0.829
Year 2006	0.498	0.421	1.184	0.237
Year 2007	0.028	0.495	0.057	0.954
Year 2008	−0.171	0.519	−0.328	0.743
Year 2009	0.407	0.459	0.887	0.375
Year 2010	0.352	0.461	0.764	0.445
Year 2011	−0.826	0.530	−1.560	0.119
Year 2012	0.172	0.459	0.375	0.708
Year 2013	−0.007	0.482	−0.014	0.989
Year 2014	0.369	0.457	0.807	0.420
Year 2015	−0.050	0.482	−0.104	0.917
Year 2016	0.065	0.495	0.131	0.896
Year 2017	−0.387	0.571	−0.679	0.497
Year 2018	−0.200	0.534	−0.375	0.708
Year 2019	−0.141	0.532	−0.265	0.791
Sin	0.106	0.078	1.368	0.171
Cos	−0.111	0.118	−0.941	0.347
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.952	49.583	<0.001
s(Elevation)		1.284	41.739	<0.001
s(Slope)		0.642	1.655	0.098
s(C110)		1.049	27.820	<0.001
s(C112)		0.983	20.901	<0.001
s(C211)		1.278	42.891	<0.001
s(C213)		0.952	12.459	<0.001
s(C221)		0.890	7.124	0.005
s(C222)		0	0	0.863
s(C223)		0	0	0.693
s(C224)		0.320	0.446	0.236
s(C231)		0	0	0.334
s(C311)		1.455	53.163	<0.001
s(C312)		0.957	11.462	<0.001
s(C313)		1.021	26.835	<0.001
s(C320)		0.670	1.828	0.097
s(C321)		0	0	0.889
s(C330)		0	0	0.883
s(C410)		0	0	0.759
s(C511)		0.942	14.729	<0.001

Common Buzzard (*Buteo buteo*) — Model C-P-GAM				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−4.698	0.451	−10.414	<0.001
Year 1995	0.617	0.517	1.194	0.232
Year 1996	0.373	0.527	0.708	0.479
Year 1999	1.368	0.463	2.956	0.003
Year 2000	1.442	0.459	3.141	0.002
Year 2001	1.302	0.469	2.775	0.006
Year 2002	1.676	0.472	3.554	<0.001
Year 2003	1.152	0.496	2.322	0.020
Year 2004	1.499	0.499	3.007	0.003
Year 2005	1.061	0.476	2.232	0.026
Year 2006	1.292	0.468	2.759	0.006
Year 2007	0.554	0.513	1.080	0.280
Year 2008	1.002	0.496	2.021	0.043
Year 2009	0.996	0.494	2.016	0.044
Year 2010	1.234	0.484	2.553	0.011
Year 2011	0.762	0.494	1.544	0.123
Year 2012	0.971	0.490	1.980	0.048
Year 2013	1.752	0.469	3.737	<0.001
Year 2014	1.180	0.485	2.435	0.015
Year 2015	1.488	0.476	3.124	0.002
Year 2016	1.492	0.476	3.137	0.002
Year 2017	1.000	0.506	1.975	0.048
Year 2018	0.729	0.521	1.398	0.162
Year 2019	1.167	0.496	2.353	0.019
Sin	−0.013	0.053	−0.250	0.802
Cos	−0.035	0.080	−0.434	0.664
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		2.959	48.721	<0.001
s(Elevation)		2.575	75.756	<0.001
s(Slope)		0.675	3.120	0.027
s(C110)		1.027	47.106	<0.001
s(C112)		0.986	19.469	<0.001
s(C211)		0.001	0	0.737
s(C213)		2.269	17.428	<0.001
s(C221)		0.012	0.012	0.305
s(C222)		0	0	0.529
s(C223)		0	0	0.498
s(C224)		0.003	0.003	0.348
s(C231)		0.892	16.076	<0.001
s(C311)		2.034	5.661	0.041
s(C312)		0	0	0.463
s(C313)		0.797	3.220	0.041
s(C320)		2.823	7.859	0.039
s(C321)		0	0	0.545
s(C330)		0	0	0.495
s(C410)		0.854	6.808	0.005
s(C511)		1.614	6.214	0.022

Common Kestrel (*Falcon tinnunculus*) — Model C-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−4.287	0.358	−11.964	<0.001
Year 1995	−0.286	0.465	−0.614	0.539
Year 1996	−0.514	0.475	−1.083	0.279
Year 1999	0.254	0.414	0.614	0.539
Year 2000	0.630	0.384	1.642	0.101
Year 2001	0.946	0.378	2.502	0.012
Year 2002	0.633	0.414	1.531	0.126
Year 2003	0.868	0.399	2.176	0.030
Year 2004	1.137	0.404	2.814	0.005
Year 2005	1.043	0.373	2.797	0.005
Year 2006	1.278	0.371	3.442	<0.001
Year 2007	0.970	0.387	2.506	0.012
Year 2008	1.145	0.384	2.985	0.003
Year 2009	0.670	0.395	1.696	0.090
Year 2010	0.992	0.386	2.568	0.010
Year 2011	0.764	0.389	1.966	0.049
Year 2012	0.906	0.386	2.349	0.019
Year 2013	1.022	0.382	2.676	0.007
Year 2014	1.158	0.379	3.052	0.002
Year 2015	1.212	0.378	3.205	0.001
Year 2016	1.361	0.376	3.617	<0.001
Year 2017	1.383	0.384	3.604	<0.001
Year 2018	0.475	0.425	1.117	0.264
Year 2019	1.019	0.396	2.575	0.010
Sin	0.030	0.051	0.590	0.555
Cos	−0.080	0.077	−1.041	0.298
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		1.533	9.015	0.002
s(Elevation)		1.828	3.207	0.127
s(Slope)		2.620	22.790	<0.001
s(C110)		0.656	4.368	0.006
s(C112)		0.437	0.964	0.126
s(C211)		0.967	26.608	<0.001
s(C213)		0	0	0.533
s(C221)		0.807	3.283	0.040
s(C222)		0	0	0.688
s(C223)		0.004	0	0.959
s(C224)		0	0	0.987
s(C231)		1.179	48.353	<0.001
s(C311)		1.985	13.373	<0.001
s(C312)		0.940	14.292	<0.001
s(C313)		0.854	9.731	<0.001
s(C320)		0.391	0.652	0.186
s(C321)		0.921	14.734	0
s(C330)		0.911	11.302	<0.001
s(C410)		0.001	0	0.552
s(C511)		0.894	4.980	0.017

Common Quail (*Coturnix coturnix*) — Model C-ZIP-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.455	0.023	−62.340	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.990	480.600	<0.001
s(Urb$_{2500}$)		1.106	179.800	<0.001
s(For$_{2500}$)		1.907	502.200	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.430	0.334	−10.270	<0.001
Year 1995	0.562	0.347	1.621	0.105
Year 1996	−1.285	0.509	−2.524	0.012
Year 1999	0.208	0.380	0.547	0.585
Year 2000	0.660	0.338	1.953	0.051
Year 2001	0.762	0.334	2.281	0.023
Year 2002	0.168	0.395	0.425	0.671
Year 2003	0.237	0.400	0.592	0.554
Year 2004	0.113	0.440	0.256	0.798
Year 2005	1.370	0.316	4.339	<0.001
Year 2006	0.741	0.334	2.222	0.026
Year 2007	0.115	0.366	0.313	0.754
Year 2008	0.269	0.381	0.706	0.480
Year 2009	0.157	0.375	0.418	0.676
Year 2010	0.797	0.342	2.328	0.020
Year 2011	0.094	0.371	0.253	0.800
Year 2012	−0.035	0.378	−0.093	0.926
Year 2013	−0.250	0.394	−0.636	0.525
Year 2014	−0.486	0.439	−1.107	0.268
Year 2015	−0.281	0.412	−0.684	0.494
Year 2016	−0.490	0.429	−1.143	0.253
Year 2017	−0.573	0.485	−1.182	0.237
Year 2018	−1.049	0.585	−1.793	0.073
Year 2019	0.240	0.394	0.609	0.543
Sin	0.013	0.064	0.202	0.840
Cos	−0.039	0.095	−0.411	0.681
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.907	25.309	<0.001
s(Elevation)		1.197	25.483	<0.001
s(Slope)		1.035	7.790	0.002
s(C110)		0.808	6.106	0.004
s(C112)		0.869	7.004	0.004
s(C211)		1.090	42.005	<0.001
s(C213)		0.861	9.760	<0.001
s(C221)		2.506	21.686	<0.001
s(C222)		0.929	12.181	<0.001
s(C223)		0	0	0.534
s(C224)		0.001	0	0.724
s(C231)		1.665	63.280	<0.001
s(C311)		2.629	17.432	<0.001
s(C312)		1.809	8.574	0.007
s(C313)		0.877	5.583	0.011
s(C320)		0	0	0.706
s(C321)		0.193	0.235	0.261
s(C330)		2.907	25.309	<0.001
s(C410)		1.197	25.483	<0.001
s(C511)		1.035	7.790	0.002

Common Pheasant (*Phasianus colchicus*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−4.305	0.222	−19.389	<0.001
Year 1995	−1.141	0.272	−4.193	<0.001
Year 1996	−0.584	0.241	−2.426	0.015
Year 1999	−0.046	0.200	−0.230	0.818
Year 2000	0.300	0.194	1.546	0.122
Year 2001	0.087	0.202	0.430	0.667
Year 2002	−0.048	0.232	−0.205	0.837
Year 2003	0.314	0.216	1.452	0.147
Year 2004	−0.290	0.294	−0.986	0.324
Year 2005	−0.012	0.201	−0.060	0.952
Year 2006	0.337	0.194	1.735	0.083
Year 2007	0.748	0.198	3.775	<0.001
Year 2008	0.622	0.205	3.040	0.002
Year 2009	0.942	0.194	4.858	<0.001
Year 2010	0.927	0.195	4.748	<0.001
Year 2011	0.806	0.193	4.171	<0.001
Year 2012	0.872	0.195	4.466	<0.001
Year 2013	0.979	0.191	5.125	<0.001
Year 2014	0.782	0.197	3.960	<0.001
Year 2015	0.926	0.196	4.733	<0.001
Year 2016	0.874	0.196	4.452	<0.001
Year 2017	0.750	0.208	3.610	<0.001
Year 2018	0.772	0.208	3.714	<0.001
Year 2019	0.604	0.213	2.839	0.005
Sin	−0.001	0.034	−0.031	0.975
Cos	0.039	0.051	0.767	0.443
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		1.981	101.266	<0.001
s(Elevation)		1.395	93.493	<0.001
s(Slope)		1.977	22.295	<0.001
s(C110)		1.377	177.353	<0.001
s(C112)		1.104	74.221	<0.001
s(C211)		0.001	0	0.752
s(C213)		0.949	13.721	<0.001
s(C221)		0.225	0.293	0.249
s(C222)		0.001	0	0.789
s(C223)		0.001	0	0.713
s(C224)		2.213	123.386	<0.001
s(C231)		0.731	2.575	0.058
s(C311)		2.640	130.881	<0.001
s(C312)		0.143	0.182	0.259
s(C313)		0.001	0	0.936
s(C320)		0.448	0.856	0.166
s(C321)		0.002	0.001	0.403
s(C330)		0.005	0.005	0.329
s(C410)		0.001	0	0.759
s(C511)		0.741	2.803	0.050

Common Moorhen (*Gallinula chloropus*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−5.900	0.969	−6.086	<0.001
Year 1995	−0.097	0.228	−0.426	0.670
Year 1996	0.248	0.221	1.125	0.261
Year 1999	−0.317	0.233	−1.363	0.173
Year 2000	0.461	0.206	2.235	0.025
Year 2001	0.416	0.207	2.010	0.044
Year 2002	0.026	0.243	0.109	0.913
Year 2003	0.140	0.250	0.560	0.576
Year 2004	−0.089	0.305	−0.291	0.771
Year 2005	0.272	0.207	1.312	0.189
Year 2006	0.158	0.215	0.737	0.461
Year 2007	−0.306	0.248	−1.236	0.217
Year 2008	0.211	0.229	0.922	0.357
Year 2009	0.187	0.220	0.851	0.395
Year 2010	0.436	0.215	2.025	0.043
Year 2011	−0.281	0.244	−1.154	0.248
Year 2012	0.050	0.238	0.210	0.834
Year 2013	0.228	0.226	1.012	0.312
Year 2014	0.047	0.239	0.195	0.846
Year 2015	0.223	0.224	0.995	0.320
Year 2016	0.227	0.228	0.996	0.320
Year 2017	0.380	0.243	1.559	0.119
Year 2018	0.132	0.245	0.540	0.589
Year 2019	0.081	0.257	0.314	0.753
Sin	0.018	0.042	0.438	0.661
Cos	0.049	0.063	0.769	0.442
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		1.640	23.987	<0.001
s(Elevation)		1.142	62.351	<0.001
s(Slope)		0.876	5.000	0.013
s(C110)		1.184	79.117	<0.001
s(C112)		0.959	13.000	<0.001
s(C211)		0.088	0.098	0.276
s(C213)		1.316	253.632	<0.001
s(C221)		0.006	0.004	0.370
s(C222)		0.579	1.204	0.149
s(C223)		0.632	0.144	0.633
s(C224)		0.669	1.944	0.085
s(C231)		0.001	0	0.772
s(C311)		2.484	26.561	<0.001
s(C312)		0	0	0.786
s(C313)		0.839	3.918	0.030
s(C320)		0.666	1.842	0.095
s(C321)		0	0	0.634
s(C330)		0.857	5.362	0.012
s(C410)		2.848	371.328	<0.001
s(C511)		2.891	107.743	<0.001

Northern Lapwing (*Vanellus vanellus*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−15.198	2.237	−6.794	<0.001
Year 1996	−2.095	0.863	−2.428	0.015
Year 1999	−0.003	0.599	−0.004	0.997
Year 2000	0.074	0.513	0.145	0.885
Year 2001	0.651	0.492	1.322	0.186
Year 2002	0.494	0.547	0.903	0.367
Year 2003	1.027	0.582	1.765	0.078
Year 2004	1.425	0.572	2.489	0.013
Year 2005	1.036	0.482	2.150	0.032
Year 2006	0.443	0.524	0.846	0.398
Year 2007	0.922	0.514	1.793	0.073
Year 2008	1.345	0.500	2.692	0.007
Year 2009	1.105	0.488	2.267	0.023
Year 2010	1.510	0.481	3.135	0.002
Year 2011	1.102	0.502	2.194	0.028
Year 2012	0.923	0.511	1.808	0.071
Year 2013	1.573	0.499	3.154	0.002
Year 2014	2.585	0.481	5.375	<0.001
Year 2015	1.679	0.490	3.429	<0.001
Year 2016	1.962	0.482	4.069	<0.001
Year 2017	2.134	0.525	4.063	<0.001
Year 2018	1.338	0.534	2.506	0.012
Year 2019	1.780	0.526	3.388	<0.001
Sin	0.343	0.097	3.520	<0.001
Cos	−0.338	0.155	−2.176	0.030
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		1.924	32.105	<0.001
s(Elevation)		0	0	0.830
s(Slope)		0.952	17.976	<0.001
s(C110)		0.911	7.397	0.004
s(C112)		0	0	0.481
s(C211)		1.773	85.008	<0.001
s(C213)		2.475	257.576	<0.001
s(C221)		0	0	0.966
s(C222)		0	0	0.651
s(C223)		0	0	0.816
s(C224)		0.946	14.829	<0.001
s(C231)		0	0	0.827
s(C311)		0.002	0.002	0.327
s(C312)		0.002	0.001	0.455
s(C313)		0.673	1.615	0.121
s(C320)		0.586	1.094	0.172
s(C321)		0.604	2.243	0.054
s(C330)		0.778	2.644	0.065
s(C410)		0.955	20.504	<0.001
s(C511)		0.974	29.611	<0.001

Feral Pigeon (*Columba livia*) — Model C-ZINB-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.502	0.027	18.950	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.988	757.300	<0.001
s(Urb$_{2500}$)		1.162	1,017.600	<0.001
s(For$_{2500}$)		2.723	464.300	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.205	0.174	−12.654	<0.001
Year 1995	0.099	0.179	0.553	0.580
Year 1996	−0.297	0.178	−1.666	0.096
Year 1999	0.107	0.180	0.593	0.553
Year 2000	0.897	0.162	5.526	<0.001
Year 2001	0.946	0.162	5.832	<0.001
Year 2002	1.316	0.177	7.456	<0.001
Year 2003	0.373	0.184	2.023	0.043
Year 2004	1.519	0.190	7.995	<0.001
Year 2005	0.942	0.161	5.843	<0.001
Year 2006	1.052	0.162	6.513	<0.001
Year 2007	0.039	0.177	0.220	0.826
Year 2008	−0.039	0.178	−0.222	0.824
Year 2009	0.024	0.173	0.136	0.892
Year 2010	0.241	0.171	1.409	0.159
Year 2011	0.523	0.167	3.125	0.002
Year 2012	0.206	0.174	1.186	0.235
Year 2013	0.319	0.170	1.872	0.061
Year 2014	0.453	0.166	2.738	0.006
Year 2015	0.438	0.170	2.580	0.010
Year 2016	0.390	0.171	2.272	0.023
Year 2017	0.431	0.185	2.335	0.020
Year 2018	0.478	0.184	2.603	0.009
Year 2019	0.502	0.183	2.739	0.006
Sin	0.052	0.031	1.707	0.088
Cos	−0.060	0.047	−1.290	0.197
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.996	323.828	<0.001
s(Elevation)		1.138	11.942	<0.001
s(Slope)		1.035	15.402	<0.001
s(C110)		0.652	1.716	0.094
s(C112)		2.600	33.562	<0.001
s(C211)		0.924	6.811	0.003
s(C213)		0.034	0.022	0.396
s(C221)		0.950	17.385	<0.001
s(C222)		0.004	0.003	0.418
s(C223)		0.850	5.136	0.014
s(C224)		0.999	47.638	<0.001
s(C231)		0.001	0	0.356
s(C311)		1.669	254.304	<0.001
s(C312)		1.003	22.758	<0.001
s(C313)		1.063	47.353	<0.001
s(C320)		0.906	8.368	0.002
s(C321)		0.797	3.127	0.044
s(C330)		0.001	0	0.784
s(C410)		0.970	28.490	<0.001
s(C511)		0.949	17.730	<0.001

Common Wood Pigeon (*Columba palumbus*) — Model C-ZIP-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.575	0.020	28.700	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.170	737.300	<0.001
s(Urb$_{2500}$)		2.981	647.900	<0.001
s(For$_{2500}$)		2.990	480.700	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.529	0.174	−14.505	<0.001
Year 1995	−1.087	0.235	−4.626	<0.001
Year 1996	−0.308	0.179	−1.720	0.085
Year 1999	−0.019	0.169	−0.110	0.912
Year 2000	−0.462	0.185	−2.494	0.013
Year 2001	−0.634	0.225	−2.818	0.005
Year 2002	−0.572	0.225	−2.540	0.011
Year 2003	−0.644	0.264	−2.440	0.015
Year 2004	−0.374	0.182	−2.057	0.040
Year 2005	0.327	0.163	2.007	0.045
Year 2006	0.072	0.180	0.402	0.688
Year 2007	0.272	0.175	1.554	0.120
Year 2008	0.420	0.171	2.461	0.014
Year 2009	0.684	0.165	4.139	<0.001
Year 2010	0.963	0.159	6.054	<0.001
Year 2011	0.832	0.165	5.057	<0.001
Year 2012	1.007	0.161	6.269	<0.001
Year 2013	1.086	0.157	6.897	<0.001
Year 2014	1.058	0.160	6.602	<0.001
Year 2015	1.299	0.158	8.233	<0.001
Year 2016	1.177	0.163	7.216	<0.001
Year 2017	1.334	0.161	8.274	<0.001
Year 2018	1.333	0.161	8.276	<0.001
Year 2019	0.006	0.027	0.219	0.827
Sin	−0.199	0.043	−4.605	<0.001
Cos	−2.529	0.174	−14.505	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.950	72.541	<0.001
s(Elevation)		2.587	39.005	<0.001
s(Slope)		1.306	54.017	<0.001
s(C110)		0.001	0	0.753
s(C112)		0.988	21.845	<0.001
s(C211)		2.090	12.796	<0.001
s(C213)		1.009	34.233	<0.001
s(C221)		0.888	7.562	0.003
s(C222)		0.002	0	0.828
s(C223)		0.666	1.789	0.101
s(C224)		0.386	0.639	0.197
s(C231)		0.001	0	0.729
s(C311)		2.702	82.454	<0.001
s(C312)		0.043	0.043	0.316
s(C313)		0.856	5.323	0.012
s(C320)		0.173	0.212	0.266
s(C321)		0.847	4.372	0.022
s(C330)		0.804	3.792	0.029
s(C410)		0.315	0.438	0.238
s(C511)		0.002	0	0.891

Eurasian Collared Dove (*Streptopelia decaocto*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.667	0.020	33.510	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.206	857.000	<0.001
s(Urb_{2500})		2.835	469.300	<0.001
s(For_{2500})		2.522	1,479.500	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.987	0.609	−6.547	<0.001
Year 1995	−0.267	0.155	−1.723	0.085
Year 1996	−0.076	0.137	−0.553	0.581
Year 1999	0.441	0.137	3.205	0.001
Year 2000	0.816	0.123	6.625	<0.001
Year 2001	0.793	0.124	6.409	<0.001
Year 2002	0.859	0.130	6.612	<0.001
Year 2003	0.789	0.130	6.049	<0.001
Year 2004	0.782	0.141	5.558	<0.001
Year 2005	0.999	0.120	8.328	<0.001
Year 2006	0.920	0.121	7.572	<0.001
Year 2007	0.784	0.126	6.243	<0.001
Year 2008	0.723	0.126	5.739	<0.001
Year 2009	0.932	0.123	7.592	<0.001
Year 2010	0.888	0.124	7.139	<0.001
Year 2011	0.754	0.123	6.146	<0.001
Year 2012	0.951	0.123	7.710	<0.001
Year 2013	0.792	0.123	6.462	<0.001
Year 2014	0.721	0.122	5.893	<0.001
Year 2015	0.666	0.124	5.391	<0.001
Year 2016	0.810	0.123	6.564	<0.001
Year 2017	0.895	0.128	6.977	<0.001
Year 2018	0.938	0.127	7.368	<0.001
Year 2019	0.977	0.127	7.712	<0.001
Sin	0.018	0.018	0.990	0.322
Cos	−0.041	0.027	−1.521	0.128
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.967	289.032	<0.001
s(Elevation)		2.906	20.032	<0.001
s(Slope)		2.010	66.178	<0.001
s(C110)		2.590	1,069.957	<0.001
s(C112)		2.942	1,047.404	<0.001
s(C211)		0.005	0.001	0.661
s(C213)		1.831	62.062	<0.001
s(C221)		0.269	0.379	0.233
s(C222)		2.739	5.245	0.125
s(C223)		0	0	0.552
s(C224)		0.956	24.219	<0.001
s(C231)		0.886	8.591	0.002
s(C311)		2.159	96.835	<0.001
s(C312)		0.001	0	0.543
s(C313)		0.932	11.455	<0.001
s(C320)		1.291	3.072	0.101
s(C321)		0.229	0.315	0.241
s(C330)		0.944	18.358	<0.001
s(C410)		2.109	25.165	<0.001
s(C511)		0.958	23.479	<0.001

European Turtle Dove (*Streptopelia turtur*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.469	0.019	−24.720	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		3.000	2,447.200	<0.001
s(Urb$_{2500}$)		1.157	288.500	<0.001
s(For$_{2500}$)		2.999	1,788.800	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.546	0.209	−12.160	<0.001
Year 1995	0.037	0.152	0.244	0.807
Year 1996	−1.128	0.211	−5.349	<0.001
Year 1999	0.071	0.145	0.488	0.626
Year 2000	0.147	0.141	1.044	0.297
Year 2001	−0.386	0.162	−2.381	0.017
Year 2002	−0.075	0.162	−0.464	0.643
Year 2003	−0.687	0.202	−3.398	<0.001
Year 2004	−0.371	0.243	−1.528	0.126
Year 2005	−0.355	0.154	−2.306	0.021
Year 2006	−0.332	0.153	−2.171	0.030
Year 2007	−0.010	0.151	−0.065	0.948
Year 2008	0.023	0.156	0.148	0.882
Year 2009	0.252	0.148	1.704	0.088
Year 2010	0.248	0.146	1.701	0.089
Year 2011	−0.302	0.155	−1.953	0.051
Year 2012	0.072	0.153	0.469	0.639
Year 2013	−0.149	0.157	−0.948	0.343
Year 2014	0.034	0.152	0.225	0.822
Year 2015	−0.204	0.162	−1.263	0.206
Year 2016	−0.103	0.157	−0.659	0.510
Year 2017	−0.107	0.168	−0.633	0.527
Year 2018	−0.246	0.172	−1.429	0.153
Year 2019	−0.323	0.178	−1.812	0.070
Sin	−0.047	0.031	−1.510	0.131
Cos	−0.080	0.050	−1.605	0.108
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.996	458.094	<0.001
s(Elevation)		2.654	39.242	<0.001
s(Slope)		2.225	46.249	<0.001
s(C110)		1.043	80.131	<0.001
s(C112)		2.531	71.924	<0.001
s(C211)		1.971	7.464	0.016
s(C213)		1.946	8.695	0.008
s(C221)		2.223	5.833	0.055
s(C222)		0.001	0.001	0.457
s(C223)		0.615	2.097	0.064
s(C224)		0	0	0.742
s(C231)		0.002	0	0.924
s(C311)		2.659	77.273	<0.001
s(C312)		0.763	3.165	0.041
s(C313)		0.002	0	0.877
s(C320)		1.244	27.083	0
s(C321)		0.002	0.002	0.423
s(C330)		0.001	0	0.682
s(C410)		0.847	7.111	0.004
s(C511)		1.704	2.530	0.218

Common Cuckoo (*Cuculus canorus*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	4.987	0.317	15.740	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.946	1,076.000	<0.001
s(Urb$_{2500}$)		2.984	1,132.000	<0.001
s(For$_{2500}$)		2.991	1,636.000	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.789	0.075	−10.538	<0.001
Year 1995	−0.086	0.097	−0.887	0.375
Year 1996	−0.650	0.110	−5.937	<0.001
Year 1999	−0.198	0.086	−2.308	0.021
Year 2000	−0.344	0.085	−4.042	<0.001
Year 2001	−0.361	0.094	−3.838	<0.001
Year 2002	−0.274	0.099	−2.781	0.005
Year 2003	−0.148	0.101	−1.473	0.141
Year 2004	−0.100	0.114	−0.875	0.382
Year 2005	0.018	0.087	0.211	0.833
Year 2006	−0.151	0.090	−1.692	0.091
Year 2007	−0.139	0.094	−1.481	0.139
Year 2008	−0.383	0.100	−3.812	<0.001
Year 2009	−0.269	0.098	−2.757	0.006
Year 2010	−0.050	0.093	−0.537	0.591
Year 2011	−0.006	0.088	−0.071	0.943
Year 2012	−0.296	0.096	−3.066	0.002
Year 2013	−0.195	0.094	−2.081	0.037
Year 2014	0.096	0.090	1.070	0.285
Year 2015	0.009	0.092	0.097	0.922
Year 2016	−0.036	0.092	−0.390	0.696
Year 2017	−0.199	0.101	−1.968	0.049
Year 2018	−0.262	0.102	−2.573	0.010
Year 2019	−0.337	0.104	−3.233	0.001
Sin	−0.008	0.018	−0.463	0.643
Cos	0.015	0.027	0.549	0.583
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.971	335.601	<0.001
s(Elevation)		2.643	32.400	<0.001
s(Slope)		2.795	77.192	<0.001
s(C110)		2.941	90.119	<0.001
s(C112)		2.885	16.403	0.001
s(C211)		0.001	0	0.571
s(C213)		2.365	31.445	<0.001
s(C221)		0.954	19.392	<0.001
s(C222)		0.496	1.006	0.154
s(C223)		0	0	0.753
s(C224)		2.236	99.193	<0.001
s(C231)		1.013	40.345	<0.001
s(C311)		2.887	119.877	<0.001
s(C312)		0.718	4.209	0.014
s(C313)		1.812	27.925	<0.001
s(C320)		0.961	12.854	0
s(C321)		2.847	50.306	0
s(C330)		2.255	25.863	<0.001
s(C410)		2.924	209.291	<0.001
s(C511)		0.940	14.920	<0.001

Common Swift (*Apus apus*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.831	0.022	37.700	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.170	665.070	<0.001
s(Urb$_{2500}$)		1.112	1,027.400	<0.001
s(For$_{2500}$)		2.833	60.010	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.922	0.127	7.258	<0.001
Year 1995	−0.780	0.159	−4.908	<0.001
Year 1996	−0.669	0.156	−4.284	<0.001
Year 1999	−0.278	0.147	−1.887	0.059
Year 2000	−0.601	0.142	−4.237	<0.001
Year 2001	−0.594	0.148	−4.005	<0.001
Year 2002	−0.458	0.162	−2.834	0.005
Year 2003	−0.217	0.163	−1.334	0.182
Year 2004	−0.335	0.178	−1.884	0.060
Year 2005	−0.485	0.146	−3.319	<0.001
Year 2006	−0.601	0.144	−4.167	<0.001
Year 2007	−1.300	0.162	−8.042	<0.001
Year 2008	−0.949	0.159	−5.971	<0.001
Year 2009	−1.072	0.157	−6.836	<0.001
Year 2010	−0.561	0.154	−3.644	<0.001
Year 2011	−0.793	0.150	−5.298	<0.001
Year 2012	−0.834	0.156	−5.341	<0.001
Year 2013	−0.886	0.155	−5.710	<0.001
Year 2014	−0.848	0.150	−5.646	<0.001
Year 2015	−0.853	0.155	−5.520	<0.001
Year 2016	−1.361	0.159	−8.573	<0.001
Year 2017	−1.510	0.175	−8.652	<0.001
Year 2018	−1.113	0.171	−6.503	<0.001
Year 2019	−0.453	0.167	−2.716	0.007
Sin	0.065	0.030	2.214	0.027
Cos	−0.127	0.044	−2.889	0.004
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.906	52.724	<0.001
s(Elevation)		2.895	50.998	<0.001
s(Slope)		0.411	0.680	0.194
s(C110)		1.022	16.871	0
s(C112)		0.876	6.340	0.005
s(C211)		1.979	29.953	0
s(C213)		0.903	7.950	0.002
s(C221)		0.956	19.609	0
s(C222)		0.800	4.087	0.023
s(C223)		0.851	5.823	0.009
s(C224)		0.905	9.191	0.001
s(C231)		0.619	1.562	0.094
s(C311)		2.679	160.801	0
s(C312)		1.237	108.943	0
s(C313)		1.269	147.769	0
s(C320)		0.956	16.345	0
s(C321)		0.001	0	0.907
s(C330)		0.003	0.002	0.411
s(C410)		0.002	0	0.755
s(C511)		0.002	0	0.811

European Bee-eater (*Merops apiaster*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−8.994	0.936	−9.608	<0.001
Year 1995	0.906	0.917	0.989	0.323
Year 1996	−0.162	1.035	−0.157	0.875
Year 1999	1.951	0.857	2.276	0.023
Year 2000	1.608	0.869	1.851	0.064
Year 2001	1.745	0.863	2.022	0.043
Year 2002	1.867	0.886	2.108	0.035
Year 2003	2.746	0.864	3.178	0.001
Year 2004	1.430	0.996	1.437	0.151
Year 2005	2.495	0.843	2.959	0.003
Year 2006	0.904	0.895	1.009	0.313
Year 2007	2.532	0.860	2.944	0.003
Year 2008	2.023	0.886	2.283	0.022
Year 2009	1.956	0.877	2.229	0.026
Year 2010	3.261	0.850	3.838	<0.001
Year 2011	2.418	0.857	2.821	0.005
Year 2012	2.152	0.870	2.474	0.013
Year 2013	2.944	0.849	3.467	<0.001
Year 2014	2.853	0.855	3.338	<0.001
Year 2015	2.744	0.860	3.192	0.001
Year 2016	2.826	0.855	3.306	<0.001
Year 2017	2.987	0.867	3.444	<0.001
Year 2018	3.262	0.865	3.771	<0.001
Year 2019	3.177	0.865	3.675	<0.001
Sin	−0.208	0.093	−2.246	0.025
Cos	0.140	0.138	1.014	0.311
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		1.999	125.125	<0.001
s(Elevation)		1.161	48.712	<0.001
s(Slope)		2.311	22.706	<0.001
s(C110)		2.144	18.500	<0.001
s(C112)		0.956	13.830	<0.001
s(C211)		0.003	0.002	0.394
s(C213)		1.017	37.487	<0.001
s(C221)		0.855	5.454	0.011
s(C222)		0.740	2.881	0.048
s(C223)		0	0	0.558
s(C224)		0.158	0.169	0.301
s(C231)		0.046	0.042	0.336
s(C311)		2.604	22.156	<0.001
s(C312)		0.001	0.001	0.470
s(C313)		0	0	0.580
s(C320)		0	0	0.490
s(C321)		0	0	0.585
s(C330)		0.939	12.666	<0.001
s(C410)		0	0	0.373
s(C511)		0.931	12.223	<0.001

Eurasian Wryneck (*Jynx torquilla*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.106	0.035	−60.520	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.994	818.020	<0.001
s(Urb$_{2500}$)		2.979	72.450	<0.001
s(For$_{2500}$)		2.974	332.040	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.928	0.723	−4.052	<0.001
Year 1995	0.072	0.298	0.242	0.809
Year 1996	−0.347	0.344	−1.008	0.313
Year 1999	0.310	0.286	1.081	0.280
Year 2000	0.146	0.267	0.545	0.586
Year 2001	−0.044	0.299	−0.147	0.883
Year 2002	0.208	0.332	0.626	0.532
Year 2003	0.271	0.349	0.776	0.438
Year 2004	0.120	0.411	0.293	0.770
Year 2005	−0.309	0.302	−1.023	0.306
Year 2006	−0.898	0.350	−2.561	0.010
Year 2007	0.298	0.285	1.045	0.296
Year 2008	−0.060	0.302	−0.197	0.844
Year 2009	−0.384	0.349	−1.100	0.271
Year 2010	−0.414	0.319	−1.299	0.194
Year 2011	−0.837	0.349	−2.399	0.016
Year 2012	−0.691	0.364	−1.898	0.058
Year 2013	−0.392	0.339	−1.159	0.246
Year 2014	−0.605	0.357	−1.693	0.090
Year 2015	−1.011	0.395	−2.561	0.010
Year 2016	−1.660	0.505	−3.287	0.001
Year 2017	−1.167	0.471	−2.477	0.013
Year 2018	−1.562	0.552	−2.828	0.005
Year 2019	−1.681	0.552	−3.043	0.002
Sin	−0.145	0.071	−2.029	0.042
Cos	−0.092	0.108	−0.855	0.393
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.956	111.980	<0.001
s(Elevation)		0	0	0.536
S(Slope)		0.928	7.061	0.004
s(C110)		0.049	0.055	0.284
s(C112)		2.681	4.330	0.182
s(C211)		0	0	0.746
s(C213)		0.734	2.549	0.062
s(C221)		2.680	98.820	<0.001
s(C222)		0.842	5.123	0.013
s(C223)		0.889	8.045	0.003
s(C224)		2.567	15.429	<0.001
s(C231)		1.527	40.971	<0.001
s(C311)		2.446	51.158	<0.001
s(C312)		0.330	0.499	0.217
s(C313)		0	0	0.803
s(C320)		0.674	2.167	0.072
s(C321)		1.787	6.650	0.024
s(C330)		0.750	3.748	0.025
s(C410)		0.001	0.001	0.411
s(C511)		0.906	19.469	<0.001

European Green Woodpecker (*Picus viridis*) — Model C-P-GAM				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−4.031	0.293	−13.736	<0.001
Year 1995	−0.622	0.429	−1.450	0.147
Year 1996	−0.097	0.378	−0.258	0.797
Year 1999	0.349	0.318	1.097	0.273
Year 2000	0.943	0.304	3.100	0.002
Year 2001	0.903	0.316	2.859	0.004
Year 2002	0.673	0.332	2.028	0.043
Year 2003	0.822	0.338	2.429	0.015
Year 2004	−0.015	0.442	−0.034	0.973
Year 2005	0.583	0.323	1.807	0.071
Year 2006	0.804	0.312	2.575	0.010
Year 2007	0.785	0.326	2.410	0.016
Year 2008	0.738	0.335	2.202	0.028
Year 2009	0.571	0.339	1.684	0.092
Year 2010	0.662	0.332	1.995	0.046
Year 2011	1.253	0.308	4.062	<0.001
Year 2012	1.117	0.318	3.517	<0.001
Year 2013	1.168	0.315	3.715	<0.001
Year 2014	1.109	0.316	3.510	<0.001
Year 2015	1.324	0.313	4.227	<0.001
Year 2016	1.161	0.316	3.671	<0.001
Year 2017	1.201	0.323	3.721	<0.001
Year 2018	0.991	0.330	3.005	0.003
Year 2019	1.255	0.321	3.902	0
Sin	−0.018	0.043	−0.418	0.676
Cos	0.057	0.066	0.858	0.391
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		2.973	137.189	<0.001
s(Elevation)		2.942	72.707	<0.001
s(Slope)		2.840	16.272	<0.001
s(C110)		0.931	7.285	0.003
s(C112)		0.846	4.172	0.022
s(C211)		2.260	15.935	<0.001
s(C213)		0.909	8.216	0.002
s(C221)		1.485	24.963	<0.001
s(C222)		0	0	0.665
s(C223)		0.533	0.860	0.203
s(C224)		2.632	29.737	<0.001
s(C231)		2.471	14.594	<0.001
s(C311)		2.741	70.003	<0.001
s(C312)		0.907	18.311	<0.001
s(C313)		2.043	25.906	<0.001
s(C320)		0	0	0.670
s(C321)		1.649	6.263	0.021
s(C330)		0	0	0.764
s(C410)		0.507	0.792	0.208
s(C511)		2.758	5.791	0.095

Great Spotted Woodpecker (*Dendrocopos major*) — Model C-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.562	0.245	−14.544	<0.001
Year 1995	−0.514	0.338	−1.518	0.129
Year 1996	−0.714	0.361	−1.977	0.048
Year 1999	0.768	0.256	2.993	0.003
Year 2000	0.481	0.260	1.847	0.065
Year 2001	0.630	0.268	2.351	0.019
Year 2002	0.767	0.277	2.766	0.006
Year 2003	1.032	0.273	3.788	<0.001
Year 2004	0.724	0.308	2.350	0.019
Year 2005	0.967	0.262	3.695	<0.001
Year 2006	1.155	0.255	4.531	<0.001
Year 2007	1.195	0.265	4.519	<0.001
Year 2008	1.035	0.270	3.827	<0.001
Year 2009	0.880	0.273	3.227	0.001
Year 2010	1.196	0.264	4.525	<0.001
Year 2011	1.465	0.256	5.715	<0.001
Year 2012	1.369	0.262	5.227	<0.001
Year 2013	1.535	0.258	5.943	<0.001
Year 2014	1.584	0.257	6.163	<0.001
Year 2015	1.405	0.261	5.380	<0.001
Year 2016	1.567	0.259	6.055	<0.001
Year 2017	1.623	0.261	6.213	<0.001
Year 2018	1.201	0.270	4.443	<0.001
Year 2019	1.631	0.261	6.240	<0.001
Sin	−0.025	0.032	−0.773	0.440
Cos	0.055	0.048	1.147	0.251
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.984	116.397	<0.001
s(Elevation)		2.976	124.603	<0.001
s(Slope)		0.975	17.158	<0.001
s(C110)		2.162	18.054	<0.001
s(C112)		1.721	10.527	0.001
s(C211)		2.118	11.104	0.001
s(C213)		0.931	25.415	<0.001
s(C221)		1.302	0.432	0.667
s(C222)		0	0	0.357
s(C223)		0.844	4.641	0.019
s(C224)		1.849	61.231	<0.001
s(C231)		0.762	5.004	0.006
s(C311)		2.924	192.659	<0.001
s(C312)		1.044	63.092	<0.001
s(C313)		2.439	141.736	<0.001
s(C320)		0.642	1.448	0.122
s(C321)		0.869	9.923	<0.001
s(C330)		0.772	4.357	0.016
s(C410)		0	0	0.901
s(C511)		0	0	0.541

Eurasian Skylark (*Alauda arvensis*) — Model C-ZIP-GAM

Binomial component

Parametric terms	Estimate	Standard error	z-value	p-value
Intercept	0.168	0.018	9.125	<0.001

Smooth terms		edf	Chi-square	p-value
s(Elevation)		2.991	618.800	<0.001
s(Urb$_{2500}$)		1.121	295.900	<0.001
s(For$_{2500}$)		2.110	193.900	<0.001

Count component

Parametric terms	Estimate	Standard error	z-value	p-value
Intercept	−1.124	0.107	−10.466	<0.001
Year 1995	−0.645	0.085	−7.623	<0.001
Year 1996	−0.861	0.084	−10.286	<0.001
Year 1999	−0.661	0.094	−7.067	<0.001
Year 2000	−0.748	0.082	−9.161	<0.001
Year 2001	−0.919	0.084	−10.953	<0.001
Year 2002	−0.939	0.101	−9.250	<0.001
Year 2003	−1.083	0.103	−10.488	<0.001
Year 2004	−1.391	0.127	−10.973	<0.001
Year 2005	−1.163	0.082	−14.132	<0.001
Year 2006	−1.349	0.093	−14.544	<0.001
Year 2007	−1.777	0.113	−15.709	<0.001
Year 2008	−1.767	0.121	−14.652	<0.001
Year 2009	−1.676	0.108	−15.491	<0.001
Year 2010	−1.836	0.122	−15.035	<0.001
Year 2011	−2.245	0.134	−16.783	<0.001
Year 2012	−2.199	0.128	−17.136	<0.001
Year 2013	−2.506	0.147	−17.029	<0.001
Year 2014	−2.463	0.152	−16.191	<0.001
Year 2015	−2.564	0.154	−16.608	<0.001
Year 2016	−2.146	0.130	−16.560	<0.001
Year 2017	−2.586	0.181	−14.321	<0.001
Year 2018	−2.280	0.161	−14.195	<0.001
Year 2019	−2.513	0.176	−14.259	<0.001
Sin	0.020	0.026	0.793	0.428
Cos	0.040	0.038	1.063	0.288

Smooth terms		edf	Chi-square	p-value
s(X, Y)		2.979	267.814	<0.001
s(Elevation)		2.940	183.753	<0.001
S(Slope)		2.553	170.265	<0.001
s(C110)		1.048	81.880	<0.001
s(C112)		2.736	50.882	<0.001
s(C211)		2.742	62.335	<0.001
s(C213)		1.671	31.182	<0.001
s(C221)		1.955	6.344	0.029
s(C222)		0.001	0	0.871
s(C223)		0.878	5.259	0.014
s(C224)		2.638	40.149	<0.001
s(C231)		0.992	44.294	<0.001
s(C311)		1.849	117.667	<0.001
s(C312)		2.820	54.836	<0.001
s(C313)		2.941	32.039	<0.001
s(C320)		1.635	42.053	<0.001
s(C321)		2.641	104.323	<0.001
s(C330)		2.376	59.652	<0.001
s(C410)		0.884	8.908	0.001
s(C511)		0.246	0.389	0.201

Eurasian Crag Martin (*Ptyonoprogne rupestris*) — Model C-NB-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−7.042	4.740	−1.486	0.137
Year 1995	0.577	0.576	1.001	0.317
Year 1996	0.237	0.595	0.397	0.691
Year 1999	0.350	0.548	0.639	0.523
Year 2000	0.047	0.548	0.085	0.932
Year 2001	0.983	0.547	1.797	0.072
Year 2002	0.384	0.624	0.616	0.538
Year 2003	0.561	0.580	0.967	0.334
Year 2004	0.041	0.653	0.062	0.950
Year 2005	−0.187	0.579	−0.323	0.747
Year 2006	0.237	0.566	0.419	0.675
Year 2007	−0.628	0.664	−0.946	0.344
Year 2008	−0.006	0.623	−0.009	0.993
Year 2009	0.102	0.612	0.167	0.867
Year 2010	0.490	0.582	0.841	0.401
Year 2011	0.650	0.557	1.167	0.243
Year 2012	0.092	0.584	0.157	0.875
Year 2013	0.906	0.554	1.637	0.102
Year 2014	0.456	0.566	0.806	0.420
Year 2015	0.895	0.548	1.634	0.102
Year 2016	0.895	0.553	1.619	0.105
Year 2017	0.474	0.606	0.782	0.434
Year 2018	0.268	0.618	0.433	0.665
Year 2019	0.841	0.580	1.449	0.147
Sin	−0.062	0.083	−0.746	0.455
Cos	−0.264	0.124	−2.132	0.033
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.993	153.522	<0.001
s(Elevation)		2.600	94.491	<0.001
s(Slope)		2.778	68.499	<0.001
s(C110)		1.881	4.913	0.055
s(C112)		2.191	19.357	<0.001
s(C211)		1.119	19.901	<0.001
s(C213)		0.717	0.048	0.795
s(C221)		0.847	4.982	0.015
s(C222)		0.897	6.973	0.005
s(C223)		0.872	4.835	0.018
s(C224)		0	0	0.920
s(C231)		1.109	21.828	<0.001
s(C311)		2.174	64.035	<0.001
s(C312)		2.057	41.727	<0.001
s(C313)		1.453	52.537	<0.001
s(C320)		0.939	11.846	<0.001
s(C321)		0.967	14.382	<0.001
s(C330)		0.337	0.451	0.235
s(C410)		0.001	0.001	0.361
s(C511)		0.877	6.802	0.005

Barn Swallow (*Hirundo rustica*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	2.130	0.043	50	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.248	1,648.500	<0.001
s(Urb$_{2500}$)		2.925	697.400	<0.001
s(For$_{2500}$)		2.991	1,062.300	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.224	0.097	−2.315	0.021
Year 1995	−0.432	0.101	−4.271	<0.001
Year 1996	−0.245	0.098	−2.492	0.013
Year 1999	−0.074	0.097	−0.764	0.445
Year 2000	−0.158	0.092	−1.710	0.087
Year 2001	−0.366	0.095	−3.844	<0.001
Year 2002	−0.294	0.107	−2.738	0.006
Year 2003	−0.556	0.110	−5.051	<0.001
Year 2004	−0.656	0.127	−5.182	<0.001
Year 2005	−0.697	0.095	−7.325	<0.001
Year 2006	−0.567	0.095	−5.969	<0.001
Year 2007	−0.838	0.104	−8.031	<0.001
Year 2008	−1.053	0.108	−9.788	<0.001
Year 2009	−1.040	0.104	−9.989	<0.001
Year 2010	−0.595	0.101	−5.882	<0.001
Year 2011	−0.998	0.101	−9.889	<0.001
Year 2012	−1.343	0.108	−12.394	<0.001
Year 2013	−0.910	0.103	−8.871	<0.001
Year 2014	−1.155	0.104	−11.140	<0.001
Year 2015	−1.169	0.105	−11.130	<0.001
Year 2016	−0.765	0.103	−7.452	<0.001
Year 2017	−1.153	0.117	−9.844	<0.001
Year 2018	−0.858	0.113	−7.593	<0.001
Year 2019	−0.908	0.114	−8.003	<0.001
Sin	0.052	0.021	2.532	0.011
Cos	−0.172	0.031	−5.485	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.951	63.796	<0.001
s(Elevation)		2.887	94.594	<0.001
S(Slope)		1.292	32.069	<0.001
s(C110)		2.466	140.681	<0.001
s(C112)		2.873	109.102	<0.001
s(C211)		1.308	33.685	<0.001
s(C213)		1.020	35.423	<0.001
s(C221)		0.984	37.342	<0.001
s(C222)		0.039	0.037	0.330
s(C223)		0.337	0.463	0.240
s(C224)		1.016	72.137	<0.001
s(C231)		0.301	0.405	0.223
s(C311)		2.538	463.975	<0.001
s(C312)		2.700	62.920	<0.001
s(C313)		1.508	215.796	<0.001
s(C320)		1.012	48.342	<0.001
s(C321)		0.916	9.275	0.001
s(C330)		0.864	6.274	0.007
s(C410)		0.007	0.005	0.411
s(C511)		0.694	2.240	0.068

Common House Martin (*Delichon urbicum*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.136	0.018	7.698	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.183	776.100	<0.001
s(Urb_{2500})		2.812	1,310.600	<0.001
s(For_{2500})		2.977	1,117.300	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.209	0.160	−1.311	0.190
Year 1995	−0.734	0.203	−3.619	<0.001
Year 1996	−0.091	0.192	−0.476	0.634
Year 1999	0.014	0.183	0.078	0.938
Year 2000	0.040	0.175	0.229	0.819
Year 2001	−0.042	0.184	−0.226	0.821
Year 2002	−0.042	0.202	−0.209	0.834
Year 2003	−0.079	0.202	−0.391	0.696
Year 2004	−0.567	0.230	−2.468	0.014
Year 2005	−0.553	0.185	−2.981	0.003
Year 2006	−0.210	0.179	−1.174	0.240
Year 2007	−0.405	0.195	−2.077	0.038
Year 2008	−0.494	0.196	−2.516	0.012
Year 2009	−0.827	0.198	−4.179	0
Year 2010	−0.117	0.191	−0.611	0.541
Year 2011	−0.469	0.186	−2.522	0.012
Year 2012	−0.598	0.194	−3.084	0.002
Year 2013	−0.733	0.194	−3.773	<0.001
Year 2014	−0.819	0.189	−4.342	<0.001
Year 2015	−0.840	0.193	−4.350	<0.001
Year 2016	−0.813	0.195	−4.164	<0.001
Year 2017	−1.016	0.216	−4.708	<0.001
Year 2018	−0.865	0.212	−4.073	<0.001
Year 2019	−0.433	0.205	−2.110	0.035
Sin	0.124	0.036	3.460	0.001
Cos	−0.097	0.054	−1.805	0.071
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.861	38.888	<0.001
s(Elevation)		0.006	0.004	0.384
s(Slope)		0.714	2.206	0.072
s(C110)		2.675	43.802	<0.001
s(C112)		1.059	52.284	<0.001
s(C211)		1.131	22.634	<0.001
s(C213)		0.402	0.603	0.215
s(C221)		0.420	0.634	0.216
s(C222)		0.002	0.001	0.409
s(C223)		0.001	0	0.751
s(C224)		0.902	8.998	0.001
s(C231)		0.001	0	0.478
s(C311)		2.327	194.343	<0.001
s(C312)		1.132	78.190	<0.001
s(C313)		1.069	56.371	<0.001
s(C320)		0	0	0.670
s(C321)		0.889	7.069	0.004
s(C330)		0.846	5.084	0.014
s(C410)		0.002	0	0.646
s(C511)		0.698	2.184	0.075

Tree Pipit (*Anthus trivialis*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.504	0.041	−61.520	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.999	2,002.800	<0.001
s(Urb$_{2500}$)		2.935	169.500	<0.001
s(For$_{2500}$)		2.930	1,322.400	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−4.531	0.601	−7.537	<0.001
Year 1995	−0.954	0.392	−2.433	0.015
Year 1996	−0.717	0.351	−2.042	0.041
Year 1999	−0.417	0.294	−1.422	0.155
Year 2000	−0.480	0.286	−1.676	0.094
Year 2001	−0.590	0.301	−1.962	0.050
Year 2002	−0.446	0.308	−1.448	0.148
Year 2003	−0.560	0.305	−1.833	0.067
Year 2004	−0.464	0.312	−1.491	0.136
Year 2005	−0.054	0.286	−0.189	0.850
Year 2006	−0.357	0.300	−1.191	0.234
Year 2007	−0.403	0.293	−1.378	0.168
Year 2008	0.068	0.284	0.241	0.810
Year 2009	−0.243	0.294	−0.828	0.408
Year 2010	−0.529	0.305	−1.734	0.083
Year 2011	−0.125	0.285	−0.436	0.663
Year 2012	−0.062	0.288	−0.216	0.829
Year 2013	−0.419	0.294	−1.425	0.154
Year 2014	−0.272	0.288	−0.944	0.345
Year 2015	−0.497	0.298	−1.670	0.095
Year 2016	−0.436	0.293	−1.489	0.136
Year 2017	−0.465	0.299	−1.554	0.120
Year 2018	−0.461	0.298	−1.546	0.122
Year 2019	−0.513	0.300	−1.708	0.088
Sin	−0.073	0.039	−1.847	0.065
Cos	0.191	0.062	3.091	0.002
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.934	95.377	<0.001
s(Elevation)		2.829	81.805	<0.001
s(Slope)		2.486	25.543	<0.001
s(C110)		0.658	1.832	0.094
s(C112)		1.843	13.770	<0.001
s(C211)		0	0	0.683
s(C213)		0	0	0.778
s(C221)		0.760	3.863	0.023
s(C222)		0.723	0.541	0.387
s(C223)		0	0	0.862
s(C224)		0.001	0	0.941
s(C231)		2.159	207.516	<0.001
s(C311)		0.001	0	0.583
s(C312)		2.839	24.556	<0.001
s(C313)		2.269	20.518	<0.001
s(C320)		0.005	0	0.871
s(C321)		2.842	252.486	<0.001
s(C330)		1.916	13.918	<0.001
s(C410)		0.196	0.249	0.259
s(C511)		0.946	17.296	<0.001

Water Pipit (*Anthus spinoletta*) — Model C-ZINB-GAM

		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.936	0.047	−62.850	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.957	2245.000	<0.001
s(Urb$_{2500}$)		0	0	0.927
s(For$_{2500}$)		2.989	193.600	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−6.617	1.323	−5.003	<0.001
Year 1995	0.271	0.432	0.628	0.530
Year 1996	0.028	0.445	0.064	0.949
Year 1999	−0.469	0.466	−1.007	0.314
Year 2000	−0.444	0.427	−1.039	0.299
Year 2001	−0.388	0.434	−0.894	0.371
Year 2002	−0.210	0.428	−0.490	0.624
Year 2003	−0.763	0.433	−1.764	0.078
Year 2004	−0.513	0.432	−1.188	0.235
Year 2005	−0.258	0.422	−0.612	0.541
Year 2006	−0.584	0.434	−1.347	0.178
Year 2007	−0.156	0.429	−0.363	0.717
Year 2008	0.014	0.425	0.032	0.974
Year 2009	0.064	0.424	0.150	0.881
Year 2010	−0.094	0.430	−0.219	0.827
Year 2011	0.006	0.428	0.013	0.989
Year 2012	−0.273	0.425	−0.643	0.520
Year 2013	−0.187	0.428	−0.438	0.662
Year 2014	−0.240	0.427	−0.563	0.574
Year 2015	−0.098	0.425	−0.230	0.818
Year 2016	−0.270	0.429	−0.630	0.529
Year 2017	−0.258	0.429	−0.601	0.548
Year 2018	−0.149	0.428	−0.348	0.728
Year 2019	−0.203	0.429	−0.472	0.637
Sin	−0.124	0.043	−2.911	0.004
Cos	−0.049	0.063	−0.766	0.444
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.989	195.963	<0.001
s(Elevation)		2.335	121.779	<0.001
s(Slope)		1.841	44.518	<0.001
s(C110)		0.324	0.510	0.208
s(C112)		0.735	2.662	0.052
s(C211)		0	0	0.644
s(C213)		0	0	0.872
s(C221)		0.349	1.046	0.079
s(C222)		0	0	0.806
s(C223)		0	0	0.967
s(C224)		0	0	0.630
s(C231)		0	0	0.646
s(C311)		0.764	2.799	0.048
s(C312)		1.235	163.133	<0.001
s(C313)		1.026	23.254	<0.001
s(C320)		0.920	9.697	<0.001
s(C321)		1.034	21.497	<0.001
s(C330)		0.578	1.359	0.111
s(C410)		0.284	0.422	0.222
s(C511)		0.842	5.120	0.014

Western Yellow Wagtail (*Motacilla flava*) — Model C-ZIP-GAM

Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.986	0.024	−41.700	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.869	798.400	<0.001
s(Urb$_{2500}$)		1.177	767.400	<0.001
s(For$_{2500}$)		2.989	1,371.500	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.260	0.337	−9.663	<0.001
Year 1995	−0.350	0.133	−2.640	0.008
Year 1996	−0.467	0.129	−3.624	<0.001
Year 1999	−0.232	0.142	−1.638	0.101
Year 2000	−0.087	0.119	−0.732	0.464
Year 2001	−0.291	0.120	−2.422	0.015
Year 2002	−0.273	0.139	−1.969	0.049
Year 2003	−0.223	0.133	−1.681	0.093
Year 2004	−0.596	0.156	−3.823	<0.001
Year 2005	−0.425	0.117	−3.626	<0.001
Year 2006	−0.373	0.123	−3.029	0.002
Year 2007	−0.524	0.133	−3.947	<0.001
Year 2008	−0.499	0.138	−3.620	<0.001
Year 2009	−0.361	0.125	−2.899	0.004
Year 2010	−0.564	0.139	−4.046	<0.001
Year 2011	−0.686	0.137	−5.020	<0.001
Year 2012	−0.936	0.145	−6.435	<0.001
Year 2013	−0.487	0.133	−3.670	<0.001
Year 2014	−1.250	0.172	−7.266	<0.001
Year 2015	−0.731	0.143	−5.123	<0.001
Year 2016	−0.864	0.147	−5.894	<0.001
Year 2017	−0.698	0.161	−4.335	<0.001
Year 2018	−0.511	0.158	−3.242	0.001
Year 2019	−0.656	0.160	−4.098	0
Sin	−0.031	0.028	−1.114	0.265
Cos	0.127	0.040	3.138	0.002
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.386	36.306	<0.001
s(Elevation)		0.001	0.001	0.189
s(Slope)		0.989	31.566	<0.001
s(C110)		2.583	63.728	<0.001
s(C112)		1.796	46.375	<0.001
s(C211)		2.971	113.624	<0.001
s(C213)		0.704	1.437	0.145
s(C221)		0.972	12.057	<0.001
s(C222)		0.001	0	0.616
s(C223)		0.721	1.679	0.127
s(C224)		2.243	30.767	<0.001
s(C231)		2.569	26.944	<0.001
s(C311)		1.147	62.737	<0.001
s(C312)		0.830	3.497	0.040
s(C313)		0.859	4.196	0.026
s(C320)		2.746	27.263	<0.001
s(C321)		0.819	2.882	0.060
s(C330)		1.803	7.215	0.015
s(C410)		0.873	3.647	0.039
s(C511)		0.993	8.382	0.003

Grey Wagtail (*Motacilla cinerea*) — Model C-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−5.006	0.335	−14.950	<0.001
Year 1995	0.417	0.367	1.137	0.255
Year 1996	0.555	0.363	1.527	0.127
Year 1999	−0.028	0.357	−0.078	0.938
Year 2000	0.818	0.334	2.446	0.014
Year 2001	0.527	0.358	1.470	0.142
Year 2002	0.293	0.398	0.735	0.462
Year 2003	0.056	0.390	0.142	0.887
Year 2004	0.150	0.411	0.365	0.715
Year 2005	0.198	0.364	0.543	0.587
Year 2006	0.251	0.364	0.690	0.490
Year 2007	0.344	0.377	0.911	0.362
Year 2008	0.313	0.375	0.835	0.404
Year 2009	0.444	0.372	1.195	0.232
Year 2010	0.347	0.375	0.927	0.354
Year 2011	0.032	0.379	0.085	0.932
Year 2012	0.293	0.373	0.785	0.433
Year 2013	0.263	0.365	0.720	0.472
Year 2014	0.389	0.367	1.060	0.289
Year 2015	0.183	0.363	0.506	0.613
Year 2016	0.349	0.360	0.969	0.332
Year 2017	0.312	0.388	0.804	0.421
Year 2018	0.334	0.382	0.875	0.382
Year 2019	0.166	0.390	0.425	0.671
Sin	−0.042	0.059	−0.706	0.481
Cos	−0.428	0.094	−4.546	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		2.943	74.973	<0.001
s(Elevation)		2.808	11.297	0.007
s(Slope)		2.924	42.278	<0.001
s(C110)		2.866	10.761	0.010
s(C112)		2.051	15.864	<0.001
s(C211)		0.001	0	0.489
s(C213)		0.566	1.463	0.107
s(C221)		0.763	2.947	0.049
s(C222)		0.740	2.168	0.087
s(C223)		0.700	1.529	0.139
s(C224)		0.001	0	0.833
s(C231)		0.001	0.001	0.332
s(C311)		2.871	11.252	0.008
s(C312)		2.881	50.661	<0.001
s(C313)		1.623	2.997	0.149
s(C320)		1.465	1.151	0.426
s(C321)		0.001	0.001	0.412
s(C330)		2.673	34.371	<0.001
s(C410)		0.001	0	0.593
s(C511)		2.958	407.525	<0.001

White Wagtail (*Motacilla alba*) — Model C-P-GAM				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.005	0.137	−14.678	<0.001
Year 1995	−0.686	0.186	−3.690	<0.001
Year 1996	−0.623	0.177	−3.531	<0.001
Year 1999	−0.610	0.161	−3.794	<0.001
Year 2000	−0.318	0.153	−2.088	0.037
Year 2001	−0.280	0.160	−1.754	0.079
Year 2002	−0.341	0.179	−1.908	0.056
Year 2003	−0.486	0.175	−2.778	0.005
Year 2004	−0.617	0.199	−3.095	0.002
Year 2005	−0.795	0.167	−4.768	<0.001
Year 2006	−0.654	0.165	−3.969	<0.001
Year 2007	−0.723	0.182	−3.979	<0.001
Year 2008	−0.820	0.187	−4.382	<0.001
Year 2009	−0.875	0.188	−4.659	<0.001
Year 2010	−0.965	0.189	−5.119	<0.001
Year 2011	−0.590	0.166	−3.560	<0.001
Year 2012	−0.991	0.187	−5.298	<0.001
Year 2013	−0.573	0.168	−3.407	<0.001
Year 2014	−0.753	0.171	−4.398	<0.001
Year 2015	−0.829	0.174	−4.762	<0.001
Year 2016	−0.584	0.167	−3.503	<0.001
Year 2017	−0.979	0.201	−4.865	<0.001
Year 2018	−0.696	0.186	−3.739	<0.001
Year 2019	−0.636	0.182	−3.492	<0.001
Sin	−0.059	0.034	−1.757	0.079
Cos	0.073	0.051	1.438	0.150
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		1.905	75.686	<0.001
s(Elevation)		2.893	120.572	<0.001
s(Slope)		2.656	45.114	<0.001
s(C110)		1.929	6.750	0.022
s(C112)		2.270	29.553	<0.001
s(C211)		0.920	10.535	<0.001
s(C213)		0.884	7.721	0.003
s(C221)		1.236	14.036	<0.001
s(C222)		0.901	6.280	0.008
s(C223)		0.609	1.197	0.160
s(C224)		0.834	5.396	0.011
s(C231)		0	0	0.616
s(C311)		2.472	205.990	<0.001
s(C312)		2.142	172.025	<0.001
s(C313)		2.055	132.343	<0.001
s(C320)		1.015	76.723	<0.001
s(C321)		2.781	41.179	<0.001
s(C330)		2.076	41.001	<0.001
s(C410)		0.001	0	0.447
s(C511)		2.761	189.471	<0.001

Eurasian Wren (*Troglodytes troglodytes*) — Model C-ZIP-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.648	0.052	12.550	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.992	1194.390	<0.001
s(Urb$_{2500}$)		2.927	97.270	<0.001
s(For$_{2500}$)		2.990	1050.900	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.295	0.105	−12.325	<0.001
Year 1995	−0.137	0.130	−1.058	0.290
Year 1996	−0.098	0.130	−0.753	0.452
Year 1999	0.070	0.109	0.644	0.520
Year 2000	0.085	0.106	0.799	0.425
Year 2001	0.213	0.113	1.883	0.060
Year 2002	0.033	0.124	0.265	0.791
Year 2003	−0.097	0.127	−0.761	0.447
Year 2004	−0.102	0.140	−0.728	0.466
Year 2005	−0.245	0.122	−2.015	0.044
Year 2006	−0.277	0.121	−2.284	0.022
Year 2007	−0.376	0.132	−2.857	0.004
Year 2008	0.050	0.120	0.413	0.679
Year 2009	−0.352	0.132	−2.665	0.008
Year 2010	−0.249	0.130	−1.920	0.055
Year 2011	−0.058	0.118	−0.497	0.619
Year 2012	−0.314	0.129	−2.436	0.015
Year 2013	−0.516	0.132	−3.898	<0.001
Year 2014	−0.359	0.128	−2.798	0.005
Year 2015	0.020	0.119	0.171	0.865
Year 2016	0.058	0.118	0.487	0.626
Year 2017	0.196	0.122	1.605	0.108
Year 2018	−0.018	0.127	−0.138	0.890
Year 2019	−0.218	0.133	−1.640	0.101
Sin	−0.083	0.022	−3.805	<0.001
Cos	−0.091	0.032	−2.849	0.004
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.336	4.695	0.029
s(Elevation)		2.999	114.151	<0.001
s(Slope)		2.704	72.199	<0.001
s(C110)		2.913	13.473	0.002
s(C112)		0.619	2.201	0.050
s(C211)		0.754	4.787	0.008
s(C213)		0.001	0	0.762
s(C221)		0.703	2.316	0.066
s(C222)		0.002	0.001	0.575
s(C223)		0.882	5.962	0.009
s(C224)		1.843	23.095	<0.001
s(C231)		1.710	38.390	<0.001
s(C311)		2.609	183.394	<0.001
s(C312)		2.926	208.747	<0.001
s(C313)		2.097	180.425	<0.001
s(C320)		2.615	94.183	<0.001
s(C321)		2.603	102.242	<0.001
s(C330)		0.971	35.375	0
s(C410)		0.001	0	0.613
s(C511)		2.884	121.164	< 2e−16

Dunnock (*Prunella modularis*) — Model C-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−7.917	3.509	−2.256	0.024
Year 1995	−1.697	0.559	−3.037	0.002
Year 1996	0.286	0.393	0.726	0.468
Year 1999	−0.151	0.373	−0.405	0.686
Year 2000	0.254	0.362	0.700	0.484
Year 2001	0.419	0.364	1.153	0.249
Year 2002	0.783	0.368	2.124	0.034
Year 2003	0.131	0.372	0.352	0.725
Year 2004	0.259	0.384	0.674	0.500
Year 2005	0.287	0.357	0.803	0.422
Year 2006	0.241	0.381	0.632	0.528
Year 2007	0.285	0.364	0.785	0.433
Year 2008	0.275	0.360	0.765	0.444
Year 2009	0.428	0.360	1.191	0.234
Year 2010	0.374	0.362	1.032	0.302
Year 2011	0.512	0.354	1.447	0.148
Year 2012	0.699	0.352	1.985	0.047
Year 2013	0.679	0.351	1.936	0.053
Year 2014	0.740	0.350	2.114	0.035
Year 2015	0.877	0.348	2.524	0.012
Year 2016	0.580	0.352	1.651	0.099
Year 2017	0.468	0.360	1.300	0.194
Year 2018	0.469	0.360	1.303	0.193
Year 2019	0.628	0.357	1.758	0.079
Sin	−0.134	0.041	−3.247	0.001
Cos	0.001	0.058	0.009	0.993
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		1.864	17.912	<0.001
s(Elevation)		2.982	299.735	<0.001
s(Slope)		2.485	21.832	<0.001
s(C110)		2.807	15.766	<0.001
s(C112)		1.825	10.233	0.003
s(C211)		0.057	0.056	0.317
s(C213)		0.710	0.043	0.807
s(C221)		0.559	0.319	0.450
s(C222)		0.001	0	0.743
s(C223)		0	0	0.867
s(C224)		0.001	0	0.492
s(C231)		2.245	17.772	<0.001
s(C311)		0.894	8.162	0.002
s(C312)		2.778	32.628	<0.001
s(C313)		2.239	7.858	0.018
s(C320)		2.255	40.383	<0.001
s(C321)		2.433	35.524	<0.001
s(C330)		0.002	0.001	0.493
s(C410)		0.004	0.003	0.396
s(C511)		0.001	0.001	0.435

European Robin (*Erithacus rubecula*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.030	0.034	−0.875	0.382
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.985	515.800	<0.001
s(Urb$_{2500}$)		2.963	441.300	<0.001
s(For$_{2500}$)		2.976	1563.600	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.284	0.140	−16.281	<0.001
Year 1995	0.016	0.142	0.115	0.909
Year 1996	0.173	0.138	1.261	0.207
Year 1999	0.285	0.115	2.467	0.014
Year 2000	0.221	0.113	1.948	0.051
Year 2001	0.497	0.118	4.205	<0.001
Year 2002	0.300	0.123	2.440	0.015
Year 2003	0.056	0.132	0.425	0.671
Year 2004	0.090	0.143	0.628	0.530
Year 2005	0.267	0.123	2.166	0.030
Year 2006	0.115	0.123	0.937	0.349
Year 2007	0.316	0.126	2.513	0.012
Year 2008	0.139	0.131	1.062	0.288
Year 2009	0.054	0.134	0.404	0.686
Year 2010	0.076	0.135	0.562	0.574
Year 2011	0.355	0.122	2.904	0.004
Year 2012	0.106	0.131	0.805	0.421
Year 2013	−0.002	0.133	−0.012	0.990
Year 2014	0.194	0.128	1.512	0.131
Year 2015	0.410	0.125	3.285	0.001
Year 2016	0.415	0.124	3.355	0.001
Year 2017	0.417	0.130	3.215	<0.001
Year 2018	0.402	0.131	3.070	0.002
Year 2019	0.152	0.138	1.101	0.271
Sin	0.020	0.020	1.012	0.312
Cos	−0.024	0.029	−0.821	0.411
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.900	159.031	<0.001
s(Elevation)		2.868	146.902	<0.001
s(Slope)		0.001	0	0.594
s(C110)		1.057	96.924	<0.001
s(C112)		1.031	93.059	<0.001
s(C211)		2.189	42.451	<0.001
s(C213)		0.937	10.092	<0.001
s(C221)		0.001	0	0.889
s(C222)		0.001	0	0.604
s(C223)		0.870	5.067	0.016
s(C224)		0.181	0.240	0.248
s(C231)		0.001	0	0.565
s(C311)		2.551	399.320	<0.001
s(C312)		1.388	376.424	<0.001
s(C313)		2.147	412.555	<0.001
s(C320)		2.152	58.493	<0.001
s(C321)		2.818	26.209	<0.001
s(C330)		1.208	1.970	0.189
s(C410)		0.882	6.815	0.005
s(C511)		1.817	10.741	0.003

Common Nigthingale (*Luscinia megarhynchos*) — Model C-ZIP-GAM

		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	1.323	0.041	32.000	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.991	2,115.900	<0.001
s(Urb_{2500})		2.991	1,970.500	<0.001
s(For_{2500})		2.651	936.900	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.057	0.106	−9.924	<0.001
Year 1995	−0.546	0.065	−8.352	<0.001
Year 1996	−0.562	0.069	−8.108	<0.001
Year 1999	−0.441	0.063	−6.969	<0.001
Year 2000	−0.518	0.062	−8.414	<0.001
Year 2001	−0.665	0.064	−10.408	<0.001
Year 2002	−0.802	0.081	−9.858	<0.001
Year 2003	−0.615	0.078	−7.911	<0.001
Year 2004	−0.594	0.095	−6.249	<0.001
Year 2005	−0.488	0.062	−7.927	<0.001
Year 2006	−0.592	0.064	−9.236	<0.001
Year 2007	−0.300	0.066	−4.544	<0.001
Year 2008	−0.390	0.070	−5.595	<0.001
Year 2009	−0.473	0.068	−6.912	<0.001
Year 2010	−0.457	0.068	−6.699	<0.001
Year 2011	−0.623	0.071	−8.821	<0.001
Year 2012	−0.699	0.074	−9.476	<0.001
Year 2013	−0.473	0.068	−6.947	<0.001
Year 2014	−0.537	0.072	−7.511	<0.001
Year 2015	−0.722	0.075	−9.663	<0.001
Year 2016	−0.594	0.072	−8.270	<0.001
Year 2017	−0.460	0.076	−6.026	<0.001
Year 2018	−0.496	0.077	−6.473	<0.001
Year 2019	−0.435	0.076	−5.728	<0.001
Sin	−0.046	0.016	−2.923	0.003
Cos	−0.007	0.024	−0.280	0.779
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.957	37.354	<0.001
s(Elevation)		2.114	110.467	<0.001
s(Slope)		2.954	111.076	<0.001
s(C110)		2.952	181.908	<0.001
s(C112)		1.021	180.278	<0.001
s(C211)		1.721	32.042	<0.001
s(C213)		2.813	15.533	<0.001
s(C221)		0.547	1.104	0.148
s(C222)		0	0	0.660
s(C223)		1.826	4.165	0.094
s(C224)		1.913	33.165	<0.001
s(C231)		1.061	28.730	<0.001
s(C311)		2.924	280.454	<0.001
s(C312)		0	0	0.917
s(C313)		2.594	6.399	0.061
s(C320)		1.011	64.455	<0.001
s(C321)		0	0	0.704
s(C330)		0	0	0.962
s(C410)		0.875	10.867	<0.001
s(C511)		1.966	51.633	<0.001

Black Redstart (*Phoenicurus ochruros*) — Model C-ZIP-GAM

Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.441	0.048	−9.120	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.962	1147.600	<0.001
s(Urb$_{2500}$)		1.095	212.100	<0.001
s(For$_{2500}$)		2.342	27.200	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.120	0.326	−9.582	<0.001
Year 1995	−0.020	0.365	−0.056	0.955
Year 1996	−0.196	0.389	−0.504	0.614
Year 1999	0.180	0.348	0.517	0.605
Year 2000	0.280	0.336	0.834	0.405
Year 2001	0.347	0.343	1.011	0.312
Year 2002	0.400	0.348	1.151	0.250
Year 2003	0.484	0.336	1.440	0.150
Year 2004	0.531	0.340	1.562	0.118
Year 2005	0.599	0.330	1.812	0.070
Year 2006	0.343	0.341	1.006	0.314
Year 2007	0.562	0.338	1.662	0.097
Year 2008	0.443	0.338	1.312	0.190
Year 2009	0.551	0.337	1.633	0.102
Year 2010	0.502	0.338	1.487	0.137
Year 2011	0.732	0.332	2.204	0.028
Year 2012	0.621	0.333	1.866	0.062
Year 2013	0.712	0.332	2.141	0.032
Year 2014	0.778	0.329	2.365	0.018
Year 2015	0.534	0.332	1.605	0.109
Year 2016	0.597	0.332	1.799	0.072
Year 2017	0.440	0.340	1.296	0.195
Year 2018	0.653	0.337	1.934	0.053
Year 2019	0.505	0.339	1.488	0.137
Sin	−0.009	0.034	−0.265	0.791
Cos	0.017	0.052	0.320	0.749
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.771	27.221	<0.001
s(Elevation)		2.906	186.283	<0.001
s(Slope)		0	0	0.540
s(C110)		1.767	82.392	<0.001
s(C112)		2.788	157.183	<0.001
s(C211)		0	0	0.830
s(C213)		0	0	0.806
s(C221)		0.031	0.032	0.306
s(C222)		0.001	0	0.466
s(C223)		0.658	1.125	0.191
s(C224)		0	0	0.553
s(C231)		1.921	10.728	<0.001
s(C311)		2.178	52.404	<0.001
s(C312)		2.180	39.294	<0.001
s(C313)		2.559	34.261	<0.001
s(C320)		2.266	14.930	<0.001
s(C321)		0.815	3.559	0.032
s(C330)		2.471	53.138	<0.001
s(C410)		0.464	0.827	0.180
s(C511)		0.670	2.013	0.082

Common Redstart (*Phoenicurus Phoenicurus*) — Model C-ZIP-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.268	0.024	11.020	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.999	1672.400	<0.001
s(Urb_{2500})		0.981	24.140	<0.001
s(For_{2500})		2.335	133.800	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.772	0.213	−12.989	<0.001
Year 1995	0.327	0.250	1.307	0.191
Year 1996	−0.224	0.262	−0.854	0.393
Year 1999	0.594	0.222	2.677	0.007
Year 2000	0.923	0.215	4.288	<0.001
Year 2001	0.753	0.226	3.329	<0.001
Year 2002	0.675	0.238	2.840	0.005
Year 2003	0.415	0.246	1.688	0.091
Year 2004	0.240	0.276	0.870	0.384
Year 2005	0.868	0.221	3.925	<0.001
Year 2006	0.716	0.222	3.220	0.001
Year 2007	0.824	0.226	3.647	<0.001
Year 2008	0.867	0.228	3.796	<0.001
Year 2009	0.644	0.234	2.751	0.006
Year 2010	0.792	0.227	3.481	<0.001
Year 2011	0.865	0.220	3.940	<0.001
Year 2012	0.826	0.224	3.694	<0.001
Year 2013	1.004	0.220	4.559	<0.001
Year 2014	0.995	0.218	4.558	<0.001
Year 2015	0.836	0.224	3.740	<0.001
Year 2016	0.666	0.225	2.968	0.003
Year 2017	0.667	0.237	2.819	0.005
Year 2018	0.541	0.241	2.245	0.025
Year 2019	0.642	0.236	2.716	0.007
Sin	−0.077	0.030	−2.588	0.010
Cos	0.029	0.045	0.657	0.511
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.290	4.697	0.025
s(Elevation)		2.548	59.882	<0.001
s(Slope)		2.524	53.958	<0.001
s(C110)		1.107	243.910	<0.001
s(C112)		2.924	312.361	<0.001
s(C211)		0.133	0.249	0.163
s(C213)		0.878	7.432	0.003
s(C221)		2.267	85.016	<0.001
s(C222)		0.872	10.295	<0.001
s(C223)		1.783	2.915	0.185
s(C224)		0	0	0.777
s(C231)		2.325	118.859	<0.001
s(C311)		2.707	35.278	<0.001
s(C312)		0.002	0	0.853
s(C313)		1.873	5.090	0.053
s(C320)		0.833	5.676	0.008
s(C321)		2.738	44.594	<0.001
s(C330)		0.011	0.011	0.314
s(C410)		0.892	7.395	0.004
s(C511)		0.679	1.978	0.087

European Stonechat (*Saxicola rubicola*) — Model C-ZIP-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.162	0.020	−57.030	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.127	494.500	<0.001
s(Urb$_{2500}$)		0.002	0	1.000
s(For$_{2500}$)		2.943	451.500	<0.001

Count component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.886	0.258	−11.180	<0.001
Year 1995	−0.337	0.316	−1.067	0.286
Year 1996	0.550	0.273	2.013	0.044
Year 1999	0.506	0.281	1.796	0.073
Year 2000	0.538	0.265	2.027	0.043
Year 2001	0.769	0.265	2.901	0.004
Year 2002	0.568	0.294	1.934	0.053
Year 2003	0.443	0.303	1.461	0.144
Year 2004	0.813	0.298	2.724	0.006
Year 2005	0.742	0.259	2.870	0.004
Year 2006	−0.485	0.308	−1.574	0.116
Year 2007	0.205	0.287	0.715	0.475
Year 2008	0.047	0.300	0.158	0.874
Year 2009	−0.751	0.359	−2.092	0.036
Year 2010	−0.369	0.326	−1.132	0.258
Year 2011	−1.109	0.366	−3.032	0.002
Year 2012	−1.311	0.410	−3.197	0.001
Year 2013	−0.418	0.320	−1.307	0.191
Year 2014	−0.851	0.375	−2.273	0.023
Year 2015	−0.580	0.336	−1.728	0.084
Year 2016	−0.645	0.340	−1.894	0.058
Year 2017	−1.150	0.447	−2.576	0.010
Year 2018	−0.670	0.384	−1.745	0.081
Year 2019	−1.455	0.507	−2.871	0.004
Sin	0.033	0.056	0.592	0.554
Cos	−0.002	0.083	−0.026	0.979
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.970	95.359	<0.001
s(Elevation)		2.784	76.100	<0.001
s(Slope)		1.001	8.161	0.003
s(C110)		1.656	36.969	<0.001
s(C112)		1.870	11.101	0.002
s(C211)		2.835	44.528	<0.001
s(C213)		0	0	0.905
s(C221)		2.529	31.753	<0.001
s(C222)		0.002	0	0.968
s(C223)		0.004	0.003	0.350
s(C224)		0	0	0.507
s(C231)		1.971	64.175	<0.001
s(C311)		2.105	30.630	<0.001
s(C312)		0.838	5.439	0.010
s(C313)		0.844	4.919	0.015
s(C320)		0.919	14.975	<0.001
s(C321)		0.001	0	0.456
s(C330)		0.001	0	0.409
s(C410)		1.562	3.312	0.115
s(C511)		0	0	0.532

Northern Wheatear (*Oenanthe oenanthe*) — Model C-P-GAM				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−46.028	16.412	−2.805	0.005
Year 1995	−0.007	0.621	−0.011	0.991
Year 1996	−0.253	0.637	−0.397	0.691
Year 1999	−0.584	0.646	−0.904	0.366
Year 2000	−0.869	0.618	−1.407	0.159
Year 2001	−0.631	0.630	−1.001	0.317
Year 2002	−0.914	0.634	−1.442	0.149
Year 2003	−1.308	0.635	−2.058	0.040
Year 2004	−1.120	0.639	−1.753	0.080
Year 2005	−0.325	0.601	−0.541	0.589
Year 2006	−0.411	0.611	−0.672	0.502
Year 2007	−0.383	0.611	−0.626	0.531
Year 2008	−0.400	0.608	−0.658	0.510
Year 2009	−0.153	0.603	−0.253	0.800
Year 2010	−0.210	0.608	−0.346	0.729
Year 2011	−0.170	0.608	−0.279	0.780
Year 2012	−0.494	0.605	−0.817	0.414
Year 2013	−0.393	0.609	−0.646	0.518
Year 2014	−0.511	0.608	−0.840	0.401
Year 2015	−0.371	0.606	−0.611	0.541
Year 2016	−0.764	0.619	−1.234	0.217
Year 2017	−0.733	0.617	−1.188	0.235
Year 2018	−0.824	0.621	−1.327	0.184
Year 2019	−0.973	0.626	−1.554	0.120
Sin	−0.096	0.064	−1.504	0.132
Cos	−0.120	0.097	−1.245	0.213
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		1.971	80.389	<0.001
s(Elevation)		2.838	91.077	<0.001
s(Slope)		1.647	26.696	<0.001
s(C110)		0.002	0	0.930
s(C112)		1.890	6.191	0.034
s(C211)		0.661	0.703	0.302
s(C213)		0	0	1.000
s(C221)		1.258	15.182	<0.001
s(C222)		0	0	0.929
s(C223)		0	0	0.967
s(C224)		0.001	0	0.755
s(C231)		0.001	0.001	0.315
s(C311)		1.054	15.231	<0.001
s(C312)		2.455	50.942	<0.001
s(C313)		0.960	13.382	<0.001
s(C320)		2.072	5.880	0.041
s(C321)		1.779	22.435	<0.001
s(C330)		2.350	4.676	0.106
s(C410)		0.002	0.001	0.560
s(C511)		0.772	3.066	0.046

Common Blackbird (*Turdus merula*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	6.102	0.186	32.800	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.973	614.400	<0.001
s(Urb$_{2500}$)		1.019	417.700	<0.001
s(For$_{2500}$)		2.970	300.700	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.341	0.042	8.152	<0.001
Year 1995	−0.366	0.055	−6.632	<0.001
Year 1996	−0.437	0.055	−7.916	<0.001
Year 1999	−0.150	0.048	−3.133	0.002
Year 2000	−0.465	0.048	−9.701	<0.001
Year 2001	−0.382	0.051	−7.435	<0.001
Year 2002	−0.410	0.057	−7.158	<0.001
Year 2003	−0.517	0.061	−8.534	<0.001
Year 2004	−0.671	0.071	−9.442	<0.001
Year 2005	−0.514	0.052	−9.936	<0.001
Year 2006	−0.491	0.050	−9.765	<0.001
Year 2007	−0.434	0.055	−7.909	<0.001
Year 2008	−0.442	0.055	−7.980	<0.001
Year 2009	−0.242	0.052	−4.618	<0.001
Year 2010	−0.300	0.053	−5.690	<0.001
Year 2011	−0.339	0.051	−6.710	<0.001
Year 2012	−0.337	0.053	−6.384	<0.001
Year 2013	−0.290	0.052	−5.547	<0.001
Year 2014	−0.312	0.051	−6.165	<0.001
Year 2015	−0.284	0.052	−5.487	<0.001
Year 2016	−0.176	0.051	−3.453	<0.001
Year 2017	−0.102	0.054	−1.880	0.060
Year 2018	−0.161	0.055	−2.936	0.003
Year 2019	−0.125	0.054	−2.308	0.021
Sin	0.002	0.011	0.213	0.831
Cos	−0.018	0.016	−1.124	0.261
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.741	18.702	<0.001
s(Elevation)		2.940	517.923	<0.001
s(Slope)		2.787	71.669	<0.001
s(C110)		1.117	31.062	<0.001
s(C112)		2.793	14.185	0.001
s(C211)		2.436	48.299	<0.001
s(C213)		1.460	114.755	<0.001
s(C221)		2.670	13.395	0.002
s(C222)		0.004	0.004	0.288
s(C223)		0.531	1.258	0.123
s(C224)		0.466	1.174	0.110
s(C231)		2.841	11.630	0.005
s(C311)		2.483	45.685	<0.001
s(C312)		1.776	15.874	<0.001
s(C313)		2.314	22.360	<0.001
s(C320)		1.913	9.153	0.006
s(C321)		2.942	41.454	<0.001
s(C330)		0.967	22.912	<0.001
s(C410)		0.001	0	0.474
s(C511)		2.049	15.411	<0.001

Song Thrush (*Turdus philomelos*) — Model C-ZIP-GAM

Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.425	0.084	−40.980	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.314	2,405.000	<0.001
s(Urb$_{2500}$)		0	0	0.564
s(For$_{2500}$)		2.996	1,408.000	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−4.322	0.822	−5.259	<0.001
Year 1995	1.274	0.564	2.259	0.024
Year 1996	0.294	0.629	0.468	0.640
Year 1999	1.321	0.519	2.544	0.011
Year 2000	1.060	0.519	2.041	0.041
Year 2001	1.449	0.521	2.783	0.005
Year 2002	1.540	0.532	2.897	0.004
Year 2003	1.706	0.526	3.245	0.001
Year 2004	1.170	0.573	2.042	0.041
Year 2005	1.436	0.526	2.731	0.006
Year 2006	1.724	0.525	3.284	0.001
Year 2007	1.757	0.520	3.379	<0.001
Year 2008	2.142	0.516	4.153	<0.001
Year 2009	1.903	0.521	3.652	<0.001
Year 2010	1.690	0.526	3.214	0.001
Year 2011	1.965	0.517	3.801	<0.001
Year 2012	2.103	0.516	4.077	<0.001
Year 2013	2.593	0.509	5.098	<0.001
Year 2014	2.055	0.514	3.998	<0.001
Year 2015	2.300	0.512	4.491	<0.001
Year 2016	2.436	0.510	4.773	<0.001
Year 2017	2.452	0.514	4.768	<0.001
Year 2018	2.590	0.513	5.049	<0.001
Year 2019	2.475	0.515	4.811	<0.001
Sin	−0.007	0.039	−0.174	0.862
Cos	0.065	0.054	1.210	0.226
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.999	114.672	<0.001
s(Elevation)		2.254	37.870	<0.001
s(Slope)		1.961	10.915	0.002
s(C110)		2.795	11.671	0.005
s(C112)		1.825	3.752	0.108
s(C211)		0.006	0.009	0.206
s(C213)		0	0	0.530
s(C221)		0	0	0.705
s(C222)		0	0	0.782
s(C223)		0.608	0.163	0.605
s(C224)		0	0	0.758
s(C231)		0.977	6.032	0.006
s(C311)		2.718	42.245	<0.001
s(C312)		2.297	75.536	<0.001
s(C313)		1.232	47.050	<0.001
s(C320)		0.855	2.588	0.067
s(C321)		2.296	21.632	<0.001
s(C330)		0	0	0.760
s(C410)		0	0	0.620
s(C511)		0	0	0.350

Mistle Thrush (*Turdus viscivorus*) — Model C-ZIP-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.050	0.045	−67.660	<0.001

Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.999	3,103.800	<0.001
s(Urb$_{2500}$)		0	0	0.888
s(For$_{2500}$)		1.437	186.200	<0.001

Count component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−13.327	45.476	−0.293	0.769
Year 1995	0.769	0.804	0.957	0.338
Year 1996	0.641	0.805	0.796	0.426
Year 1999	1.168	0.734	1.591	0.112
Year 2000	0.513	0.751	0.684	0.494
Year 2001	−0.337	0.820	−0.411	0.681
Year 2002	0.942	0.767	1.228	0.219
Year 2003	0.612	0.767	0.798	0.425
Year 2004	0.685	0.820	0.835	0.404
Year 2005	0.896	0.746	1.202	0.229
Year 2006	1.292	0.759	1.701	0.089
Year 2007	0.835	0.750	1.114	0.265
Year 2008	0.999	0.750	1.332	0.183
Year 2009	1.201	0.745	1.611	0.107
Year 2010	1.399	0.740	1.891	0.059
Year 2011	1.658	0.726	2.283	0.022
Year 2012	1.104	0.748	1.476	0.140
Year 2013	1.485	0.730	2.035	0.042
Year 2014	1.774	0.724	2.451	0.014
Year 2015	1.417	0.734	1.931	0.053
Year 2016	1.525	0.730	2.090	0.037
Year 2017	1.453	0.744	1.954	0.051
Year 2018	1.526	0.742	2.058	0.040
Year 2019	1.220	0.751	1.625	0.104
Sin	−0.195	0.069	−2.839	0.005
Cos	0.127	0.097	1.300	0.194

Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.085	2.118	0.138
s(Elevation)		2.754	25.728	<0.001
s(Slope)		1.617	11.042	0.001
s(C110)		0	0	0.692
s(C112)		0.854	3.282	0.047
s(C211)		0	0	0.377
s(C213)		0.002	0	0.741
s(C221)		0.001	0	0.346
s(C222)		0	0	0.721
s(C223)		0	0	0.875
s(C224)		0.398	0.036	0.763
s(C231)		1.765	12.243	<0.001
s(C311)		0	0	0.561
s(C312)		2.803	77.756	<0.001
s(C313)		1.694	30.072	<0.001
s(C320)		2.466	9.793	0.008
s(C321)		2.432	20.050	<0.001
s(C330)		0	0	0.419
s(C410)		0	0	0.797
s(C511)		0.003	0.003	0.331

Cetti's Warbler (*Cettia cetti*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.328	0.026	−50.340	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.148	533.500	<0.001
s(Urb$_{2500}$)		2.989	1,014.300	<0.001
s(For$_{2500}$)		2.997	863.100	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−4.385	0.823	−5.325	<0.001
Year 1995	−0.070	0.229	−0.305	0.761
Year 1996	0.138	0.245	0.565	0.572
Year 1999	0.561	0.221	2.542	0.011
Year 2000	0.537	0.222	2.421	0.015
Year 2001	0.925	0.216	4.284	<0.001
Year 2002	−0.069	0.298	−0.230	0.818
Year 2003	−0.238	0.298	−0.796	0.426
Year 2004	0.624	0.275	2.264	0.024
Year 2005	0.419	0.219	1.913	0.056
Year 2006	−0.437	0.250	−1.753	0.080
Year 2007	0.078	0.250	0.310	0.757
Year 2008	0.438	0.241	1.820	0.069
Year 2009	−0.144	0.255	−0.566	0.572
Year 2010	−0.532	0.284	−1.873	0.061
Year 2011	−0.187	0.260	−0.721	0.471
Year 2012	−0.726	0.306	−2.371	0.018
Year 2013	−0.960	0.316	−3.040	0.002
Year 2014	−0.834	0.322	−2.592	0.010
Year 2015	−0.320	0.271	−1.184	0.236
Year 2016	−0.078	0.261	−0.300	0.764
Year 2017	−0.595	0.303	−1.967	0.049
Year 2018	−0.280	0.284	−0.986	0.324
Year 2019	−0.326	0.291	−1.121	0.262
Sin	0.044	0.045	0.978	0.328
Cos	−0.179	0.069	−2.576	0.010
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.988	258.506	<0.001
s(Elevation)		2.720	78.830	<0.001
s(Slope)		2.829	10.599	0.010
s(C110)		1.028	46.390	<0.001
s(C112)		0.996	42.708	<0.001
s(C211)		2.117	13.297	<0.001
s(C213)		0.477	0.982	0.150
s(C221)		0.856	5.460	0.011
s(C222)		0.001	0.001	0.443
s(C223)		0.001	0.001	0.486
s(C224)		2.004	8.385	0.010
s(C231)		0.001	0	0.645
s(C311)		2.246	29.157	<0.001
s(C312)		0.002	0.001	0.428
s(C313)		0.828	3.154	0.050
s(C320)		2.809	29.063	<0.001
s(C321)		0.001	0	0.690
s(C330)		0.001	0	0.824
s(C410)		2.880	293.059	<0.001
s(C511)		2.375	61.413	<0.001

Melodius Warbler (*Hippolais polyglotta*) — Model C-ZIP-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.706	0.028	−61.690	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.810	434.730	<0.001
s(Urb$_{2500}$)		1.050	39.040	<0.001
s(For$_{2500}$)		2.958	278.180	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.588	0.369	−9.721	<0.001
Year 1995	0.105	0.383	0.274	0.784
Year 1996	−0.958	0.587	−1.633	0.103
Year 1999	0.589	0.347	1.698	0.089
Year 2000	0.101	0.366	0.277	0.782
Year 2001	0.324	0.361	0.895	0.371
Year 2002	0.400	0.385	1.040	0.299
Year 2003	0.459	0.379	1.213	0.225
Year 2004	0.110	0.548	0.202	0.840
Year 2005	0.132	0.368	0.358	0.720
Year 2006	0.460	0.348	1.322	0.186
Year 2007	0.599	0.359	1.671	0.095
Year 2008	0.732	0.383	1.910	0.056
Year 2009	0.855	0.356	2.406	0.016
Year 2010	0.935	0.347	2.696	0.007
Year 2011	0.920	0.343	2.685	0.007
Year 2012	1.151	0.338	3.404	<0.001
Year 2013	0.965	0.345	2.795	0.005
Year 2014	0.958	0.348	2.756	0.006
Year 2015	1.451	0.343	4.229	<0.001
Year 2016	0.697	0.364	1.917	0.055
Year 2017	0.785	0.375	2.093	0.036
Year 2018	0.847	0.376	2.249	0.025
Year 2019	1.007	0.359	2.801	0.005
Sin	−0.097	0.062	−1.557	0.120
Cos	0.055	0.098	0.555	0.579
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.808	26.327	<0.001
s(Elevation)		2.124	12.038	0.001
s(Slope)		2.600	5.539	0.086
s(C110)		2.866	20.838	<0.001
s(C112)		0.973	43.136	<0.001
s(C211)		2.202	23.420	<0.001
s(C213)		0.951	18.540	<0.001
s(C221)		0.895	11.618	<0.001
s(C222)		0.001	0	0.738
s(C223)		0.001	0.001	0.402
s(C224)		1.975	8.857	0.008
s(C231)		0	0	0.655
s(C311)		2.341	23.101	<0.001
s(C312)		0.560	1.181	0.145
s(C313)		1.888	4.066	0.105
s(C320)		2.270	92.558	<0.001
s(C321)		0	0	0.892
s(C330)		1.867	35.193	<0.001
s(C410)		1.897	3.395	0.157
s(C511)		1.725	14.918	<0.001

Lesser Whitethroat (*Curruca curruca*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.533	0.056	−62.690	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.992	2,907.300	<0.001
s(Urb$_{2500}$)		0	0	1.000
s(For$_{2500}$)		2.983	175.800	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−12.104	33.019	−0.367	0.714
Year 1995	−0.350	0.605	−0.579	0.562
Year 1996	−0.521	0.621	−0.838	0.402
Year 1999	−0.096	0.545	−0.176	0.860
Year 2000	−0.295	0.556	−0.530	0.596
Year 2001	0.185	0.552	0.335	0.738
Year 2002	−1.289	0.771	−1.673	0.094
Year 2003	−0.426	0.576	−0.739	0.460
Year 2004	−0.669	0.635	−1.054	0.292
Year 2005	−0.276	0.546	−0.506	0.613
Year 2006	−0.021	0.568	−0.037	0.970
Year 2007	0.526	0.532	0.989	0.323
Year 2008	−0.110	0.543	−0.203	0.839
Year 2009	−0.147	0.548	−0.269	0.788
Year 2010	0.158	0.538	0.294	0.769
Year 2011	0.332	0.531	0.624	0.533
Year 2012	0.295	0.534	0.553	0.581
Year 2013	0.173	0.534	0.323	0.746
Year 2014	0.282	0.533	0.530	0.596
Year 2015	−0.043	0.535	−0.080	0.936
Year 2016	0.245	0.530	0.461	0.645
Year 2017	0.153	0.540	0.283	0.777
Year 2018	0.069	0.543	0.128	0.899
Year 2019	−0.005	0.544	−0.008	0.993
Sin	−0.254	0.064	−3.939	<0.001
Cos	−0.117	0.086	−1.355	0.176
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.875	26.971	<0.001
s(Elevation)		0.001	0	0.722
s(Slope)		2.194	14.377	<0.001
s(C110)		1.832	10.298	0.003
s(C112)		0.916	7.685	0.003
s(C211)		0.768	2.913	0.047
s(C213)		0.001	0	0.550
s(C221)		0.610	0.355	0.445
s(C222)		0.001	0	0.772
s(C223)		0.655	0.048	0.786
s(C224)		0.384	0.066	0.679
s(C231)		1.004	8.518	0.002
s(C311)		0.943	9.521	<0.001
s(C312)		2.406	33.668	<0.001
s(C313)		1.808	7.924	0.008
s(C320)		2.357	27.009	<0.001
s(C321)		2.930	29.635	<0.001
s(C330)		2.775	21.759	<0.001
s(C410)		0.007	0.008	0.289
s(C511)		0.760	2.366	0.077

Eurasian Blackcap (*Sylvia atricapilla*) — Model C-ZIP-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	8.224	0.393	20.950	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.991	1,225.920	<0.001
s(Urb$_{2500}$)		2.969	160.510	<0.001
s(For$_{2500}$)		2.549	62.870	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.243	0.043	5.587	<0.001
Year 1995	−0.248	0.056	−4.450	<0.001
Year 1996	−0.143	0.055	−2.612	0.009
Year 1999	0.001	0.048	0.025	0.980
Year 2000	−0.107	0.048	−2.246	0.025
Year 2001	−0.092	0.051	−1.814	0.070
Year 2002	−0.126	0.056	−2.257	0.024
Year 2003	−0.187	0.058	−3.221	0.001
Year 2004	−0.299	0.068	−4.422	<0.001
Year 2005	−0.145	0.051	−2.855	0.004
Year 2006	−0.126	0.050	−2.513	0.012
Year 2007	−0.066	0.054	−1.222	0.222
Year 2008	−0.015	0.054	−0.282	0.778
Year 2009	−0.008	0.053	−0.148	0.882
Year 2010	0.035	0.053	0.667	0.505
Year 2011	0.053	0.050	1.046	0.295
Year 2012	−0.015	0.053	−0.286	0.775
Year 2013	−0.102	0.054	−1.892	0.059
Year 2014	−0.103	0.053	−1.945	0.052
Year 2015	−0.111	0.054	−2.066	0.039
Year 2016	−0.120	0.054	−2.233	0.026
Year 2017	0.031	0.056	0.557	0.577
Year 2018	−0.030	0.056	−0.533	0.594
Year 2019	0.012	0.056	0.211	0.833
Sin	−0.010	0.010	−1.050	0.294
Cos	−0.030	0.015	−2.038	0.042
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.952	73.506	<0.001
s(Elevation)		2.577	206.946	<0.001
s(Slope)		2.815	67.971	<0.001
s(C110)		2.655	49.698	<0.001
s(C112)		2.927	56.104	<0.001
s(C211)		1.754	23.568	<0.001
s(C213)		0	0	0.652
s(C221)		2.249	8.264	0.015
s(C222)		0.002	0	0.709
s(C223)		2.542	10.151	0.008
s(C224)		1.950	97.983	<0.001
s(C231)		0.832	7.419	0.002
s(C311)		2.942	513.563	<0.001
s(C312)		1.808	21.421	<0.001
s(C313)		2.621	185.940	<0.001
s(C320)		2.214	49.262	<0.001
s(C321)		2.873	35.964	<0.001
s(C330)		0.919	11.937	<0.001
s(C410)		2.772	5.764	0.100
s(C511)		1.966	23.925	<0.001

Western Bonelli's Warbler (*Phylloscopus bonelli*) — Model C-ZINB-GAM

Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.444	0.037	−66.350	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.920	359.300	<0.001
s(Urb$_{2500}$)		1.067	144.900	<0.001
s(For$_{2500}$)		2.335	114.700	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−5.220	4.888	−1.068	0.286
Year 1995	1.184	0.351	3.371	<0.001
Year 1996	0.827	0.363	2.279	0.023
Year 1999	1.285	0.321	4.006	<0.001
Year 2000	1.041	0.317	3.291	0.001
Year 2001	1.148	0.329	3.486	<0.001
Year 2002	1.022	0.344	2.966	0.003
Year 2003	0.883	0.350	2.523	0.012
Year 2004	0.647	0.370	1.750	0.080
Year 2005	1.034	0.331	3.121	0.002
Year 2006	0.533	0.361	1.476	0.140
Year 2007	0.901	0.342	2.631	0.009
Year 2008	1.000	0.335	2.984	0.003
Year 2009	0.728	0.353	2.064	0.039
Year 2010	0.977	0.344	2.839	0.005
Year 2011	0.937	0.337	2.781	0.005
Year 2012	1.170	0.333	3.508	<0.001
Year 2013	1.268	0.332	3.821	<0.001
Year 2014	1.206	0.338	3.569	<0.001
Year 2015	1.236	0.338	3.661	<0.001
Year 2016	1.435	0.330	4.344	<0.001
Year 2017	1.305	0.339	3.846	<0.001
Year 2018	1.179	0.345	3.414	<0.001
Year 2019	1.225	0.343	3.567	<0.001
Sin	0.190	0.042	4.473	<0.001
Cos	−0.443	0.067	−6.581	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.000	332.708	<0.001
s(Elevation)		1.091	22.044	<0.001
s(Slope)		2.827	170.716	<0.001
s(C110)		0.860	5.078	0.014
s(C112)		0.985	22.914	<0.001
s(C211)		0.898	5.892	0.009
s(C213)		0.741	0.039	0.818
s(C221)		0.754	2.628	0.061
s(C222)		0.648	1.544	0.122
s(C223)		0	0	0.545
s(C224)		0.001	0	0.506
s(C231)		0.001	0	0.378
s(C311)		1.117	23.209	<0.001
s(C312)		0.002	0	0.842
s(C313)		0.262	0.349	0.236
s(C320)		0.937	12.215	<0.001
s(C321)		0.932	10.762	<0.001
s(C330)		0.966	23.641	<0.001
s(C410)		0	0	0.768
s(C511)		0.973	34.796	<0.001

Common Chiffchaff (*Phylloscopus collybita*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.679	0.032	−21.230	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.990	2,239.300	<0.001
s(Urb_{2500})		0	0	0.835
s(For_{2500})		2.995	968.400	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.880	0.162	−11.575	<0.001
Year 1995	0.145	0.145	1.001	0.317
Year 1996	0.527	0.134	3.930	<0.001
Year 1999	0.077	0.125	0.615	0.538
Year 2000	−0.090	0.123	−0.728	0.466
Year 2001	−0.055	0.132	−0.415	0.678
Year 2002	−0.390	0.145	−2.685	0.007
Year 2003	−0.230	0.142	−1.619	0.105
Year 2004	−0.107	0.151	−0.709	0.478
Year 2005	−0.396	0.139	−2.853	0.004
Year 2006	−0.499	0.147	−3.394	<0.001
Year 2007	−0.224	0.139	−1.609	0.108
Year 2008	−0.106	0.136	−0.778	0.437
Year 2009	−0.493	0.151	−3.265	0.001
Year 2010	−0.191	0.142	−1.353	0.176
Year 2011	−0.234	0.136	−1.727	0.084
Year 2012	−0.770	0.157	−4.913	<0.001
Year 2013	−0.572	0.146	−3.907	<0.001
Year 2014	−0.423	0.144	−2.948	0.003
Year 2015	−0.203	0.137	−1.475	0.140
Year 2016	−0.114	0.134	−0.848	0.397
Year 2017	−0.380	0.148	−2.574	0.010
Year 2018	−0.409	0.149	−2.735	0.006
Year 2019	−0.341	0.148	−2.305	0.021
Sin	0.003	0.024	0.115	0.909
Cos	−0.007	0.035	−0.194	0.846
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.938	199.344	<0.001
s(Elevation)		2.999	187.752	<0.001
s(Slope)		2.206	42.085	<0.001
s(C110)		1.020	48.577	<0.001
s(C112)		0.987	50.352	<0.001
s(C211)		0.933	12.981	<0.001
s(C213)		0.863	4.100	0.029
s(C221)		0.780	3.195	0.042
s(C222)		0.842	4.788	0.017
s(C223)		0.796	2.820	0.060
s(C224)		0.003	0.003	0.334
s(C231)		0	0	0.389
s(C311)		1.976	42.642	<0.001
s(C312)		2.426	57.767	<0.001
s(C313)		2.455	75.281	<0.001
s(C320)		2.065	91.614	<0.001
s(C321)		2.800	36.050	<0.001
s(C330)		0.905	9.699	<0.001
s(C410)		0.671	2.327	0.062
s(C511)		2.836	36.915	<0.001

Goldcrest (*Regulus regulus*) — Model C-ZIP-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.747	0.032	−54.360	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.993	3335.700	<0.001
s(Urb_{2500})		0.002	0	0.787
s(For_{2500})		2.372	158.900	<0.001

Count component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−17.281	50.304	−0.344	0.731
Year 1995	−0.327	0.289	−1.131	0.258
Year 1996	0.480	0.238	2.012	0.044
Year 1999	0.237	0.222	1.070	0.285
Year 2000	0.237	0.217	1.095	0.274
Year 2001	0.187	0.226	0.826	0.409
Year 2002	0.297	0.231	1.283	0.199
Year 2003	−0.025	0.248	−0.103	0.918
Year 2004	−0.539	0.330	−1.635	0.102
Year 2005	−0.266	0.249	−1.069	0.285
Year 2006	−0.297	0.263	−1.130	0.258
Year 2007	−0.011	0.240	−0.046	0.963
Year 2008	−0.139	0.254	−0.546	0.585
Year 2009	−0.794	0.316	−2.513	0.012
Year 2010	−0.147	0.255	−0.577	0.564
Year 2011	−0.248	0.250	−0.994	0.320
Year 2012	0.090	0.246	0.364	0.716
Year 2013	−0.478	0.262	−1.821	0.069
Year 2014	−0.447	0.263	−1.701	0.089
Year 2015	−0.084	0.246	−0.342	0.732
Year 2016	−0.355	0.251	−1.414	0.157
Year 2017	0.183	0.252	0.727	0.468
Year 2018	−0.367	0.291	−1.258	0.208
Year 2019	−0.687	0.322	−2.134	0.033
Sin	0.005	0.040	0.124	0.901
Cos	−0.033	0.055	−0.601	0.548
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.970	72.865	<0.001
s(Elevation)		0.867	4.433	0.019
s(Slope)		2.314	8.217	0.016
s(C110)		2.521	22.495	<0.001
s(C112)		1.915	5.498	0.047
s(C211)		1.814	3.307	0.160
s(C213)		0.753	0.023	0.861
s(C221)		0.492	0.043	0.767
s(C222)		0.001	0.001	0.432
s(C223)		0.611	0.024	0.843
s(C224)		0.002	0.001	0.503
s(C231)		2.768	8.453	0.025
s(C311)		2.194	6.473	0.036
s(C312)		2.854	155.391	<0.001
s(C313)		2.290	74.842	<0.001
s(C320)		0.001	0	0.885
s(C321)		1.782	11.781	0.001
s(C330)		0.954	19.631	<0.001
s(C410)		0.340	0.439	0.256
s(C511)		0.599	1.394	0.127

Common Firecrest (*Regulus ignicapilla*) — Model C-ZIP-GAM

Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.497	0.023	−66.390	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.992	787.800	<0.001
s(Urb$_{2500}$)		0.002	0	0.918
s(For$_{2500}$)		2.990	551.000	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−17.761	72.373	−0.245	0.806
Year 1995	0.755	0.416	1.814	0.070
Year 1996	−0.015	0.448	−0.033	0.974
Year 1999	−0.090	0.398	−0.225	0.822
Year 2000	0.442	0.375	1.177	0.239
Year 2001	0.696	0.386	1.803	0.071
Year 2002	0.375	0.400	0.937	0.349
Year 2003	0.041	0.425	0.096	0.924
Year 2004	0.170	0.460	0.370	0.711
Year 2005	0.442	0.400	1.107	0.268
Year 2006	0.179	0.407	0.440	0.660
Year 2007	0.643	0.394	1.633	0.102
Year 2008	0.549	0.399	1.376	0.169
Year 2009	0.246	0.428	0.575	0.566
Year 2010	0.615	0.400	1.537	0.124
Year 2011	0.861	0.383	2.246	0.025
Year 2012	−0.160	0.426	−0.377	0.706
Year 2013	0.874	0.386	2.265	0.023
Year 2014	0.797	0.388	2.053	0.040
Year 2015	0.986	0.381	2.590	0.010
Year 2016	1.161	0.376	3.091	0.002
Year 2017	1.247	0.390	3.198	0.001
Year 2018	1.315	0.392	3.354	<0.001
Year 2019	1.133	0.398	2.851	0.004
Sin	0.022	0.054	0.413	0.680
Cos	−0.208	0.076	−2.723	0.006
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.984	98.478	<0.001
s(Elevation)		2.811	18.809	<0.001
s(Slope)		2.990	78.196	<0.001
s(C110)		0.005	0.011	0.102
s(C112)		0.962	6.689	0.007
s(C211)		1.045	35.230	<0.001
s(C213)		0.760	0.070	0.762
s(C221)		0.912	6.962	0.006
s(C222)		0.820	3.547	0.037
s(C223)		0	0	0.570
s(C224)		0.477	0.031	0.797
s(C231)		1.144	52.389	<0.001
s(C311)		1.142	46.024	<0.001
s(C312)		2.867	137.639	<0.001
s(C313)		2.219	20.704	<0.001
s(C320)		1.045	33.549	<0.001
s(C321)		1.074	50.962	<0.001
s(C330)		0.902	5.160	0.016
s(C410)		0.896	5.573	0.013
s(C511)		0.939	12.601	<0.001

Spotted Flycatcher (*Muscicapa striata*) — Model C-P-GAM

Parametric terms	Estimate	Standard error	z-value	p-value
Intercept	−3.096	0.180	−17.207	<0.001
Year 1995	−0.581	0.249	−2.339	0.019
Year 1996	−0.924	0.272	−3.395	<0.001
Year 1999	0.407	0.194	2.096	0.036
Year 2000	0.186	0.191	0.972	0.331
Year 2001	0.846	0.192	4.407	<0.001
Year 2002	0.488	0.211	2.316	0.021
Year 2003	0.125	0.228	0.547	0.585
Year 2004	−0.014	0.266	−0.052	0.958
Year 2005	0.121	0.203	0.596	0.551
Year 2006	0.330	0.197	1.679	0.093
Year 2007	0.487	0.206	2.363	0.018
Year 2008	0.753	0.198	3.808	<0.001
Year 2009	0.519	0.203	2.549	0.011
Year 2010	0.211	0.211	1.000	0.317
Year 2011	0.682	0.192	3.551	<0.001
Year 2012	1.026	0.190	5.392	<0.001
Year 2013	0.912	0.194	4.708	<0.001
Year 2014	0.877	0.192	4.578	<0.001
Year 2015	0.705	0.196	3.594	<0.001
Year 2016	0.759	0.195	3.891	<0.001
Year 2017	1.137	0.194	5.860	<0.001
Year 2018	0.808	0.201	4.024	<0.001
Year 2019	0.931	0.198	4.713	<0.001
Sin	−0.030	0.030	−0.975	0.330
Cos	−0.033	0.046	−0.722	0.470
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		2.991	302.316	<0.001
s(Elevation)		2.739	101.454	<0.001
s(Slope)		2.471	32.920	<0.001
s(C110)		0.635	2.506	0.032
s(C112)		1.691	12.669	<0.001
s(C211)		0.992	32.287	<0.001
s(C213)		0.937	15.935	<0.001
s(C221)		0.858	9.394	<0.001
s(C222)		0.018	0.015	0.361
s(C223)		0.917	14.974	<0.001
s(C224)		0	0	0.459
s(C231)		2.241	10.438	0.002
s(C311)		2.736	44.717	<0.001
s(C312)		2.503	12.527	0.002
s(C313)		2.128	11.300	0.001
s(C320)		0.002	0	0.603
s(C321)		0.890	11.502	<0.001
s(C330)		0.806	4.328	0.019
s(C410)		1.774	4.493	0.070
s(C511)		1.839	4.244	0.090

Long-tailed Tit (*Aegithalos caudatus*) — Model C-P-GAM

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−4.025	0.293	−13.755	<0.001
Year 1995	0.912	0.321	2.837	0.005
Year 1996	0.359	0.344	1.045	0.296
Year 1999	0.825	0.305	2.707	0.007
Year 2000	0.456	0.307	1.485	0.138
Year 2001	1.233	0.306	4.026	<0.001
Year 2002	0.974	0.320	3.039	0.002
Year 2003	0.858	0.330	2.600	0.009
Year 2004	0.708	0.360	1.966	0.049
Year 2005	0.614	0.319	1.922	0.055
Year 2006	0.900	0.307	2.928	0.003
Year 2007	1.098	0.317	3.459	<0.001
Year 2008	1.007	0.321	3.138	0.002
Year 2009	0.683	0.330	2.068	0.039
Year 2010	0.643	0.331	1.941	0.052
Year 2011	1.283	0.307	4.181	<0.001
Year 2012	0.927	0.321	2.886	0.004
Year 2013	0.947	0.322	2.942	0.003
Year 2014	1.163	0.314	3.706	<0.001
Year 2015	1.186	0.315	3.767	<0.001
Year 2016	0.999	0.321	3.117	0.002
Year 2017	1.542	0.313	4.930	<0.001
Year 2018	0.858	0.334	2.572	0.010
Year 2019	1.020	0.328	3.114	0.002
Sin	−0.084	0.040	−2.109	0.035
Cos	0.004	0.059	0.075	0.940
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		0.003	0.003	0.369
s(Elevation)		2.219	67.388	<0.001
s(Slope)		2.871	18.680	<0.001
s(C110)		0.001	0.001	0.453
s(C112)		0.955	17.269	<0.001
s(C211)		2.215	13.138	<0.001
s(C213)		0.869	7.351	0.003
s(C221)		0.056	0.059	0.307
s(C222)		0.002	0.001	0.543
s(C223)		0.005	0.001	0.648
s(C224)		0.003	0.002	0.421
s(C231)		1.734	7.360	0.011
s(C311)		2.691	226.157	<0.001
s(C312)		1.778	35.482	<0.001
s(C313)		2.039	77.152	<0.001
s(C320)		0.869	8.040	0.002
s(C321)		0.734	3.286	0.032
s(C330)		0.002	0	0.702
s(C410)		0.887	9.246	0.001
s(C511)		0.963	20.142	<0.001

Marsh Tit (*Poecile palustris*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.118	0.042	−50.010	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.984	750.600	<0.001
s(Urb$_{2500}$)		2.978	538.200	<0.001
s(For$_{2500}$)		2.985	1,006.400	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.897	0.388	−10.031	<0.001
Year 1995	1.045	0.430	2.429	0.015
Year 1996	0.491	0.459	1.071	0.284
Year 1999	1.040	0.395	2.636	0.008
Year 2000	0.642	0.398	1.614	0.106
Year 2001	1.506	0.400	3.764	<0.001
Year 2002	1.631	0.398	4.096	<0.001
Year 2003	1.482	0.407	3.644	<0.001
Year 2004	1.706	0.412	4.145	<0.001
Year 2005	1.278	0.406	3.151	0.002
Year 2006	1.386	0.395	3.511	<0.001
Year 2007	1.677	0.399	4.200	<0.001
Year 2008	1.420	0.408	3.482	<0.001
Year 2009	1.826	0.397	4.599	<0.001
Year 2010	1.848	0.400	4.620	<0.001
Year 2011	2.331	0.387	6.022	<0.001
Year 2012	1.760	0.399	4.416	<0.001
Year 2013	1.730	0.399	4.333	<0.001
Year 2014	1.927	0.394	4.894	<0.001
Year 2015	1.558	0.402	3.874	<0.001
Year 2016	1.644	0.401	4.104	<0.001
Year 2017	1.439	0.411	3.502	<0.001
Year 2018	1.554	0.407	3.815	<0.001
Year 2019	1.951	0.399	4.887	<0.001
Sin	0.059	0.038	1.536	0.124
Cos	0.234	0.053	4.392	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.992	194.740	<0.001
s(Elevation)		0.423	0.612	0.225
s(Slope)		0.001	0	0.509
s(C110)		0.604	2.558	0.035
s(C112)		0.001	0.001	0.396
s(C211)		1.723	7.268	0.012
s(C213)		0	0	0.501
s(C221)		0	0	0.879
s(C222)		0	0	0.871
s(C223)		0	0	0.634
s(C224)		0	0	0.670
s(C231)		1.297	13.503	<0.001
s(C311)		2.415	293.817	<0.001
s(C312)		1.021	30.814	<0.001
s(C313)		1.858	266.747	<0.001
s(C320)		0.362	0.574	0.201
s(C321)		0	0	0.443
s(C330)		0.770	3.551	0.031
s(C410)		0	0	0.923
s(C511)		0	0	0.919

Willow Tit (*Poecile montanus*) — Model C-ZIP-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.750	0.067	−55.560	<0.001

Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.996	1,676.880	<0.001
s(Urb$_{2500}$)		0.927	11.560	<0.001
s(For$_{2500}$)		2.990	572.420	<0.001

Count component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−38.206	53.235	−0.718	0.473
Year 1995	−0.290	0.508	−0.572	0.568
Year 1996	−0.555	0.540	−1.029	0.304
Year 1999	−0.174	0.433	−0.403	0.687
Year 2000	−0.787	0.475	−1.657	0.098
Year 2001	0.691	0.408	1.692	0.091
Year 2002	0.174	0.458	0.380	0.704
Year 2003	0.273	0.421	0.649	0.517
Year 2004	−0.246	0.500	−0.493	0.622
Year 2005	−0.316	0.434	−0.728	0.467
Year 2006	−0.634	0.542	−1.170	0.242
Year 2007	0.112	0.429	0.260	0.795
Year 2008	−0.793	0.491	−1.614	0.107
Year 2009	0.063	0.443	0.141	0.888
Year 2010	0.117	0.432	0.271	0.787
Year 2011	0.328	0.418	0.786	0.432
Year 2012	−0.876	0.491	−1.782	0.075
Year 2013	0.282	0.420	0.671	0.503
Year 2014	−0.318	0.439	−0.724	0.469
Year 2015	−0.091	0.430	−0.211	0.833
Year 2016	−0.142	0.429	−0.331	0.740
Year 2017	−0.168	0.459	−0.367	0.714
Year 2018	−0.081	0.449	−0.181	0.857
Year 2019	0.115	0.447	0.258	0.797
Sin	0.009	0.063	0.149	0.882
Cos	0.044	0.084	0.521	0.602

Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.829	95.393	<0.001
s(Elevation)		0	0	0.463
s(Slope)		0	0	0.356
s(C110)		0.912	7.866	0.003
s(C112)		0.918	9.441	0.001
s(C211)		0.642	0.437	0.410
s(C213)		0	0	0.911
s(C221)		0	0	0.650
s(C222)		0	0	0.756
s(C223)		0	0	0.827
s(C224)		0.001	0	0.864
s(C231)		1.002	25.088	<0.001
s(C311)		0	0	0.666
s(C312)		2.827	60.282	<0.001
s(C313)		0	0	0.446
s(C320)		0	0	0.748
s(C321)		2.401	30.703	<0.001
s(C330)		0.924	6.796	0.006
s(C410)		0	0	0.553
s(C511)		0.857	5.673	0.010

European Crested Tit (*Lophophanes cristatus*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.771	0.057	−48.600	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.959	1,204.730	<0.001
s(Urb$_{2500}$)		0.943	14.910	<0.001
s(For$_{2500}$)		2.970	593.070	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−7.138	8.012	−0.891	0.373
Year 1995	−0.256	0.488	−0.526	0.599
Year 1996	−0.199	0.445	−0.448	0.654
Year 1999	0.924	0.351	2.633	0.008
Year 2000	0.636	0.352	1.809	0.070
Year 2001	−0.332	0.391	−0.850	0.395
Year 2002	0.619	0.366	1.690	0.091
Year 2003	0.465	0.376	1.236	0.217
Year 2004	0.695	0.420	1.656	0.098
Year 2005	0.349	0.372	0.937	0.349
Year 2006	0.369	0.385	0.959	0.338
Year 2007	0.759	0.367	2.069	0.039
Year 2008	0.273	0.386	0.709	0.478
Year 2009	0.804	0.384	2.094	0.036
Year 2010	0.543	0.379	1.434	0.152
Year 2011	0.430	0.377	1.139	0.255
Year 2012	0.210	0.392	0.537	0.591
Year 2013	0.753	0.369	2.043	0.041
Year 2014	0.652	0.371	1.757	0.079
Year 2015	0.361	0.384	0.941	0.347
Year 2016	0.852	0.365	2.332	0.020
Year 2017	0.808	0.385	2.100	0.036
Year 2018	0.868	0.383	2.265	0.023
Year 2019	0.634	0.399	1.589	0.112
Sin	0.075	0.050	1.517	0.129
Cos	−0.003	0.064	−0.040	0.968
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.757	15.215	<0.001
s(Elevation)		0.871	5.537	0.008
s(Slope)		1.099	33.314	<0.001
s(C110)		1.209	22.095	<0.001
s(C112)		2.768	38.612	<0.001
s(C211)		0.948	10.440	<0.001
s(C213)		0.776	0.030	0.845
s(C221)		0.645	0.116	0.671
s(C222)		0.628	0.787	0.262
s(C223)		0.498	0.021	0.837
s(C224)		0.661	1.053	0.206
s(C231)		0.993	21.683	<0.001
s(C311)		1.080	48.107	<0.001
s(C312)		2.913	131.970	<0.001
s(C313)		0.640	6.136	<0.001
s(C320)		2.909	31.260	<0.001
s(C321)		1.707	49.303	<0.001
s(C330)		0.001	0	0.568
s(C410)		0.675	1.590	0.120
s(C511)		0.947	19.296	<0.001

Coal Tit (*Periparus ater*) — Model C-ZIP-GAM

		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.813	0.048	−37.660	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.992	2,645.119	<0.001
s(Urb_{2500})		0.784	3.921	0.025
s(For_{2500})		2.977	596.639	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.247	2.547	−0.882	0.378
Year 1995	−0.543	0.138	−3.934	<0.001
Year 1996	−0.137	0.122	−1.123	0.261
Year 1999	−0.181	0.106	−1.704	0.088
Year 2000	−0.416	0.106	−3.939	<0.001
Year 2001	−0.112	0.108	−1.037	0.300
Year 2002	−0.214	0.118	−1.817	0.069
Year 2003	−0.227	0.116	−1.954	0.051
Year 2004	−0.250	0.136	−1.835	0.067
Year 2005	−0.568	0.118	−4.831	<0.001
Year 2006	−0.046	0.115	−0.400	0.689
Year 2007	−0.115	0.112	−1.030	0.303
Year 2008	−0.603	0.125	−4.842	<0.001
Year 2009	−0.620	0.133	−4.663	<0.001
Year 2010	−0.310	0.120	−2.585	0.010
Year 2011	−0.221	0.113	−1.955	0.051
Year 2012	−0.329	0.117	−2.805	0.005
Year 2013	−0.232	0.113	−2.058	0.040
Year 2014	−0.362	0.115	−3.139	0.002
Year 2015	−0.449	0.118	−3.815	<0.001
Year 2016	−0.102	0.110	−0.928	0.354
Year 2017	−0.191	0.122	−1.561	0.118
Year 2018	−0.106	0.122	−0.868	0.386
Year 2019	−0.548	0.133	−4.121	<0.001
Sin	−0.019	0.020	−0.960	0.337
Cos	0.054	0.028	1.950	0.051
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.983	214.084	<0.001
s(Elevation)		2.527	93.431	<0.001
s(Slope)		2.387	17.269	<0.001
s(C110)		2.699	20.897	<0.001
s(C112)		2.065	22.912	<0.001
s(C211)		1.023	17.445	<0.001
s(C213)		0.752	0.121	0.689
s(C221)		0.904	8.814	0.002
s(C222)		0.872	5.747	0.010
s(C223)		0.784	1.818	0.128
s(C224)		0.860	4.790	0.018
s(C231)		1.562	20.596	<0.001
s(C311)		2.735	25.661	<0.001
s(C312)		2.956	281.594	<0.001
s(C313)		2.513	98.128	<0.001
s(C320)		2.842	27.074	<0.001
s(C321)		2.648	65.987	<0.001
s(C330)		2.848	10.926	0.009
s(C410)		0.887	5.414	0.013
s(C511)		0.980	23.867	<0.001

Eurasian Blue Tit (*Cyanistes caeruleus*) — Model C-ZIP-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.432	0.022	−19.920	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.796	1,698.100	<0.001
s(Urb$_{2500}$)		2.943	306.300	<0.001
s(For$_{2500}$)		2.962	1,448.100	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.293	0.166	−13.834	<0.001
Year 1995	−0.026	0.214	−0.122	0.903
Year 1996	0.584	0.188	3.105	0.002
Year 1999	0.352	0.174	2.017	0.044
Year 2000	0.534	0.170	3.142	0.002
Year 2001	0.869	0.176	4.937	<0.001
Year 2002	0.608	0.184	3.306	<0.001
Year 2003	0.937	0.182	5.144	<0.001
Year 2004	0.329	0.220	1.495	0.135
Year 2005	0.478	0.183	2.614	0.009
Year 2006	0.599	0.175	3.423	<0.001
Year 2007	0.620	0.184	3.374	<0.001
Year 2008	0.830	0.181	4.580	<0.001
Year 2009	0.696	0.184	3.791	<0.001
Year 2010	0.819	0.182	4.500	<0.001
Year 2011	0.992	0.172	5.753	<0.001
Year 2012	0.717	0.181	3.962	<0.001
Year 2013	0.621	0.182	3.406	<0.001
Year 2014	0.716	0.180	3.973	<0.001
Year 2015	0.450	0.189	2.385	0.017
Year 2016	0.572	0.186	3.071	0.002
Year 2017	0.654	0.188	3.468	<0.001
Year 2018	0.418	0.196	2.136	0.033
Year 2019	0.423	0.196	2.154	0.031
Sin	−0.052	0.026	−1.996	0.046
Cos	0.093	0.039	2.387	0.017
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.984	155.942	<0.001
s(Elevation)		2.372	48.588	<0.001
S(Slope)		1.856	4.496	0.071
s(C110)		0.979	17.841	<0.001
s(C112)		2.833	10.779	0.009
s(C211)		2.241	30.049	<0.001
s(C213)		0.980	19.241	<0.001
s(C221)		2.410	16.012	<0.001
s(C222)		0.793	6.065	0.005
s(C223)		0.553	1.106	0.156
s(C224)		1.864	13.713	<0.001
s(C231)		1.765	4.958	0.041
s(C311)		2.608	69.971	<0.001
s(C312)		1.867	8.433	0.007
s(C313)		2.221	30.566	<0.001
s(C320)		2.501	2.874	0.314
s(C321)		1.414	9.298	0.003
s(C330)		0.723	2.752	0.048
s(C410)		0.770	4.851	0.011
s(C511)		0	0	0.902

Great Tit (*Parus major*) — Model C-ZIP-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	3.033	0.061	49.620	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.941	1,262.800	<0.001
s(Urb$_{2500}$)		2.984	332.000	<0.001
s(For$_{2500}$)		2.996	829.100	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.625	0.069	−9.079	<0.001
Year 1995	−0.617	0.092	−6.679	<0.001
Year 1996	−0.707	0.094	−7.500	<0.001
Year 1999	−0.168	0.075	−2.225	0.026
Year 2000	−0.512	0.077	−6.661	<0.001
Year 2001	−0.280	0.080	−3.509	<0.001
Year 2002	−0.437	0.092	−4.755	<0.001
Year 2003	−0.021	0.086	−0.244	0.807
Year 2004	−0.259	0.102	−2.542	0.011
Year 2005	−0.194	0.078	−2.483	0.013
Year 2006	−0.152	0.076	−2.007	0.045
Year 2007	−0.075	0.082	−0.912	0.362
Year 2008	−0.128	0.084	−1.524	0.128
Year 2009	−0.027	0.081	−0.332	0.740
Year 2010	0.074	0.079	0.941	0.346
Year 2011	−0.055	0.078	−0.707	0.480
Year 2012	−0.060	0.081	−0.738	0.460
Year 2013	0.022	0.079	0.280	0.779
Year 2014	−0.093	0.080	−1.172	0.241
Year 2015	−0.015	0.080	−0.185	0.853
Year 2016	0.049	0.079	0.612	0.541
Year 2017	0.109	0.083	1.321	0.186
Year 2018	0.124	0.082	1.511	0.131
Year 2019	0.112	0.082	1.363	0.173
Sin	0.012	0.015	0.807	0.420
Cos	0.015	0.023	0.665	0.506
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.873	71.283	<0.001
s(Elevation)		2.934	202.019	<0.001
s(Slope)		2.356	13.474	<0.001
s(C110)		1.336	4.231	0.036
s(C112)		2.223	12.596	0.001
s(C211)		0.897	5.497	0.007
s(C213)		0.998	23.605	<0.001
s(C221)		0.244	0.450	0.164
s(C222)		0.002	0.001	0.381
s(C223)		0.001	0.001	0.427
s(C224)		2.627	37.439	<0.001
s(C231)		2.748	21.450	<0.001
s(C311)		2.853	204.343	<0.001
s(C312)		1.365	13.620	<0.001
s(C313)		2.285	48.279	<0.001
s(C320)		0.002	0.001	0.477
s(C321)		1.999	4.977	0.070
s(C330)		0.877	4.508	0.022
s(C410)		0.860	4.359	0.023
s(C511)		2.699	13.864	0.002

Eurasian Nuthatch (*Sitta europaea*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.286	0.045	−50.830	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.995	604.100	<0.001
s(Urb$_{2500}$)		2.996	592.900	<0.001
s(For$_{2500}$)		2.993	888.300	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.747	0.271	−10.154	<0.001
Year 1995	−0.299	0.350	−0.853	0.393
Year 1996	−1.232	0.434	−2.838	0.005
Year 1999	0.240	0.272	0.883	0.377
Year 2000	−0.144	0.276	−0.522	0.601
Year 2001	0.328	0.285	1.151	0.250
Year 2002	0.292	0.290	1.008	0.313
Year 2003	−0.079	0.333	−0.236	0.813
Year 2004	−1.285	0.481	−2.670	0.008
Year 2005	−0.038	0.306	−0.123	0.902
Year 2006	0.423	0.280	1.510	0.131
Year 2007	−0.097	0.319	−0.303	0.762
Year 2008	−0.146	0.327	−0.446	0.656
Year 2009	0.070	0.307	0.229	0.819
Year 2010	−0.248	0.344	−0.720	0.471
Year 2011	0.253	0.293	0.863	0.388
Year 2012	0.372	0.295	1.264	0.206
Year 2013	−0.291	0.340	−0.857	0.391
Year 2014	0.260	0.296	0.879	0.380
Year 2015	−0.081	0.317	−0.256	0.798
Year 2016	−0.292	0.344	−0.848	0.397
Year 2017	0.154	0.324	0.474	0.635
Year 2018	−0.392	0.367	−1.070	0.285
Year 2019	0.253	0.317	0.799	0.424
Sin	0.016	0.050	0.325	0.745
Cos	0.295	0.070	4.241	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.992	130.001	<0.001
s(Elevation)		2.882	29.477	<0.001
s(Slope)		0.755	2.916	0.045
s(C110)		2.624	12.085	0.003
s(C112)		0.003	0.001	0.648
s(C211)		0	0	0.962
s(C213)		0	0	0.540
s(C221)		0.002	0.001	0.385
s(C222)		0.002	0.001	0.387
s(C223)		0	0	0.515
s(C224)		0	0	0.439
s(C231)		0.716	2.434	0.062
s(C311)		2.498	218.444	<0.001
s(C312)		1.075	31.987	<0.001
s(C313)		1.463	137.484	<0.001
s(C320)		0	0	1.000
s(C321)		0	0	0.952
s(C330)		2.843	19.925	<0.001
s(C410)		0.757	2.363	0.077
s(C511)		2.902	41.362	<0.001

Short-toed Treecreeper (*Certhia brachydactyla*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.663	0.049	−53.940	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.988	1,005.700	<0.001
s(Urb$_{2500}$)		1.114	232.800	<0.001
s(For$_{2500}$)		2.973	741.600	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−6.025	1.011	−5.961	<0.001
Year 1995	0.724	1.157	0.626	0.531
Year 1996	2.033	1.016	2.001	0.045
Year 1999	1.758	1.021	1.722	0.085
Year 2000	1.822	1.051	1.734	0.083
Year 2001	2.707	1.019	2.657	0.008
Year 2002	2.983	1.020	2.924	0.003
Year 2003	2.684	1.043	2.573	0.010
Year 2004	2.202	1.034	2.129	0.033
Year 2005	2.980	1.008	2.956	0.003
Year 2006	2.483	1.031	2.409	0.016
Year 2007	2.741	1.028	2.666	0.008
Year 2008	1.664	1.081	1.539	0.124
Year 2009	2.293	1.046	2.194	0.028
Year 2010	2.883	1.019	2.828	0.005
Year 2011	2.965	1.021	2.904	0.004
Year 2012	3.042	1.023	2.973	0.003
Year 2013	2.937	1.021	2.877	0.004
Year 2014	2.571	1.036	2.481	0.013
Year 2015	2.937	1.025	2.866	0.004
Year 2016	3.004	1.027	2.925	0.003
Year 2017	3.236	1.022	3.167	0.002
Year 2018	3.180	1.022	3.112	0.002
Year 2019	0.065	0.069	0.941	0.347
Sin	0.135	0.102	1.319	0.187
Cos	−6.025	1.011	−5.961	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.870	114.120	<0.001
s(Elevation)		0	0	0.871
s(Slope)		2.132	22.630	<0.001
s(C110)		1.685	13.536	<0.001
s(C112)		1.981	11.735	0.001
s(C211)		0	0	0.739
s(C213)		0.001	0	0.401
s(C221)		0.840	4.347	0.023
s(C222)		0.182	0.238	0.251
s(C223)		0	0	0.612
s(C224)		0	0	0.622
s(C231)		0.635	1.946	0.074
s(C311)		2.613	82.052	<0.001
s(C312)		1.752	20.578	<0.001
s(C313)		2.098	101.850	<0.001
s(C320)		0.125	0.141	0.281
s(C321)		0	0	0.800
s(C330)		0.574	1.185	0.149
s(C410)		0.187	0.234	0.261
s(C511)		0.866	7.435	0.003

Eurasian Golden Oriole (*Oriolus oriolus*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.683	0.022	−30.830	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.949	2,012.600	<0.001
s(Urb$_{2500}$)		1.190	1,228.600	<0.001
s(For$_{2500}$)		2.994	818.900	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.696	0.205	−13.138	<0.001
Year 1995	−0.404	0.169	−2.390	0.017
Year 1996	−0.880	0.204	−4.320	<0.001
Year 1999	−0.557	0.154	−3.617	<0.001
Year 2000	−0.443	0.159	−2.794	0.005
Year 2001	−0.650	0.176	−3.699	<0.001
Year 2002	−0.374	0.185	−2.021	0.043
Year 2003	0.066	0.168	0.392	0.695
Year 2004	−0.022	0.236	−0.095	0.924
Year 2005	−0.078	0.152	−0.513	0.608
Year 2006	−0.496	0.166	−2.991	0.003
Year 2007	0.057	0.155	0.366	0.714
Year 2008	−0.078	0.170	−0.460	0.646
Year 2009	−0.174	0.169	−1.026	0.305
Year 2010	−0.076	0.165	−0.458	0.647
Year 2011	−0.348	0.166	−2.099	0.036
Year 2012	−0.120	0.164	−0.733	0.464
Year 2013	0.099	0.152	0.653	0.514
Year 2014	0.101	0.157	0.643	0.520
Year 2015	0.077	0.161	0.478	0.633
Year 2016	0.031	0.161	0.195	0.846
Year 2017	0.162	0.165	0.980	0.327
Year 2018	0.027	0.172	0.159	0.873
Year 2019	0.133	0.166	0.798	0.425
Sin	−0.016	0.034	−0.456	0.648
Cos	0.063	0.052	1.223	0.221
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.937	188.880	<0.001
s(Elevation)		1.877	8.298	0.009
s(Slope)		2.375	39.808	<0.001
s(C110)		2.886	60.827	<0.001
s(C112)		1.752	41.716	<0.001
s(C211)		2.505	72.325	<0.001
s(C213)		0.778	5.226	0.009
s(C221)		0.001	0	0.840
s(C222)		0.790	3.211	0.044
s(C223)		0.001	0	0.585
s(C224)		2.944	276.559	<0.001
s(C231)		0.001	0	0.729
s(C311)		2.634	145.798	<0.001
s(C312)		0.001	0	0.934
s(C313)		0.001	0	0.814
s(C320)		0.548	1.291	0.124
s(C321)		0	0	0.870
s(C330)		1.848	8.288	0.010
s(C410)		0.006	0.005	0.358
s(C511)		0.003	0.002	0.342

Red-backed Shrike (*Lanius collurio*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.863	0.020	−42.370	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.985	1,121.200	<0.001
s(Urb$_{2500}$)		1.558	175.900	<0.001
s(For$_{2500}$)		2.970	392.100	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.488	0.153	−9.757	<0.001
Year 1995	−0.072	0.183	−0.392	0.695
Year 1996	−0.701	0.203	−3.462	<0.001
Year 1999	−0.576	0.180	−3.194	0.001
Year 2000	−0.681	0.176	−3.873	<0.001
Year 2001	−0.387	0.180	−2.153	0.031
Year 2002	−0.881	0.227	−3.889	<0.001
Year 2003	−1.922	0.363	−5.299	<0.001
Year 2004	−1.233	0.334	−3.694	<0.001
Year 2005	−0.843	0.196	−4.299	<0.001
Year 2006	−1.119	0.212	−5.275	<0.001
Year 2007	−0.680	0.201	−3.388	<0.001
Year 2008	−0.917	0.221	−4.141	<0.001
Year 2009	−1.187	0.244	−4.866	<0.001
Year 2010	−0.987	0.223	−4.422	<0.001
Year 2011	−1.608	0.251	−6.413	<0.001
Year 2012	−1.859	0.287	−6.484	<0.001
Year 2013	−1.161	0.230	−5.044	<0.001
Year 2014	−1.323	0.248	−5.338	<0.001
Year 2015	−1.274	0.244	−5.219	<0.001
Year 2016	−1.091	0.222	−4.911	<0.001
Year 2017	−1.632	0.294	−5.548	<0.001
Year 2018	−1.739	0.311	−5.594	<0.001
Year 2019	−2.025	0.346	−5.852	<0.001
Sin	−0.055	0.051	−1.088	0.277
Cos	−0.132	0.079	−1.682	0.093
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.931	52.891	<0.001
s(Elevation)		2.320	10.213	0.004
s(Slope)		2.078	24.021	<0.001
s(C110)		1.506	31.453	<0.001
s(C112)		1.758	28.458	<0.001
s(C211)		0	0	0.866
s(C213)		0.529	1.463	0.095
s(C221)		0.795	5.718	0.007
s(C222)		0.001	0	0.481
s(C223)		0.002	0	0.912
s(C224)		1.974	5.889	0.041
s(C231)		0.990	59.606	<0.001
s(C311)		2.344	73.707	<0.001
s(C312)		1.379	39.741	<0.001
s(C313)		1.977	34.830	<0.001
s(C320)		2.494	21.804	<0.001
s(C321)		0.008	0.007	0.348
s(C330)		0.881	7.668	0.003
s(C410)		0.730	2.397	0.070
s(C511)		0.108	0.123	0.283

Eurasian Jay (*Garrulus glandarius*) — Model C-P-GAM				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.949	0.235	−16.772	<0.001
Year 1995	0.318	0.293	1.086	0.277
Year 1996	−0.303	0.315	−0.964	0.335
Year 1999	0.458	0.251	1.821	0.069
Year 2000	0.532	0.245	2.171	0.030
Year 2001	0.464	0.260	1.786	0.074
Year 2002	0.727	0.259	2.812	0.005
Year 2003	0.931	0.263	3.533	<0.001
Year 2004	0.659	0.293	2.248	0.025
Year 2005	0.642	0.257	2.503	0.012
Year 2006	0.816	0.251	3.248	0.001
Year 2007	0.854	0.255	3.349	<0.001
Year 2008	0.588	0.269	2.186	0.029
Year 2009	0.800	0.260	3.074	0.002
Year 2010	0.614	0.266	2.303	0.021
Year 2011	1.013	0.250	4.057	<0.001
Year 2012	0.871	0.256	3.409	<0.001
Year 2013	1.096	0.250	4.378	<0.001
Year 2014	0.925	0.255	3.631	<0.001
Year 2015	0.781	0.260	3.003	0.003
Year 2016	1.167	0.251	4.647	<0.001
Year 2017	1.014	0.261	3.893	<0.001
Year 2018	0.946	0.263	3.594	<0.001
Year 2019	0.847	0.266	3.178	0.001
Sin	0.068	0.035	1.965	0.049
Cos	−0.072	0.051	−1.400	0.161
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X,Y)		2.999	422.098	<0.001
s(Elevation)		2.692	161.667	<0.001
s(Slope)		2.597	40.981	<0.001
s(C110)		0.865	12.151	<0.001
s(C112)		0.767	3.796	0.020
s(C211)		2.006	6.691	0.017
s(C213)		0.887	12.070	<0.001
s(C221)		0.911	9.764	<0.001
s(C222)		0.586	1.602	0.094
s(C223)		0.003	0.002	0.421
s(C224)		2.837	18.247	<0.001
s(C231)		0.919	24.467	<0.001
s(C311)		2.735	77.426	<0.001
s(C312)		1.831	69.811	<0.001
s(C313)		2.255	62.657	<0.001
s(C320)		2.618	6.387	0.056
s(C321)		0.002	0.001	0.494
s(C330)		0.879	8.041	0.002
s(C410)		0.256	0.348	0.237
s(C511)		2.896	19.981	<0.001

Eurasian Magpie (*Pica pica*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.130	0.022	5.935	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.832	1,228.500	<0.001
s(Urb$_{2500}$)		2.991	427.300	<0.001
s(For$_{2500}$)		2.985	496.000	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−4.327	0.317	−13.663	<0.001
Year 1995	0.851	0.273	3.121	0.002
Year 1996	0.280	0.280	1.000	0.317
Year 1999	0.658	0.283	2.321	0.020
Year 2000	0.687	0.270	2.550	0.011
Year 2001	0.675	0.270	2.500	0.012
Year 2002	1.194	0.266	4.483	<0.001
Year 2003	1.203	0.265	4.532	<0.001
Year 2004	0.848	0.297	2.856	0.004
Year 2005	1.348	0.253	5.332	<0.001
Year 2006	1.366	0.255	5.359	<0.001
Year 2007	0.919	0.267	3.441	<0.001
Year 2008	1.069	0.265	4.034	<0.001
Year 2009	1.275	0.259	4.928	<0.001
Year 2010	1.321	0.259	5.106	<0.001
Year 2011	1.271	0.257	4.949	<0.001
Year 2012	1.600	0.255	6.278	<0.001
Year 2013	1.687	0.252	6.687	<0.001
Year 2014	1.345	0.256	5.254	<0.001
Year 2015	1.490	0.255	5.850	<0.001
Year 2016	1.777	0.252	7.042	<0.001
Year 2017	1.821	0.257	7.083	<0.001
Year 2018	2.158	0.254	8.488	<0.001
Year 2019	1.923	0.256	7.508	<0.001
Sin	−0.027	0.029	−0.929	0.353
Cos	0.092	0.041	2.260	0.024
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.989	538.714	<0.001
s(Elevation)		2.740	23.190	<0.001
s(Slope)		2.253	49.829	<0.001
s(C110)		2.879	98.385	<0.001
s(C112)		1.000	17.180	<0.001
s(C211)		2.693	26.948	<0.001
s(C213)		0.968	27.905	<0.001
s(C221)		1.667	6.188	0.023
s(C222)		0.897	7.571	0.004
s(C223)		0.896	18.516	<0.001
s(C224)		2.936	43.789	<0.001
s(C231)		2.342	5.083	0.077
s(C311)		2.063	14.276	<0.001
s(C312)		2.104	18.278	<0.001
s(C313)		0	0	0.200
s(C320)		0.001	0	0.549
s(C321)		0.685	2.502	0.054
s(C330)		0.710	2.785	0.045
s(C410)		0.291	0.593	0.139
s(C511)		1.985	51.380	<0.001

Carrion Crow (*Corvus corone*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.863	0.053	−54.160	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.984	1,431.700	<0.001
s(Urb$_{2500}$)		2.994	376.100	<0.001
s(For$_{2500}$)		2.996	542.100	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−5.174	0.647	−7.995	<0.001
Year 1995	−0.692	0.767	−0.903	0.367
Year 1996	0.181	0.576	0.315	0.753
Year 1999	0.282	0.532	0.530	0.596
Year 2000	0.667	0.525	1.272	0.203
Year 2001	0.632	0.522	1.211	0.226
Year 2002	0.041	0.604	0.069	0.945
Year 2003	−0.474	0.589	−0.805	0.421
Year 2004	−0.366	0.636	−0.576	0.565
Year 2005	0.373	0.526	0.709	0.478
Year 2006	1.170	0.535	2.189	0.029
Year 2007	0.229	0.543	0.422	0.673
Year 2008	0.079	0.550	0.144	0.886
Year 2009	0.464	0.535	0.867	0.386
Year 2010	0.672	0.528	1.271	0.204
Year 2011	−0.285	0.557	−0.512	0.609
Year 2012	0.326	0.532	0.612	0.540
Year 2013	0.407	0.529	0.769	0.442
Year 2014	−0.004	0.537	−0.008	0.994
Year 2015	0.057	0.530	0.108	0.914
Year 2016	−0.086	0.542	−0.159	0.873
Year 2017	−0.610	0.596	−1.024	0.306
Year 2018	−0.033	0.564	−0.059	0.953
Year 2019	0.041	0.553	0.074	0.941
Sin	0.018	0.059	0.309	0.757
Cos	0.150	0.079	1.904	0.057
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.934	259.492	<0.001
s(Elevation)		2.890	160.879	<0.001
s(Slope)		1.688	8.534	0.006
s(C110)		0	0	0.568
s(C112)		1.859	6.212	0.027
s(C211)		0	0	0.883
s(C213)		0	0	0.918
s(C221)		0.006	0.006	0.314
s(C222)		0.751	1.916	0.110
s(C223)		0.001	0	0.440
s(C224)		0	0	0.602
s(C231)		1.749	41.659	<0.001
s(C311)		0	0	0.924
s(C312)		2.810	27.190	<0.001
s(C313)		0.497	1.046	0.139
s(C320)		0.550	2.109	0.040
s(C321)		0.737	7.744	<0.001
s(C330)		1.684	2.559	0.200
s(C410)		0	0	0.828
s(C511)		0	0	0.581

Hooded Crow (*Corvus cornix*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	5.315	0.158	33.630	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.457	1,456.400	<0.001
s(Urb$_{2500}$)		0.001	0	0.910
s(For$_{2500}$)		2.980	661.300	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.088	0.062	−1.420	0.156
Year 1995	−0.471	0.080	−5.924	<0.001
Year 1996	−0.475	0.078	−6.081	<0.001
Year 1999	−0.016	0.071	−0.221	0.825
Year 2000	−0.076	0.069	−1.099	0.272
Year 2001	−0.061	0.071	−0.860	0.390
Year 2002	0.020	0.078	0.251	0.802
Year 2003	−0.231	0.083	−2.779	0.005
Year 2004	−0.123	0.091	−1.345	0.179
Year 2005	−0.092	0.071	−1.302	0.193
Year 2006	0.039	0.070	0.554	0.579
Year 2007	−0.161	0.076	−2.106	0.035
Year 2008	−0.080	0.076	−1.050	0.294
Year 2009	−0.249	0.076	−3.280	0.001
Year 2010	−0.098	0.075	−1.314	0.189
Year 2011	0.042	0.072	0.575	0.565
Year 2012	−0.041	0.075	−0.542	0.588
Year 2013	0.001	0.074	0.009	0.992
Year 2014	0.026	0.073	0.361	0.718
Year 2015	−0.057	0.075	−0.757	0.449
Year 2016	−0.038	0.075	−0.504	0.615
Year 2017	−0.075	0.082	−0.917	0.359
Year 2018	−0.106	0.081	−1.309	0.191
Year 2019	−0.162	0.082	−1.979	0.048
Sin	0.064	0.014	4.471	<0.001
Cos	0.004	0.022	0.190	0.850
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.979	241.191	<0.001
s(Elevation)		1.864	138.533	<0.001
s(Slope)		2.505	42.907	<0.001
s(C110)		1.934	36.587	<0.001
s(C112)		1.061	34.312	<0.001
s(C211)		1.861	36.774	<0.001
s(C213)		2.669	225.123	<0.001
s(C221)		0.822	4.528	0.017
s(C222)		0.515	1.050	0.151
s(C223)		0.640	1.698	0.103
s(C224)		2.389	93.992	<0.001
s(C231)		2.691	98.033	<0.001
s(C311)		2.837	117.467	<0.001
s(C312)		2.080	16.599	<0.001
s(C313)		0.967	12.294	<0.001
s(C320)		0.985	25.176	<0.001
s(C321)		0.806	4.028	0.022
s(C330)		0.915	10.360	<0.001
s(C410)		0.001	0	0.597
s(C511)		0.945	16.368	<0.001

Common Starling (*Sturnus vulgaris*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	4.055	0.115	35.330	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.933	1,429.140	<0.001
s(Urb$_{2500}$)		0.999	77.630	<0.001
s(For$_{2500}$)		1.495	561.930	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.444	0.180	−8.023	<0.001
Year 1995	−0.441	0.083	−5.316	<0.001
Year 1996	−0.876	0.086	−10.163	<0.001
Year 1999	−0.117	0.078	−1.502	0.133
Year 2000	−0.127	0.074	−1.717	0.086
Year 2001	−0.510	0.078	−6.519	<0.001
Year 2002	−0.367	0.087	−4.210	<0.001
Year 2003	−0.580	0.091	−6.363	<0.001
Year 2004	−0.473	0.103	−4.607	<0.001
Year 2005	−0.305	0.074	−4.114	<0.001
Year 2006	−0.309	0.075	−4.112	<0.001
Year 2007	−0.412	0.081	−5.087	<0.001
Year 2008	−0.331	0.081	−4.063	<0.001
Year 2009	−0.480	0.081	−5.915	<0.001
Year 2010	−0.360	0.080	−4.505	<0.001
Year 2011	−0.456	0.079	−5.801	<0.001
Year 2012	−0.340	0.080	−4.254	<0.001
Year 2013	−0.509	0.080	−6.350	<0.001
Year 2014	−0.332	0.077	−4.282	<0.001
Year 2015	−0.577	0.082	−7.067	<0.001
Year 2016	−0.380	0.080	−4.741	<0.001
Year 2017	−0.694	0.094	−7.409	<0.001
Year 2018	−0.609	0.092	−6.616	<0.001
Year 2019	−0.742	0.094	−7.868	<0.001
Sin	0.012	0.017	0.692	0.489
Cos	0.004	0.025	0.142	0.887
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.030	334.840	<0.001
s(Elevation)		2.659	69.480	<0.001
s(Slope)		1.671	176.691	<0.001
s(C110)		2.227	14.884	<0.001
s(C112)		2.303	45.970	<0.001
s(C211)		0.603	1.347	0.112
s(C213)		0.955	14.573	<0.001
s(C221)		0.974	26.401	<0.001
s(C222)		0.779	3.577	0.031
s(C223)		0.001	0	0.937
s(C224)		0.001	0	0.788
s(C231)		1.656	85.363	<0.001
s(C311)		2.446	135.150	<0.001
s(C312)		1.017	26.918	<0.001
s(C313)		2.138	65.853	<0.001
s(C320)		0.926	11.379	<0.001
s(C321)		0.654	2.098	0.072
s(C330)		0.750	2.873	0.049
s(C410)		0.013	0.009	0.402
s(C511)		0.775	3.409	0.032

Italian Sparrow (*Passer italiae*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	6.307	0.180	35.120	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.150	1,884.500	<0.001
s(Urb$_{2500}$)		0.999	729.900	<0.001
s(For$_{2500}$)		0	0	0.552
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.322	0.052	−6.163	<0.001
Year 1995	−0.351	0.058	−6.045	<0.001
Year 1996	−0.534	0.056	−9.451	<0.001
Year 1999	−0.073	0.055	−1.333	0.183
Year 2000	−0.268	0.052	−5.182	<0.001
Year 2001	−0.560	0.056	−10.082	<0.001
Year 2002	−0.393	0.064	−6.179	<0.001
Year 2003	−0.593	0.068	−8.675	<0.001
Year 2004	−0.621	0.077	−8.047	<0.001
Year 2005	−0.643	0.055	−11.637	<0.001
Year 2006	−0.791	0.057	−13.808	<0.001
Year 2007	−0.916	0.064	−14.283	<0.001
Year 2008	−0.916	0.064	−14.220	<0.001
Year 2009	−1.003	0.063	−15.837	<0.001
Year 2010	−0.998	0.064	−15.556	<0.001
Year 2011	−1.119	0.063	−17.764	<0.001
Year 2012	−1.157	0.068	−17.088	<0.001
Year 2013	−1.245	0.067	−18.446	<0.001
Year 2014	−1.388	0.067	−20.794	<0.001
Year 2015	−1.177	0.065	−18.127	<0.001
Year 2016	−1.355	0.071	−19.011	<0.001
Year 2017	−1.145	0.078	−14.722	<0.001
Year 2018	−0.977	0.073	−13.454	<0.001
Year 2019	−1.017	0.073	−13.869	<0.001
Sin	0	0.014	−0.034	0.973
Cos	0	0.022	0.010	0.992
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.964	194.297	<0.001
s(Elevation)		1.377	127.582	<0.001
S(Slope)		1.065	25.331	<0.001
s(C110)		2.300	179.201	<0.001
s(C112)		2.965	655.634	<0.001
s(C211)		1.323	33.441	<0.001
s(C213)		2.153	54.436	<0.001
s(C221)		2.490	17.050	<0.001
s(C222)		0.758	3.026	0.044
s(C223)		0.931	9.306	0.001
s(C224)		1.584	3.588	0.093
s(C231)		1.845	71.784	<0.001
s(C311)		2.905	171.857	<0.001
s(C312)		1.000	66.285	<0.001
s(C313)		2.198	94.083	<0.001
s(C320)		0.959	29.269	<0.001
s(C321)		1.836	3.547	0.129
s(C330)		1.635	8.853	0.005
s(C410)		0.897	13.400	<0.001
s(C511)		2.695	6.356	0.068

Eurasian Tree Sparrow (*Passer montanus*) — Model C-ZIP-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	2.657	0.056	47.220	<0.001

Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		1.274	1,367.000	<0.001
s(Urb$_{2500}$)		2.987	1,536.000	<0.001
s(For$_{2500}$)		2.992	1,285.000	<0.001

Count component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.851	0.140	−13.218	<0.001
Year 1995	−0.352	0.108	−3.245	0.001
Year 1996	−0.464	0.106	−4.387	<0.001
Year 1999	−0.079	0.105	−0.756	0.449
Year 2000	−0.145	0.097	−1.498	0.134
Year 2001	−0.222	0.098	−2.274	0.023
Year 2002	−0.523	0.123	−4.253	<0.001
Year 2003	−0.806	0.138	−5.845	<0.001
Year 2004	−0.526	0.148	−3.557	<0.001
Year 2005	−0.378	0.099	−3.828	<0.001
Year 2006	−0.344	0.101	−3.415	<0.001
Year 2007	−0.311	0.106	−2.945	0.003
Year 2008	−0.286	0.107	−2.681	0.007
Year 2009	−0.291	0.103	−2.835	0.005
Year 2010	−0.482	0.108	−4.444	<0.001
Year 2011	−0.660	0.108	−6.092	<0.001
Year 2012	−0.669	0.114	−5.889	<0.001
Year 2013	−0.674	0.112	−5.998	<0.001
Year 2014	−0.528	0.109	−4.862	<0.001
Year 2015	−0.517	0.107	−4.821	<0.001
Year 2016	−0.583	0.111	−5.256	<0.001
Year 2017	−0.670	0.128	−5.224	<0.001
Year 2018	−0.766	0.131	−5.853	<0.001
Year 2019	−0.921	0.137	−6.706	<0.001
Sin	0.025	0.023	1.085	0.278
Cos	0.064	0.035	1.811	0.070

Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.956	60.667	<0.001
s(Elevation)		2.791	36.345	<0.001
s(Slope)		1.047	25.221	<0.001
s(C110)		2.252	15.416	<0.001
s(C112)		2.931	120.242	<0.001
s(C211)		1.069	18.045	<0.001
s(C213)		1.121	32.702	<0.001
s(C221)		1.890	13.353	<0.001
s(C222)		0.877	5.564	0.011
s(C223)		0	0	0.531
s(C224)		1.610	1.741	0.314
s(C231)		1.717	20.534	<0.001
s(C311)		2.146	50.230	<0.001
s(C312)		2.784	23.823	<0.001
s(C313)		2.059	32.807	<0.001
s(C320)		0	0	0.304
s(C321)		0.002	0	0.903
s(C330)		0.742	3.555	0.028
s(C410)		0.897	13.829	<0.001
s(C511)		1.905	4.068	0.105

Common Chaffinch (*Fringilla coelebs*) — Model C-ZIP-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	6.300	1.912	3.296	<0.001

Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		0.003	0	1.000
s(Urb$_{2500}$)		2.981	786.300	<0.001
s(For$_{2500}$)		1.639	1,612.800	<0.001

Count component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.205	0.050	4.072	<0.001
Year 1995	−0.173	0.065	−2.672	0.008
Year 1996	−0.133	0.063	−2.093	0.036
Year 1999	−0.025	0.055	−0.455	0.649
Year 2000	−0.099	0.055	−1.817	0.069
Year 2001	−0.032	0.058	−0.547	0.584
Year 2002	−0.097	0.062	−1.553	0.120
Year 2003	−0.054	0.062	−0.873	0.383
Year 2004	−0.056	0.068	−0.823	0.411
Year 2005	0.014	0.058	0.238	0.812
Year 2006	0.025	0.056	0.440	0.660
Year 2007	0.019	0.060	0.319	0.750
Year 2008	0.011	0.061	0.174	0.862
Year 2009	0.008	0.061	0.131	0.896
Year 2010	−0.054	0.061	−0.884	0.377
Year 2011	−0.087	0.058	−1.483	0.138
Year 2012	−0.041	0.060	−0.681	0.496
Year 2013	−0.170	0.061	−2.779	0.005
Year 2014	−0.143	0.059	−2.397	0.017
Year 2015	−0.136	0.060	−2.254	0.024
Year 2016	−0.199	0.061	−3.270	0.001
Year 2017	−0.067	0.064	−1.054	0.292
Year 2018	−0.117	0.065	−1.813	0.070
Year 2019	−0.134	0.065	−2.063	0.039
Sin	−0.012	0.010	−1.142	0.254
Cos	0.009	0.015	0.584	0.559

Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.976	402.465	<0.001
s(Elevation)		2.668	110.564	<0.001
s(Slope)		2.697	66.233	<0.001
s(C110)		1.508	1.714	0.241
s(C112)		1.764	3.218	0.125
s(C211)		2.893	31.125	<0.001
s(C213)		0.907	17.705	<0.001
s(C221)		2.883	23.012	<0.001
s(C222)		1.738	3.473	0.125
s(C223)		1.781	10.761	0.002
s(C224)		1.423	24.062	<0.001
s(C231)		0.483	2.811	0.007
s(C311)		2.462	97.402	<0.001
s(C312)		2.860	209.555	<0.001
s(C313)		2.461	141.634	<0.001
s(C320)		0.697	3.709	0.011
s(C321)		2.949	136.362	<0.001
s(C330)		0.977	57.090	<0.001
s(C410)		0.912	13.229	<0.001
s(C511)		2.808	9.517	0.017

European Serin (*Serinus serinus*) — Model C-ZIP-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.357	0.026	13.560	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.999	2,188.000	<0.001
s(Urb$_{2500}$)		2.989	1,835.000	<0.001
s(For$_{2500}$)		2.985	1,446.000	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−1.300	0.114	−11.431	<0.001
Year 1995	−0.476	0.147	−3.234	0.001
Year 1996	−0.802	0.154	−5.203	<0.001
Year 1999	−0.271	0.135	−2.016	0.044
Year 2000	−0.037	0.121	−0.308	0.758
Year 2001	−0.389	0.136	−2.865	0.004
Year 2002	−0.126	0.146	−0.867	0.386
Year 2003	−0.378	0.154	−2.447	0.014
Year 2004	−0.188	0.164	−1.146	0.252
Year 2005	−0.192	0.126	−1.525	0.127
Year 2006	−0.088	0.122	−0.719	0.472
Year 2007	−0.203	0.130	−1.555	0.120
Year 2008	−0.159	0.129	−1.232	0.218
Year 2009	−0.113	0.129	−0.874	0.382
Year 2010	−0.241	0.129	−1.875	0.061
Year 2011	−0.463	0.129	−3.598	<0.001
Year 2012	−0.231	0.129	−1.790	0.073
Year 2013	−0.524	0.137	−3.824	<0.001
Year 2014	−0.555	0.128	−4.320	<0.001
Year 2015	−0.565	0.134	−4.221	<0.001
Year 2016	−0.448	0.133	−3.380	<0.001
Year 2017	−0.440	0.147	−2.997	0.003
Year 2018	−0.333	0.143	−2.329	0.020
Year 2019	−0.317	0.141	−2.250	0.024
Sin	−0.050	0.026	−1.894	0.058
Cos	−0.079	0.042	−1.878	0.060
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.988	<0.001	<0.001
s(Elevation)		0.001	0	0.604
s(Slope)		2.895	113.883	<0.001
s(C110)		2.386	121.305	<0.001
s(C112)		1.746	67.878	<0.001
s(C211)		0.542	0.944	0.164
s(C213)		0.988	29.669	<0.001
s(C221)		2.895	110.787	<0.001
s(C222)		0.909	16.834	<0.001
s(C223)		0.721	3.434	0.026
s(C224)		0.675	1.737	0.106
s(C231)		2.081	8.550	0.005
s(C311)		2.886	118.367	<0.001
s(C312)		1.860	31.369	<0.001
s(C313)		2.228	63.291	<0.001
s(C320)		0.773	2.389	0.071
s(C321)		1.911	7.472	0.015
s(C330)		1.915	15.494	<0.001
s(C410)		0.954	11.390	<0.001
s(C511)		1.291	0.428	0.665

European Greenfinch (*Chloris chloris*) — Model C-ZINB-GAM

Binomial component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.146	0.019	−7.711	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.999	1,202.150	<0.001
s(Urb$_{2500}$)		2.978	1,058.550	<0.001
s(For$_{2500}$)		1.262	54.350	<0.001

Count component

Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.632	0.109	−5.807	<0.001
Year 1995	−0.378	0.121	−3.118	0.002
Year 1996	−0.627	0.122	−5.143	<0.001
Year 1999	−0.084	0.115	−0.733	0.464
Year 2000	−0.024	0.106	−0.226	0.821
Year 2001	−0.659	0.118	−5.569	<0.001
Year 2002	−0.634	0.137	−4.641	<0.001
Year 2003	−0.767	0.141	−5.426	<0.001
Year 2004	−1.120	0.176	−6.369	<0.001
Year 2005	−1.016	0.121	−8.411	<0.001
Year 2006	−1.107	0.122	−9.098	<0.001
Year 2007	−1.093	0.134	−8.154	<0.001
Year 2008	−0.987	0.129	−7.631	<0.001
Year 2009	−1.450	0.145	−10.017	<0.001
Year 2010	−1.443	0.144	−10.047	<0.001
Year 2011	−1.255	0.129	−9.746	<0.001
Year 2012	−0.986	0.129	−7.644	<0.001
Year 2013	−1.446	0.144	−10.072	<0.001
Year 2014	−1.582	0.136	−11.645	<0.001
Year 2015	−1.429	0.137	−10.428	<0.001
Year 2016	−1.658	0.151	−11.019	<0.001
Year 2017	−1.592	0.168	−9.460	<0.001
Year 2018	−1.973	0.191	−10.323	<0.001
Year 2019	−1.691	0.173	−9.750	<0.001
Sin	0.058	0.030	1.966	0.049
Cos	−0.061	0.046	−1.329	0.184
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		2.984	329.850	<0.001
s(Elevation)		2.704	19.338	<0.001
s(Slope)		0.998	9.789	<0.001
s(C110)		2.500	125.367	<0.001
s(C112)		0.944	12.391	<0.001
s(C211)		0.825	3.710	0.027
s(C213)		0.982	22.378	<0.001
s(C221)		0.936	13.978	<0.001
s(C222)		0.028	0.029	0.305
s(C223)		0.902	9.298	0.001
s(C224)		0.920	10.673	<0.001
s(C231)		0.001	0	0.633
s(C311)		2.713	123.871	<0.001
s(C312)		0.998	21.063	<0.001
s(C313)		1.033	33.425	<0.001
s(C320)		0	0	0.845
s(C321)		0.333	0.470	0.231
s(C330)		0	0	0.903
s(C410)		0.933	12.960	<0.001
s(C511)		0.693	2.180	0.075

European Goldfinch (*Carduelis carduelis*) — Model C-ZINB-GAM				
		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	0.065	0.019	3.525	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.941	1,045.600	<0.001
s(Urb$_{2500}$)		2.984	181.300	<0.001
s(For$_{2500}$)		2.952	59.300	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−0.281	0.099	−2.850	0.004
Year 1995	−0.638	0.125	−5.087	<0.001
Year 1996	−0.316	0.115	−2.745	0.006
Year 1999	−0.168	0.112	−1.500	0.134
Year 2000	−0.131	0.107	−1.225	0.221
Year 2001	−0.298	0.112	−2.670	0.008
Year 2002	−0.503	0.130	−3.871	<0.001
Year 2003	−0.450	0.129	−3.497	<0.001
Year 2004	−0.728	0.153	−4.745	<0.001
Year 2005	−0.728	0.114	−6.369	<0.001
Year 2006	−1.077	0.123	−8.789	<0.001
Year 2007	−1.136	0.136	−8.377	<0.001
Year 2008	−1.247	0.139	−8.958	<0.001
Year 2009	−1.447	0.145	−9.992	<0.001
Year 2010	−1.541	0.148	−10.402	<0.001
Year 2011	−1.676	0.144	−11.677	<0.001
Year 2012	−1.289	0.135	−9.517	<0.001
Year 2013	−1.268	0.134	−9.449	<0.001
Year 2014	−1.549	0.139	−11.151	<0.001
Year 2015	−1.373	0.136	−10.064	<0.001
Year 2016	−1.532	0.141	−10.846	<0.001
Year 2017	−1.458	0.159	−9.188	<0.001
Year 2018	−1.871	0.181	−10.326	<0.001
Year 2019	−1.947	0.184	−10.578	<0.001
Sin	−0.023	0.028	−0.845	0.398
Cos	0.005	0.041	0.125	0.901
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.934	85.697	<0.001
s(Elevation)		2.717	68.253	<0.001
s(Slope)		2.561	35.419	<0.001
s(C110)		2.540	79.730	<0.001
s(C112)		1.005	23.050	<0.001
s(C211)		0.967	6.051	0.007
s(C213)		0.001	0.001	0.396
s(C221)		0.934	13.401	<0.001
s(C222)		0.074	0.080	0.296
s(C223)		0.352	0.571	0.202
s(C224)		0.001	0.001	0.403
s(C231)		1.850	35.231	<0.001
s(C311)		2.677	119.049	<0.001
s(C312)		1.185	56.521	<0.001
s(C313)		2.428	57.803	<0.001
s(C320)		0.897	7.960	0.003
s(C321)		0.291	0.398	0.238
s(C330)		0.003	0.001	0.530
s(C410)		0.873	6.535	0.006
s(C511)		0.801	4.036	0.023

Common Linnet (*Linaria cannabina*) — Model C-ZINB-GAM

		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.930	0.044	−67.050	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.686	3,830.038	<0.001
s(Urb$_{2500}$)		0	0	0.946
s(For$_{2500}$)		0.500	2.865	0.011
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−9.612	20.227	−0.475	0.635
Year 1996	−1.059	0.633	−1.672	0.094
Year 1999	−0.150	0.439	−0.341	0.733
Year 2000	−0.131	0.410	−0.319	0.750
Year 2001	−0.413	0.465	−0.888	0.374
Year 2002	−0.373	0.473	−0.790	0.429
Year 2003	−0.109	0.429	−0.254	0.799
Year 2004	−0.727	0.500	−1.454	0.146
Year 2005	0.552	0.388	1.423	0.155
Year 2006	0.233	0.414	0.564	0.573
Year 2007	−0.073	0.420	−0.175	0.861
Year 2008	0.183	0.406	0.449	0.653
Year 2009	−0.096	0.420	−0.228	0.820
Year 2010	−0.268	0.421	−0.637	0.524
Year 2011	0.278	0.401	0.692	0.489
Year 2012	0.150	0.402	0.373	0.709
Year 2013	−0.115	0.411	−0.280	0.780
Year 2014	−0.227	0.410	−0.553	0.580
Year 2015	−0.205	0.409	−0.501	0.616
Year 2016	−0.460	0.419	−1.098	0.272
Year 2017	−0.372	0.423	−0.880	0.379
Year 2018	−0.417	0.430	−0.969	0.333
Year 2019	0.117	0.408	0.286	0.775
Sin	−0.114	0.071	−1.598	0.110
Cos	−0.072	0.114	−0.635	0.525
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.944	56.401	<0.001
s(Elevation)		2.730	98.546	<0.001
s(Slope)		1.882	5.297	0.049
s(C110)		0	0	0.634
s(C112)		2.049	16.564	<0.001
s(C211)		0	0	0.415
s(C213)		0.705	0.012	0.899
s(C221)		0.940	13.156	<0.001
s(C222)		0	0	0.930
s(C223)		0	0	0.827
s(C224)		0.267	0.056	0.646
s(C231)		0	0	0.850
s(C311)		1.090	22.332	<0.001
s(C312)		1.964	79.921	<0.001
s(C313)		1.038	32.620	<0.001
s(C320)		2.260	15.396	<0.001
s(C321)		0	0	0.940
s(C330)		0.984	32.762	<0.001
s(C410)		0.002	0.001	0.383
s(C511)		0.823	4.278	0.022

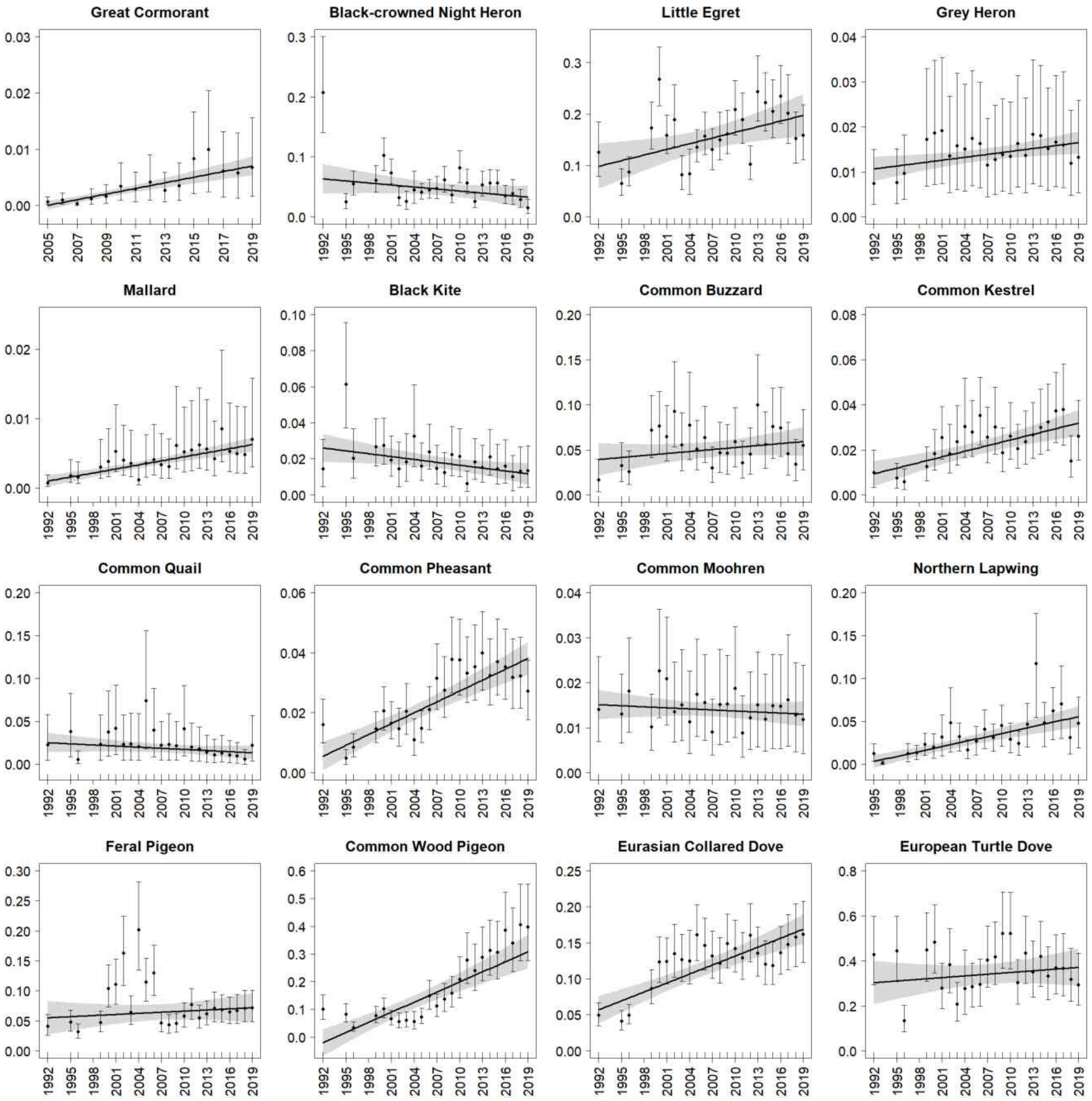
Common Redpoll (*Acanthis flammea*) — Model C-ZINB-GAM				
Binomial component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−3.551	0.067	−53.160	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.892	2,178.420	<0.001
s(Urb$_{2500}$)		0	0	0.929
s(For$_{2500}$)		2.306	42.360	<0.001
Count component				
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−7.041	25.421	−0.277	0.782
Year 1995	0.295	0.547	0.539	0.590
Year 1996	0.634	0.551	1.152	0.249
Year 1999	−0.609	0.562	−1.085	0.278
Year 2000	0.423	0.528	0.801	0.423
Year 2001	−0.185	0.548	−0.337	0.736
Year 2002	0.314	0.548	0.574	0.566
Year 2003	−0.752	0.557	−1.349	0.177
Year 2004	0.155	0.542	0.285	0.775
Year 2005	0.206	0.518	0.397	0.691
Year 2006	0.349	0.541	0.645	0.519
Year 2007	−0.378	0.543	−0.697	0.486
Year 2008	−0.574	0.544	−1.055	0.291
Year 2009	−0.701	0.549	−1.276	0.202
Year 2010	−0.875	0.561	−1.560	0.119
Year 2011	−0.022	0.527	−0.042	0.967
Year 2012	0.173	0.521	0.333	0.739
Year 2013	−0.154	0.530	−0.291	0.771
Year 2014	0.013	0.523	0.026	0.979
Year 2015	0.085	0.518	0.163	0.870
Year 2016	−0.586	0.537	−1.090	0.276
Year 2017	−0.551	0.544	−1.014	0.311
Year 2018	−0.902	0.566	−1.595	0.111
Year 2019	−0.641	0.549	−1.168	0.243
Sin	−0.124	0.064	−1.929	0.054
Cos	0.344	0.090	3.811	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.783	16.389	<0.001
s(Elevation)		2.496	34.507	<0.001
s(Slope)		2.535	25.271	<0.001
s(C110)		0.002	0.001	0.413
s(C112)		0	0	0.400
s(C211)		0.597	0.743	0.259
s(C213)		0	0	0.860
s(C221)		0	0	0.624
s(C222)		0	0	0.852
s(C223)		0	0	0.902
s(C224)		0.227	0.013	0.810
s(C231)		0	0	1.000
s(C311)		0	0	0.881
s(C312)		2.209	28.429	<0.001
s(C313)		0.831	4.305	0.021
s(C320)		2.035	7.829	0.013
s(C321)		2.198	18.131	<0.001
s(C330)		0.529	1.112	0.142
s(C410)		0	0	0.605
s(C511)		0.001	0	0.446

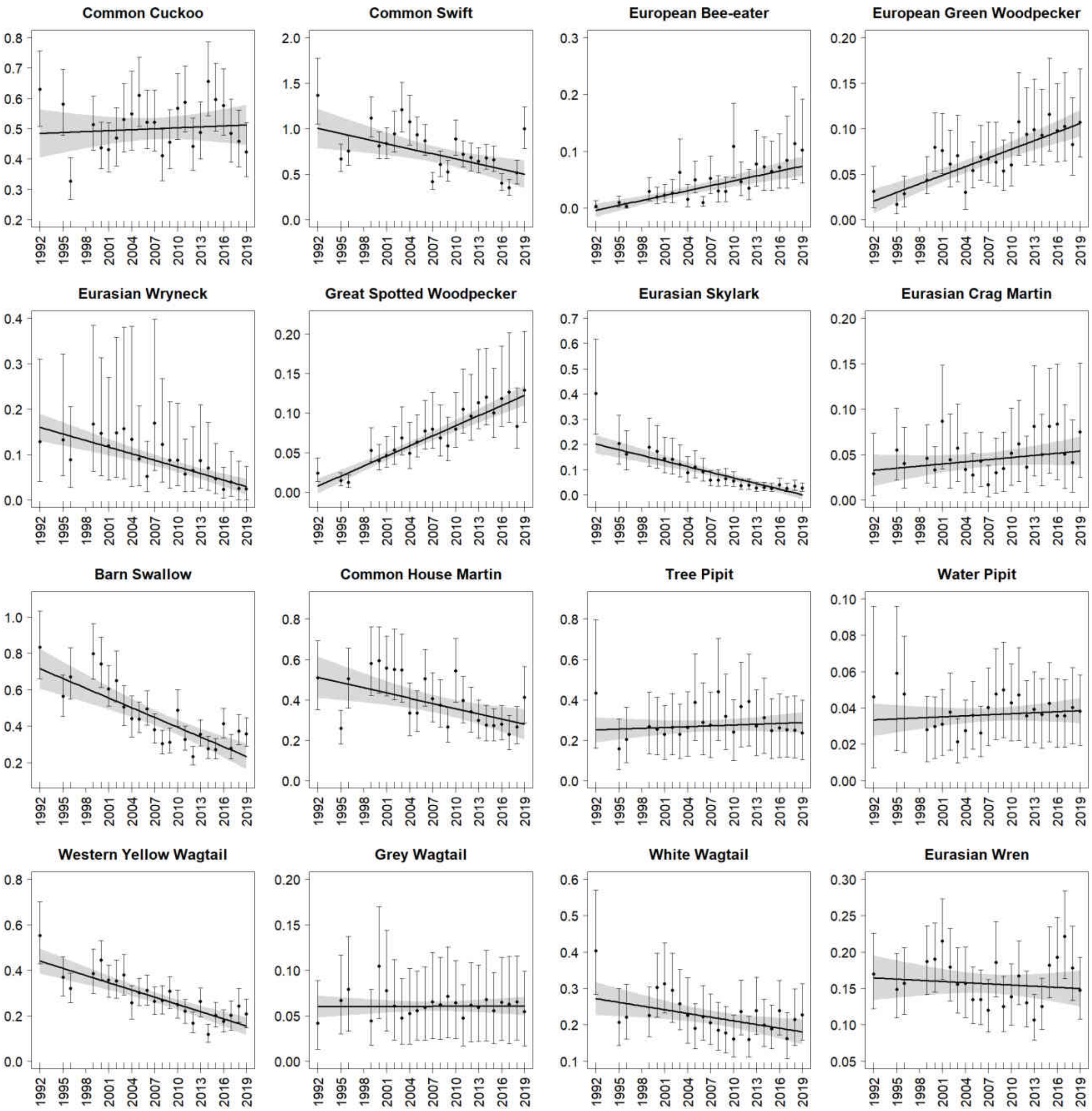
Eurasian Bullfinch (*Pyrrhula pyrrhula*) — Model C-ZIP-GAM

		Binomial component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−2.553	0.039	−64.760	<0.001
Smooth terms		**edf**	**Chi-square**	**p-value**
s(Elevation)		2.996	2,722.820	<0.001
s(Urb$_{2500}$)		0.002	0	1.000
s(For$_{2500}$)		2.006	97.430	<0.001
		Count component		
Parametric terms	**Estimate**	**Standard error**	**z-value**	**p-value**
Intercept	−6.245	3.029	−2.061	0.039
Year 1995	1.299	0.514	2.529	0.011
Year 1996	−0.663	0.734	−0.903	0.367
Year 1999	0.845	0.478	1.770	0.077
Year 2000	0.961	0.469	2.048	0.041
Year 2001	1.529	0.469	3.259	0.001
Year 2002	1.383	0.477	2.898	0.004
Year 2003	1.080	0.486	2.224	0.026
Year 2004	1.254	0.510	2.461	0.014
Year 2005	1.019	0.480	2.124	0.034
Year 2006	0.209	0.551	0.380	0.704
Year 2007	0.293	0.519	0.563	0.573
Year 2008	1.248	0.481	2.595	0.009
Year 2009	0.517	0.523	0.987	0.323
Year 2010	1.083	0.489	2.216	0.027
Year 2011	1.275	0.478	2.668	0.008
Year 2012	1.071	0.491	2.181	0.029
Year 2013	0.780	0.496	1.574	0.115
Year 2014	0.699	0.498	1.402	0.161
Year 2015	1.051	0.487	2.161	0.031
Year 2016	0.992	0.487	2.038	0.042
Year 2017	0.822	0.516	1.594	0.111
Year 2018	0.599	0.530	1.131	0.258
Year 2019	0.653	0.530	1.234	0.217
Sin	−0.008	0.056	−0.148	0.882
Cos	0.069	0.079	0.879	0.380
Smooth terms		**edf**	**Chi-square**	**p-value**
s(X, Y)		1.918	55.513	<0.001
s(Elevation)		2.835	34.892	<0.001
s(Slope)		0.931	8.684	0.002
s(C110)		1.939	14.939	<0.001
s(C112)		0.962	14.599	<0.001
s(C211)		0.821	3.303	0.042
s(C213)		0.001	0	0.595
s(C221)		0.647	0.327	0.477
s(C222)		0.609	0.040	0.797
s(C223)		0.001	0	0.820
s(C224)		0	0	0.706
s(C231)		1.426	33.316	<0.001
s(C311)		1.013	13.524	<0.001
s(C312)		2.459	28.298	<0.001
s(C313)		0	0	0.386
s(C320)		2.637	14.036	0.001
s(C321)		2.823	44.499	<0.001
s(C330)		1.774	11.105	0.002
s(C410)		0	0	0.507
s(C511)		0.882	7.720	0.003

S3.8

Population indices with confidence intervals and regression line for the 76 studied species. Y-axis represents estimated number of breeding pairs per point count (see Section 3.2.3 for details). Dot and bars represent the median and the 2.5th-97.5th percentiles of 1,000 bootstrapped values, respectively. Fitted WLS-regression lines with confidence intervals (grey area) are superimposed.

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0.6
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0.8
Common Swift
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0.5
1.0
1.5
2.0
European Bee-eater
0.0
0.1
0.2
0.3
European Green Woodpecker
0.00
0.05
0.10
0.15
0.20
Eurasian Wryneck
0.0
0.1
0.2
0.3
0.4
Great Spotted Woodpecker
0.00
0.05
0.10
0.15
0.20
Eurasian Skylark
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Eurasian Crag Martin
0.00
0.05
0.10
0.15
0.20
Barn Swallow
0.2
0.4
0.6
0.8
1.0
Common House Martin
0.0
0.2
0.4
0.6
0.8
Tree Pipit
0.0
0.2
0.4
0.6
0.8
Water Pipit
0.00
0.02
0.04
0.06
0.08
0.10
Western Yellow Wagtail
0.0
0.2
0.4
0.6
0.8
Grey Wagtail
0.00
0.05
0.10
0.15
0.20
White Wagtail
0.1
0.2
0.3
0.4
0.5
0.6
Eurasian Wren
0.05
0.10
0.15
0.20
0.25
0.30
1992
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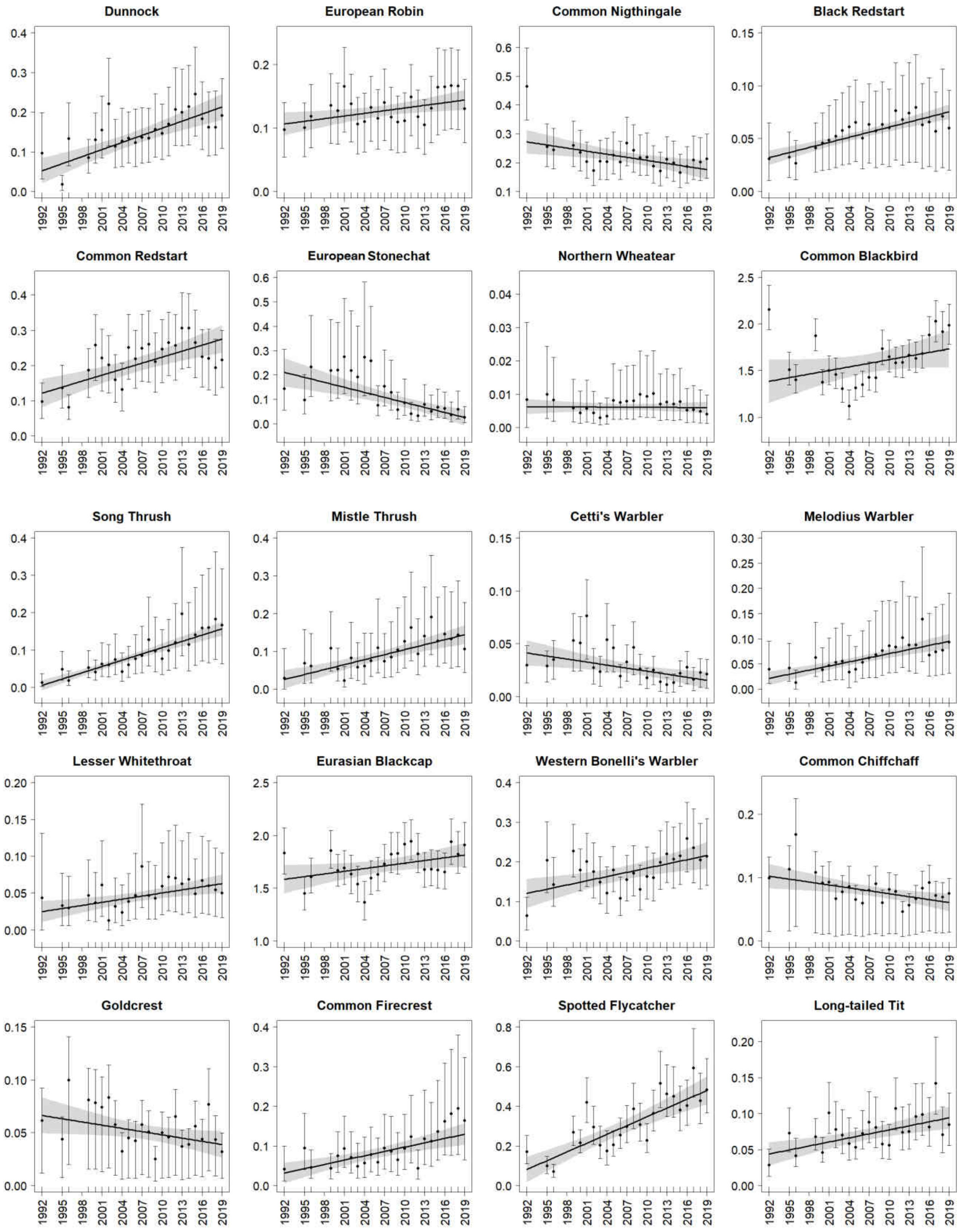
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European Robin
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0.2
Common Nigthingale
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0.2
0.3
0.4
0.5
0.6
Black Redstart
0.00
0.05
0.10
0.15
Common Redstart
0.0
0.1
0.2
0.3
0.4
European Stonechat
0.0
0.1
0.2
0.3
0.4
0.5
0.6
Northern Wheatear
0.00
0.01
0.02
0.03
0.04
Common Blackbird
1.0
1.5
2.0
2.5
Song Thrush
0.0
0.1
0.2
0.3
0.4
Mistle Thrush
0.0
0.1
0.2
0.3
0.4
Cetti's Warbler
0.00
0.05
0.10
0.15
Melodius Warbler
0.00
0.05
0.10
0.15
0.20
0.25
0.30
Lesser Whitethroat
0.00
0.05
0.10
0.15
0.20
Eurasian Blackcap
1.0
1.5
2.0
2.5
Western Bonelli's Warbler
0.0
0.1
0.2
0.3
0.4
Common Chiffchaff
0.0
0.1
0.2
Goldcrest
0.00
0.05
0.10
0.15
Common Firecrest
0.0
0.1
0.2
0.3
0.4
Spotted Flycatcher
0.0
0.2
0.4
0.6
0.8
Long-tailed Tit
0.00
0.05
0.10
0.15
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1992
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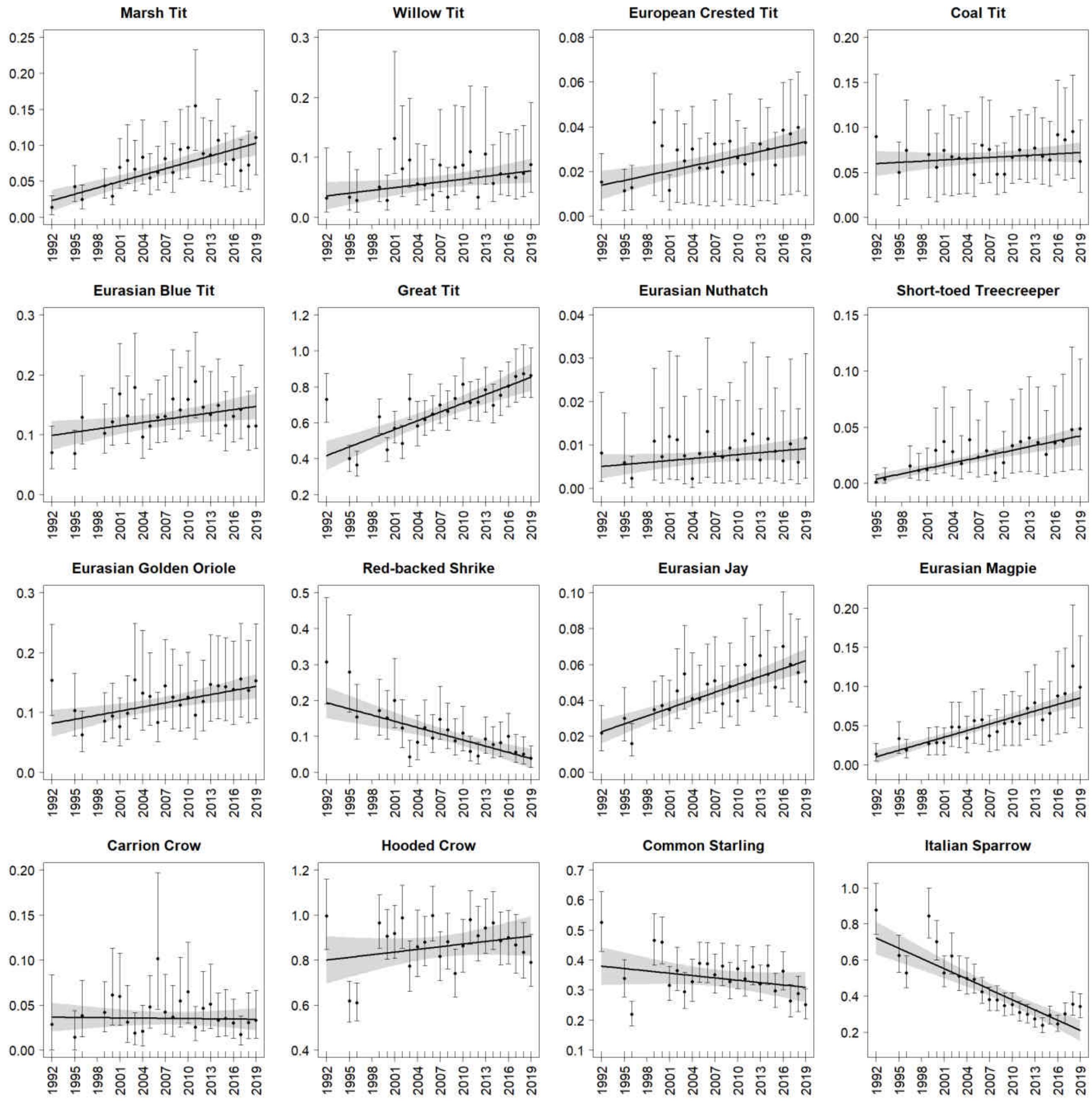
Marsh Tit
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Willow Tit
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0.0
European Crested Tit
0.08
0.06
0.04
0.02
0.00
Coal Tit
0.20
0.15
0.10
0.05
0.00
Eurasian Blue Tit
0.3
0.2
0.1
0.0
Great Tit
1.2
1.0
0.8
0.6
0.4
0.2
Eurasian Nuthatch
0.04
0.03
0.02
0.01
0.00
Short-toed Treecreeper
0.15
0.10
0.05
0.00
1995
Eurasian Golden Oriole
0.3
0.2
0.1
0.0
Red-backed Shrike
0.5
0.4
0.3
0.2
0.1
0.0
Eurasian Jay
0.10
0.08
0.06
0.04
0.02
0.00
Eurasian Magpie
0.20
0.15
0.10
0.05
0.00
Carrion Crow
0.20
0.15
0.10
0.05
0.00
Hooded Crow
1.2
1.0
0.8
0.6
0.4
Common Starling
0.7
0.6
0.5
0.4
0.3
0.2
0.1
Italian Sparrow
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0.8
0.6
0.4
0.2
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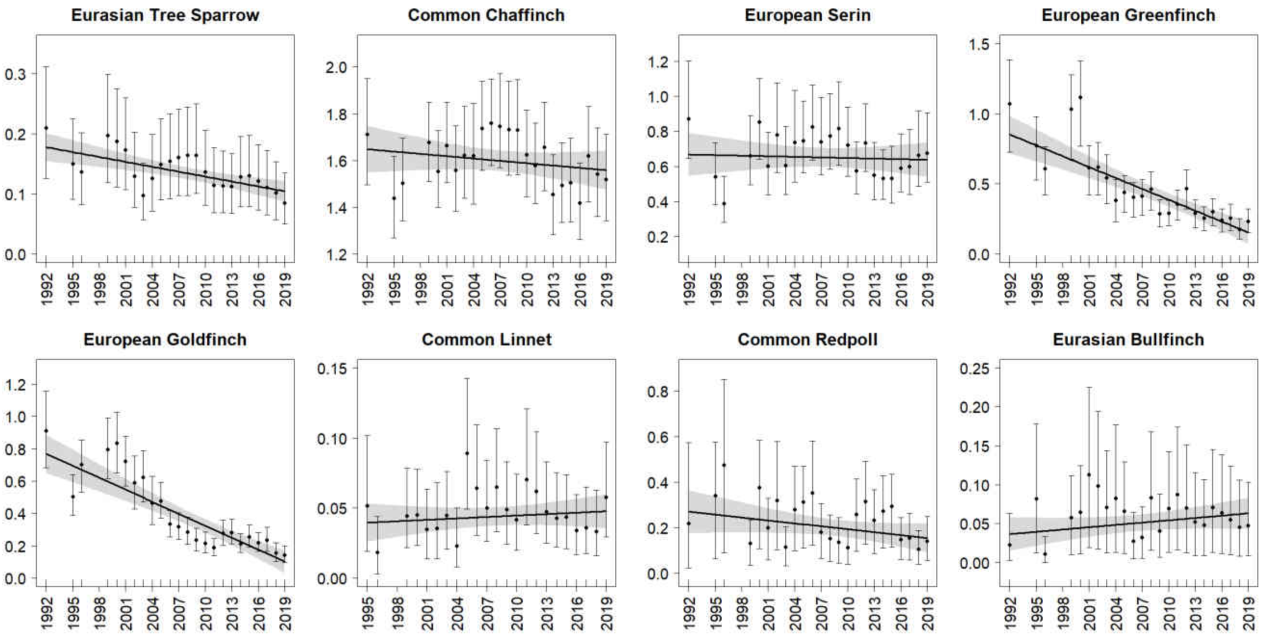
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Common Chaffinch
1.2
1.4
1.6
1.8
2.0
European Serin
0.2
0.4
0.6
0.8
1.0
1.2
European Greenfinch
0.0
0.5
1.0
1.5
1992
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European Goldfinch
0.0
0.2
0.4
0.6
0.8
1.0
1.2
Common Linnet
0.00
0.05
0.10
0.15
Common Redpoll
0.0
0.2
0.4
0.6
0.8
Eurasian Bullfinch
0.00
0.05
0.10
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0.20
0.25
1992
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2019

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Chapter 4

New evidence on the linkage of population trends and species traits to long-term niche changes

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Abstract

Despite the assessment of long-term niche dynamics could provide crucial information for investigating species responses to environmental changes, it is a poorly investigated topic in ecology. Here, we present a case study of multi-species niche analysis for 71 common breeding birds in northern Italy, exploring long-term niche changes from 1992 to 2017 and their relationship with both population trends and species traits. We (i) quantified the realised Grinnellian niche in the environmental space, (ii) compared variations in niche breadth and centroid, (iii) tested niche divergence and conservatism through equivalency and similarity tests, (iv) calculated niche overlap, expansion and unfilling indices, and (v) investigated their association with both population changes and species traits. Results supported niche divergence (equivalency test) for 32% of species, although two-thirds were not supported by the similarity test. We detected a general tendency to adjust the niche centroids towards warmer thermal conditions. Increasing populations were positively correlated with niche expansion, while negatively correlated with niche overlap, albeit at the limit of the significance threshold. We found moderate evidence for a non-random association between niche changes and species traits, especially for body size, clutch size, number of broods per year, inhabited landscape type, and migration strategy. We encourage studies correlating long-term population trends and niche changes with species traits' information and a specific focus on cause-effect relationship at both the single and multiple-species level.

4.1. Introduction

The quantification of the realised niche of a species (Hutchinson, 1957) (sensu Grinnell; Grinnel, 1914, 1917; Soberón, 2007; Soberón & Nakamura, 2009), hereafter niche) and how it varies across space and time has received increasing attention in ecological studies, with important implications in evolution, biogeography, and conservation (Wiens & Graham, 2005; Pearman et al., 2008; Petitpierre et al., 2012; Strubbe et al., 2013; Breiner et al., 2017; Mothes et al., 2019; Rather et al., 2020; Zink et al., 2020; Ahmadi et al., 2021; Liordos et al., 2021). Many studies have focused on niche evolution in related taxa (Losos, 2008; Broennimann et al., 2014a; Moreno-Contreras et al., 2020; Sillero et al., 2020; Escoriza et al., 2021; Hending et al., 2021; Lin et al., 2021; Liu et al., 2021), or on niche quantification of alien species to assess their potential as invaders in non-native ranges (Broennimann et al., 2014b; Li et al., 2014; Jänes et al., 2017; Louppe et al., 2019; Liu et al., 2020; Changjun et al., 2021; Olivera et al., 2021; Tang et al., 2021; Zachariah Atwater & Barney, 2021). However, niche quantification and change in avian species remain poorly investigated aspects, especially if compared to other research topics (e.g. population trend assessment). As well as the general tendency in ecology, in ornithology most studies on niche have focused on evolutionary aspects or on invasive species. Moreover, several studies have focused on niche-tracking under climate change by a correlative modeling approach (e.g. species distribution models; Guisan & Thuiller, 2005) in order to predict future changes in species distributional range (Devictor et al., 2008; Reino et al., 2018; Jose & Nameer, 2020; Bladon et al., 2021; Sierra-Morales et al., 2021). Both the niche-tracking concept and its application in predictive species distribution modeling assume niche conservatism (Soberón & Nakamura, 2009), which implies that in the future a species will occupy the same environmental conditions that it occupies today. Several studies have supported niche conservatism on both ecological and evolutionary timescales (Peterson et al., 1999; Wiens & Graham, 2005; Peterson, 2011). However, these studies focused on conservation of the fundamental niche, while a separate issue is whether the realised niche is also conserved. Some studies have highlighted that species may not retain their realised niche between the native and invaded range (Medley, 2010; Lauzeral et al., 2011) and that variations may be expected under climate changes (Sutton et al., 2015).

Very little attention has been given to within-species niche changes in the same geographic area over time. Assessing the change of the niche of a species in a relatively long-term period (e.g. decades) could allow measuring the environmental plasticity of the species in adapting to suboptimal environmental conditions and in colonising new habitats, as well as the tendency in moving the niche boundaries or position towards different combinations of environmental gradients. This information may be combined with population trends to shed light on mechanisms that regulate species capability in responding to environmental changes, which can be pivotal to plan effective conservation actions. We ascertained a lack of studies on this potential relationship (but see Ralston et al., 2016, 2017), although long time-series data coming from standardised bird monitoring programs (e.g. North American Breeding Bird Surveys; Sauer et al., 2017) exist. Ralston et al. (2016) found a positive association between changes in climatic niche breadth and population trends. Ralston et al. (2017) also showed that increasing species tended to show greater levels of climatic niche expansion compared to declining species, while declining species had significantly greater climatic niche unfilling compared to increasing species. Notwithstanding the relevance and the novelty of their results, these two studies did not consider the habitat characteristics (e.g. land cover variables) in niche quantification, thus omitting important scenopoetic variables, i.e. variables that are invariant to species (Hutchinson, 1978), constituting the realised Grinnellian niche. Another important question is how temporal changes in niche occupancy (i.e. variations of the density of occurrence corrected by the environmental availability in the multidimensional niche space) are related to population trends. The inference on the cause-effect relationship between niche changes and population trends needs to be carefully evaluated (Ralston et al., 2017). Indeed, it is reasonable to expect that a change (both an expansion and an unfilling) in a species niche could be the reason for the observed population trend (e.g. Cheeseman et al., 2021 for the isotopic niche). However, it is also reasonable that the variation in a species niche may be the result of a change in the species population abundance (due to niche-independent potential factors, e.g. epidemic, interspecific competition, density-dependent factors), which could have led to a niche reshaping with expansion, unfilling, centroid shift, variations in breadth or density of occurrence.

Beyond the relevance of a species-specific approach, in the past decade the increasing attention on a trait-based approach allowed highlighting emergent ecological patterns in groups of birds sharing similar life-history and ecological traits (Sullivan et al., 2015; Rocchia et al., 2018; Bowler et al., 2019; Kamp et al., 2021; Tirozzi et al., 2021 and *Chapter 3*). The relationship between the ecological niche and species traits has been mainly explored under an evolutionary perspective (Pigot et al., 2020; Pelegrin et al., 2021; Shaner et al., 2021), but there is a lack of studies focusing on ecological aspects (but see Zurell et al., 2018; Schumm et al., 2021). Revealing such types of ecological signal would point out a non-random evolution of niche changes, suggesting the existence of shared ecological pressures within groups of species sharing similar characteristics.

Here, we present a multi-species niche analysis on 71 common breeding birds in northern Italy (Lombardy region), exploring long-term niche changes from 1992 to 2017 and relating niche changes to species population trends, life-history and ecological traits. Specifically, we tried to answer the following questions: (i) did birds vary their niche over a long-term period? (ii) Are niche expansion and unfilling associated with increasing and decreasing populations, respectively? (iii) Is the intensity of niche overlap, i.e. the tendency to not vary the niche occupancy, related to population change? (iv) How do niche changes relate to species traits?

4.2. Materials and Methods

4.2.1. Study area and bird data

The study was carried out in Lombardy, a region of 23,861 km^2 in northern Italy (45° N, 9° E). The area presents diversified landscapes: mountain chains in the North (Alps and Prealps), a large West-East alluvial plain of more than 12,000 km^2 in the central part (Po Plain), and a portion of Apennines mountains in the southwestern corner. Overall, land use is characterised by urban areas (14.7%), agricultural lands (42.2%), and natural and semi-natural lands (39.6%, of which 61.4% are forests; data derived from digital land cover map DUSAF; ERSAF, 2018). Continuous forests and meadows occupy the territory of Alps and Prealps up to the wood limit, where natural shrublands and grasslands extend at higher altitudes. The Po Plain is heavily men-modified, with intensive cereal cultivations (mainly maize) in the central and eastern part, and dense urban areas and paddy fields in the West. Extensive farming and deciduous and mixed forests characterise the Apennines. During the time span considered in this study, the region underwent some land-use changes. Forest cover increased (+1%), agricultural lands declined (−3.3%), and urban areas increased (+2.1%) (comparison of digital land-cover maps DUSAF; ERSAF, 1999, 2018).

Bird data were obtained from the Long-Term Monitoring Program of Breeding Birds in Lombardy (Bani et al., 2009). The project has been carrying out yearly surveys since 1992 (no data are available for 1993, 1994, 1997, 1998) following a stratified random design (Tirozzi et al., 2021 and *Chapter 3*). Data were collected through a single-visit point-count method with unlimited distance (Blondel et al., 1981), whereby all birds heard or seen (including over-flying individuals) in 10 min were recorded (Fornasari et al., 1998). Surveys were carried out each year during the breeding season (10 May-20 June), from sunrise to 11 a.m. and only in good weather conditions. The technique is effective in detecting bird species belonging to the orders Columbiformes, Cuculiformes, Apodiformes, Coraciiformes, Piciformes, and Passeriformes, but can also be used to survey some other common species, such as the Common Buzzard (*Buteo buteo*) and the Common Kestrel (*Falco tinnunculus*) (Bani et al., 2009). To investigate the long-term changes of species niche, we defined two temporal windows (T_1 and T_2) of a three-year time interval: T_1 includes point counts performed in 1992 (n = 373), 1995 (n = 650), and 1996 (n = 696), while T_2 includes point counts performed in 2015 (n = 855), 2016 (n = 749), and 2017 (n = 542) (Figure 4.1). This procedure allows limiting the effect of inter-annual abundance variability and obtaining a more representative sample (Ralston et al., 2016; Rocchia et al., 2018; Dondina et al., 2022). Since the project did not include multiple surveys within the same season, species detection probability could not be explicitly considered. Nevertheless, the large amount of data used for this study and their aggregation into three-year time intervals overcomes the potential limit of imperfect detection, lowering the noise generated by stochasticity in species detection (Dondina et al., 2017; Bani et al., 2019). Moreover, 10-min point counts have been indicated as an effective survey technique to detect a sufficiently high percentage of the species present in a site (Fuller & Langslow, 1984), and surveys were performed by a restricted pool of expert surveyors, thus limiting the presence of inter-observer detection bias. For the purpose of this study, we retained the most common species with a frequency of occurrence higher than or equal to 1% in both T_1 and T_2 (number of species = 71).

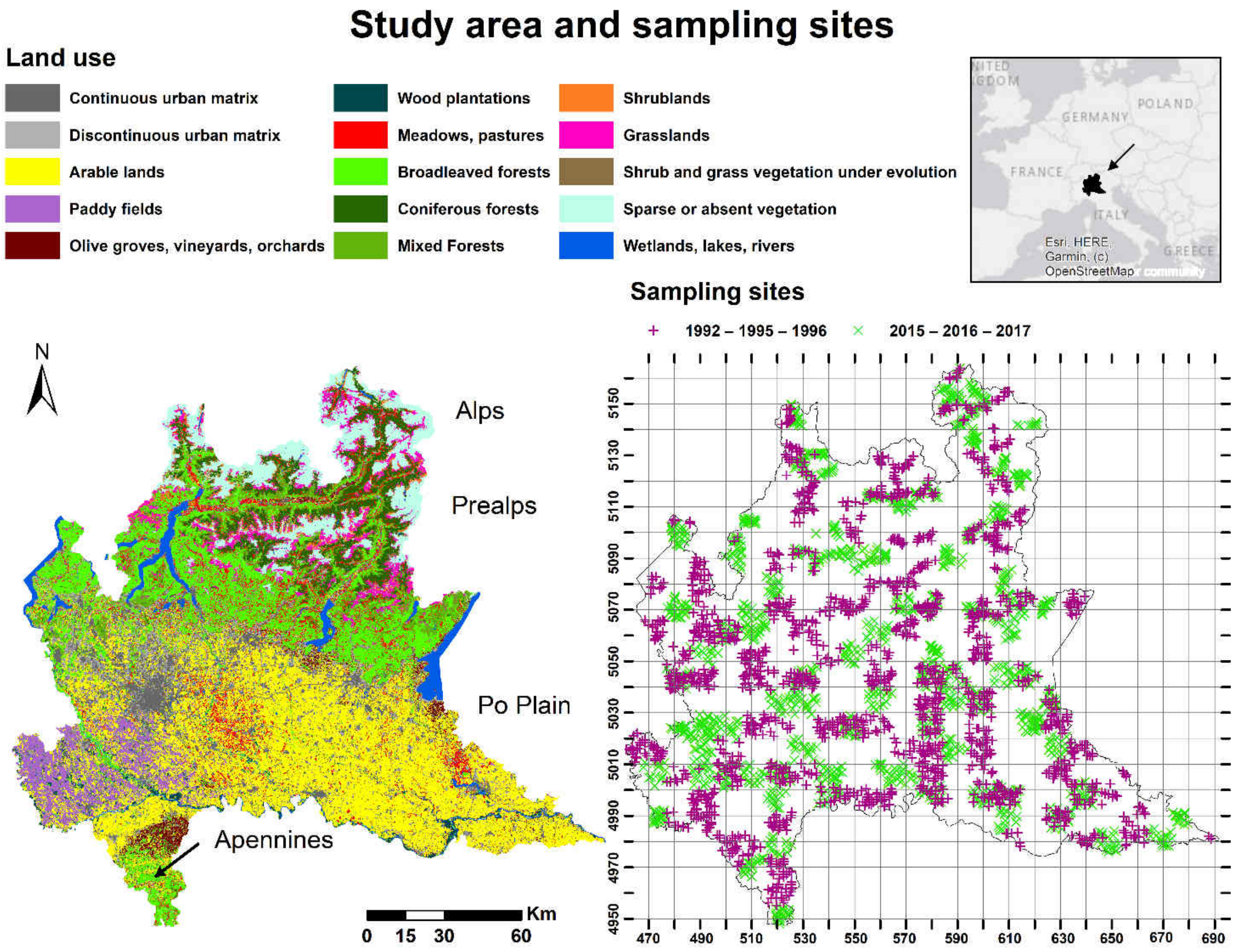

Figure 4.1. Land covers in the study area and locations of the sampling sites. Land covers are represented according to 3rd-level of DUSAF land-cover map (ERSAF, 2018) with some mergers (see S4.1 in Supplementary materials). 10-km square grid (WGS84, UTM 32N) is superimposed on sampling sites. X and Y coordinates are in km.

4.2.2. Habitat and climatic variables

Species niche was quantified by using 17 land-cover variables, four topographic variables and four climatic variables. Land-cover variables were recorded on the field as fractional cover within a 250-m circular buffer around each point count and were classified according to the 3rd-level of DUSAF digital map (ERSAF, 2018). Some variables were merged because they were strongly underrepresented in the dataset and indicated similar types of land covers (S4.1). Land-cover variables included continuous urban matrix (e.g. dense urban areas, industrial areas, infrastructures; C110), discontinuous urban matrix (e.g. farmsteads; C112), arable lands (e.g. maize, wheat, horticulture; C211) paddy fields (C213), permanent orchard plantations (olive groves, vineyards, orchards; C220), wood plantations (C224), meadows and pastures (C231), broadleaved forests

(C311), coniferous forests (C312), mixed forests (C313), grasslands (C321), shrublands (C322), no tree vegetation under evolution (C324), areas with sparse or absent vegetation (e.g. outcrops, debris deposits, glaciers; C330), wetland vegetation (C410), rivers and streams (C511), and natural and artificial lakes (C512). Topographic variables were derived from the Digital Elevation Model (DEM, 20-m ground-resolution, downloadable from http://www.geoportale.regione.lombardia.it/, accessed on 21 September 2021), and included sine (sin) and cosine (cos) of the aspect (adimensional), slope (grades) and elevation (m), all measured by averaging pixel values within a 250-m circular buffer around each survey site. Climatic variables were obtained from the European Climate Assessment & Dataset (ECAD) with a resolution of 0.1 degree (ECAD, 2021). They included the annual cumulative rainfall (rr), and the annual average (tavg), minimum (tmin) and maximum (tmax) temperature. For each period, after trimming the original grid by our study area, we spatially associated the value of each climatic variable to the corresponding point count, by averaging values within a period between the two years immediately preceding the first year of the time interval and the last year, i.e. 1990-1996 for T_1 and 2013-2017 for T_2. This way, we obtained values representative of climatic conditions in the two periods, limiting the effects of climatic oscillation that might be detected during a single year and taking into account that birds could have exhibited a delayed response to climatic parameters (Lindström et al., 2013).

Geospatial analyses were conducted in ESRI ArcMap v. 10.7.1 (ESRI, 2019) and in R software v. 4.0.2 (R Core Development Team, 2020).

4.2.3. Niche quantification and temporal changes

In recent years, the quantification and the analysis of spatio-temporal niche changes benefited from novel methodological insights (Broennimann et al., 2012; Qiao et al., 2016; Di Cola et al., 2017; Nunes & Pearson, 2017; Brown & Carnaval, 2019; Warren et al., 2021). The most important progress concerns the use of the environmental space (E-space; Broennimann et al., 2012; Qiao et al., 2016; Di Cola et al., 2017; Brown & Carnaval, 2019) instead of the geographical space (G-space; Guisan & Thuiller, 2005; Warren et al., 2008, 2010). This way, no assumptions are required for the model-based approach (Broennimann et al., 2012; Di Cola et al., 2017). The use of the E-space permits better assessment of the niche overlap because it takes into account the environmental availability and the analogy between ranges (Broennimann et al., 2012; Guisan et al., 2014), and it overcomes some limitations on the inference of niche similarity (Brown & Carnaval, 2019).

Niche analysis was performed separately for the 71 bird species using the R package *ecospat* (Broennimann et al., 2020) The E-space was assessed through an ordination technique using a PCA-environment framework, retaining the two main axes resulting from the input of the 25 habitat and climatic variables presented in Section 4.2.2. The axes of the PCA maximise the ecological variance present in the study area for both periods. The PCA scores of species occurrence in each period were projected onto a grid of cells bounded by the minimum and maximum PCA scores of both periods, i.e. gridded E-space, and a kernel density function was used to estimate the density of occurrence of the species in each cell of the grid (Di Cola et al., 2017).

We evaluated the species niche breadth and centroid along each of the PCA axes for each period, by computing the variance and the median of the scores along the principal components, respectively. To detect a significant variation in the niche breadth and centroid between the two periods across all species, we performed the Wilcoxon rank sum test. To compare the overlap of the environmental niche of each species between T_1 and T_2, we used the metric Schoener's D (Schoener, 1968; Broennimann et al., 2012). This index quantifies the amount of niche overlap by computing, for every grid cell in the E-space, the absolute differences in densities of occurrence corrected by the prevalence of the environments in their range, i.e. niche occupancy, between the two periods. It varies from zero (no overlap) to one (complete overlap). Additionally, we calculated three niche dynamic indices between the two periods, namely the expansion, unfilling, and stability index (all varying from a minimum of zero to a maximum of one). The expansion index represents the E-space occupied by the species in T_2 only, the unfilling index indicates the E-space occupied by the species in T_1 only, and the stability index represents the E-space where the species occurred in both periods ($T_1 \cap T2$) (Petitpierre et al., 2012). This decomposition can provide more information about the drivers of niche change between the two periods. We computed the three indices by limiting their calculation to the shared available E-space (*intersection* = 0), in order to exclude that the observed values were due to differences in the accessible E-space (Brown & Carnaval, 2019). Since the stability index is complementary to the expansion index, it was not reported in the results to avoid redundant information. We evaluated the correlation among Schoener's D, expansion and unfilling indices by the non-parametric Kendall test (Kendall, 1938). To test the statistical significance of niche overlap (Schoener's D), we ran equivalency and similarity tests, comparing the overlap of the two observed niches to the overlap of simulated niches. The equivalency test assesses whether two niches are more or less equivalent than expected by chance when randomly reallocating all occurrences between the two ranges. The similarity test assesses whether the overlap between observed niches in two ranges is different from the overlap between niches when their occurrence density grids are randomly shifted in the background environment (Warren et al., 2008; Broennimann et al., 2012; Di Cola et al., 2017). To ensure a robust statistical inference, each test was performed based on 1,000 simulations (Koma et al., 2021; Lei & Liu, 2021). For both tests, we assessed the hypotheses of both niche divergence and niche conservatism, i.e. one-side tests, and for the similarity test both niches were randomly shifted. For both the equivalency and similarity tests, a significant p-value (≤ 0.05) means that the two niches are less (niche divergence) or more (niche conservatism) equivalent/similar than a random expectation.

4.2.4. Relationship between niche temporal changes, population trends and species traits

To assess the relationship between niche temporal changes and population trends we performed a Kendall non-parametric correlation analysis (Kendall, 1938) between each of the niche metrics (Schoener's D, expansion and unfilling indices) and the species population trends (% change). Compared to the Spearman *rho* tatistic, Kendall *tau* provides more accurate p-values when the sample dimension is small and there are many ties in the data (Kedall, 1945), as in our case. We derived species trends from Tirozzi et al. (2021) (*Chapter 3*), where long-term trends (1992-2019) for the species considered in this study were assessed in the same study area, using data derived from the same bird monitoring program. We assigned a zero value to species with non-significant trends.

To investigate the relationship between niche metrics (Schoener's D, expansion and unfilling indices) and species traits, we performed distinct analyses for continuous traits (12 life-history traits, namely body length, wing length, tail length, bill length, tarsus length, body weight, clutch size, incubation period, fledging period [Storchová & Hořák, 2018]; number of broods per breeding season [Storchová & Hořák, 2018; Tirozzi et al., 2021 and *Chapter 3*]; annual fecundity [Jiguet et al., 2007]; dispersal ratio [Fischer & Lindenmayer, 2005; Li et al., 2019]; and six species specialisation indices, namely foraging habitat, acquisition behavior, nesting habitat, foraging substrate, diet [Julliard et al., 2006; Pearman et al., 2014; Tirozzi et al., 2021 and *Chapter 3*]; overall [Tirozzi et al., 2021 and *Chapter 3*]) and categorical traits (four uncorrelated traits of interest [Tirozzi et al., 2021 and *Chapter 3*], namely migration strategy [Tirozzi et al., 2021 and *Chapter 3*], nest type [Storchová & Hořák, 2018; Tirozzi et al., 2021 and *Chapter 3*], landscape type, i.e. habitat preferences at landscape scales [Tirozzi et al., 2021 and *Chapter 3*], and diet [Wilman et al., 2014; Tirozzi et al., 2021 and *Chapter 3*]). For continuous traits, we performed a principal component analysis (PCA) using all 18 traits as input variables. This way, we reduced the dimensionality of traits into new uncorrelated components representing species life-history and ecological characteristics. Then, we analyzed the correlation between the main axes of the PCA, picked out through eigenvalues, scree plots and percentage of variance explained, and the niche metrics, which were input as supplementary quantitative variables. PCA was performed using the R packages *FactoMineR* (Lê et al., 2014) and *factoextra* (Kassambara et al., 2020). For categorical traits, we performed a Kruskal–Wallis rank sum test separately for each combination of niche metric and trait. In the case of overall significance (p-value ≤ 0.05), we ran a Dunn's test (significant threshold = 0.05) for pairwise comparisons between trait levels with the Bonferroni adjustment (Dunn, 1964). See S4.2 in Supplementary materials for details and referencing literature about traits. All statistical analyses were performed in R software v. 4.0.2 (R Core Development Team, 2020).

4.3. Results

4.3.1. Niche quantification and temporal changes

In defining the E-space, the first two PCA axes explained 31.3% of the total variance. PC1 explained 24.2% of the variance, while PC2 7.1%. The first axis represents a thermal gradient, showing a strong negative correlation with elevation and a strong positive correlation with temperatures (Figure 4.2, S4.3 and S4.4A in Supplementary materials). The major contributions to PC2 were given by nine variables (S4.4B in Supplementary materials). Annual rainfall (rr), broadleaved forests (C311), mixed forests (C313), meadows and pastures (C231), and slope were positively correlated with this component, while arable lands (C211), grasslands (C321), shrublands (C322), and areas with sparse or absent vegetation (C330), showed a negative correlation (Figure 4.2 and S4.3). The second niche component reflects habitat characteristics along an ecological gradient of open (variables negatively correlated with PC2) vs closed (variables positively correlated with PC2) habitats, despite the inclusion of meadows and pastures in the latter group. The strong contribution of annual rainfall to PC2 could reflect the major water requirements of natural habitats such as broadleaved and mixed forests.

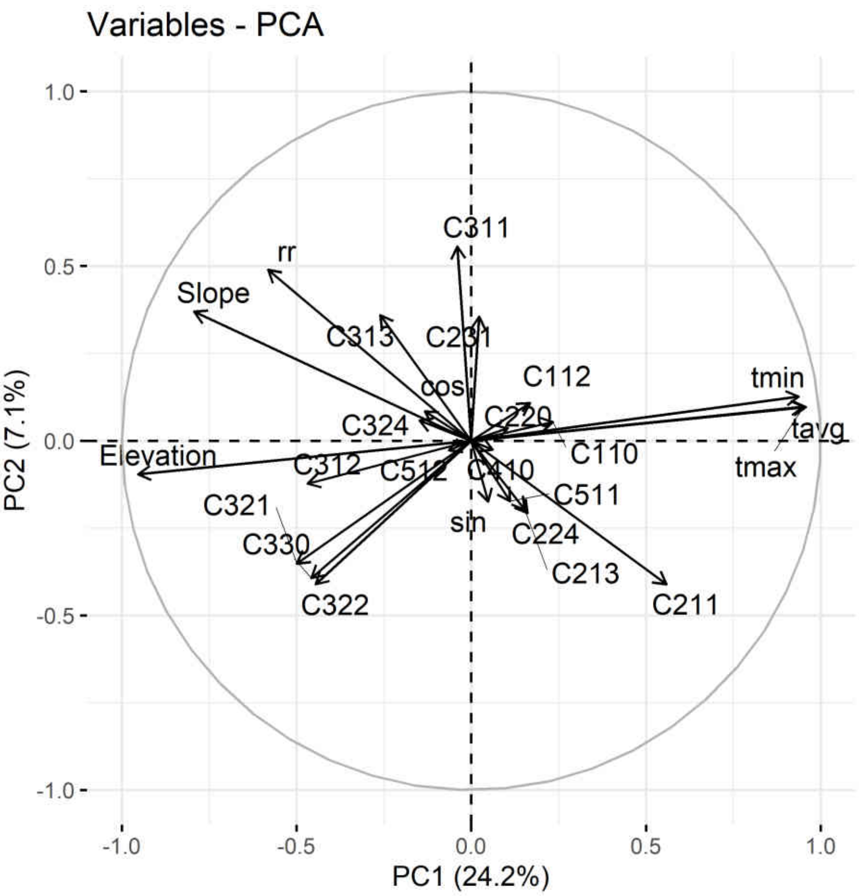

Figure 4.2. First two axes of the principal component analysis (PCA) that define the E-space, based on 25 input variables. See Section 4.2.2 and S4.1 for variables' abbreviations and S4.3 for variables' coordinates.

Niche breadths and centroids showed a large variability across species along each of the two PCA axes (S4.5 in Supplementary materials). Despite differences within species, we detected a general change only for the niche centroid along PC1 between T_1 and T_2, representing a shift towards warmer climatic conditions (W = 1,991, p-value = 0.031; S4.6 in Supplementary materials).

Niche quantification in T_1 and T_2, and niche temporal changes of the 71 species were reported in S4.7 in Supplementary materials. The whole extent and the centroids' position of the available E-space (solid lines and dashed arrows in Figure 4.3A-D and in S4.7) were largely similar between T_1 and T_2, meaning that the background E-space in the two periods was comparable. Only a small portion in the bottom area of the available E-space in T_2 did not match with the E-space in T_1 (shrublands, grasslands and areas with sparse or absent vegetation at higher altitudes). Some species (e.g. Common Quail *Coturnix coturnix*, Western Yellow Wagtail *Motacilla flava*, and Cetti's Warbler *Cettia cetti*) tended to fill a small portion of the total available E-space, while others (e.g.

Common Cuckoo *Cuculus canorus*, Grey Wagtail *Motacilla cinerea*, Eurasian Wren *Troglodytes troglodytes*, Common Chaffinch *Fringilla coelebs*) occurred in most of the available E-space. Regarding changes between T_1 and T_2 of the density of occurrence and the occupied E-space, different types of patterns can be identified (S4.7). Some species, such as the Song Thrush (*Turdus philomelos*, Figure 4.3A), extended their niche in most of the whole E-space. Other species exhibited a directional expansion along one of the niche components. For example, the Great Spotted Woodpecker (*Dendrocopos major*, Figure 4.3B) showed an expansion (without remarkable niche unfilling) towards coniferous forests and scattered vegetation at higher altitudes. Conversely, other species mainly showed a shift with unfilling and expansion along the same dimension, such as the Eurasian Bullfinch *Pyrrhula pyrrhula* along PC1 towards warmer climatic conditions, lower altitudes and mixed/broadleaved forests (Figure 4.3C). Other species showed a relatively stable niche, with moderate areas of unfilling/expansion and non-directional patterns (e.g. the Eurasian Blackcap *Sylvia atricapilla*, S4.7). Finally, 17 species (e.g. the Eurasian Wryneck *Jynx torquilla*, Figure 4.3D) exhibited an overall niche contraction.

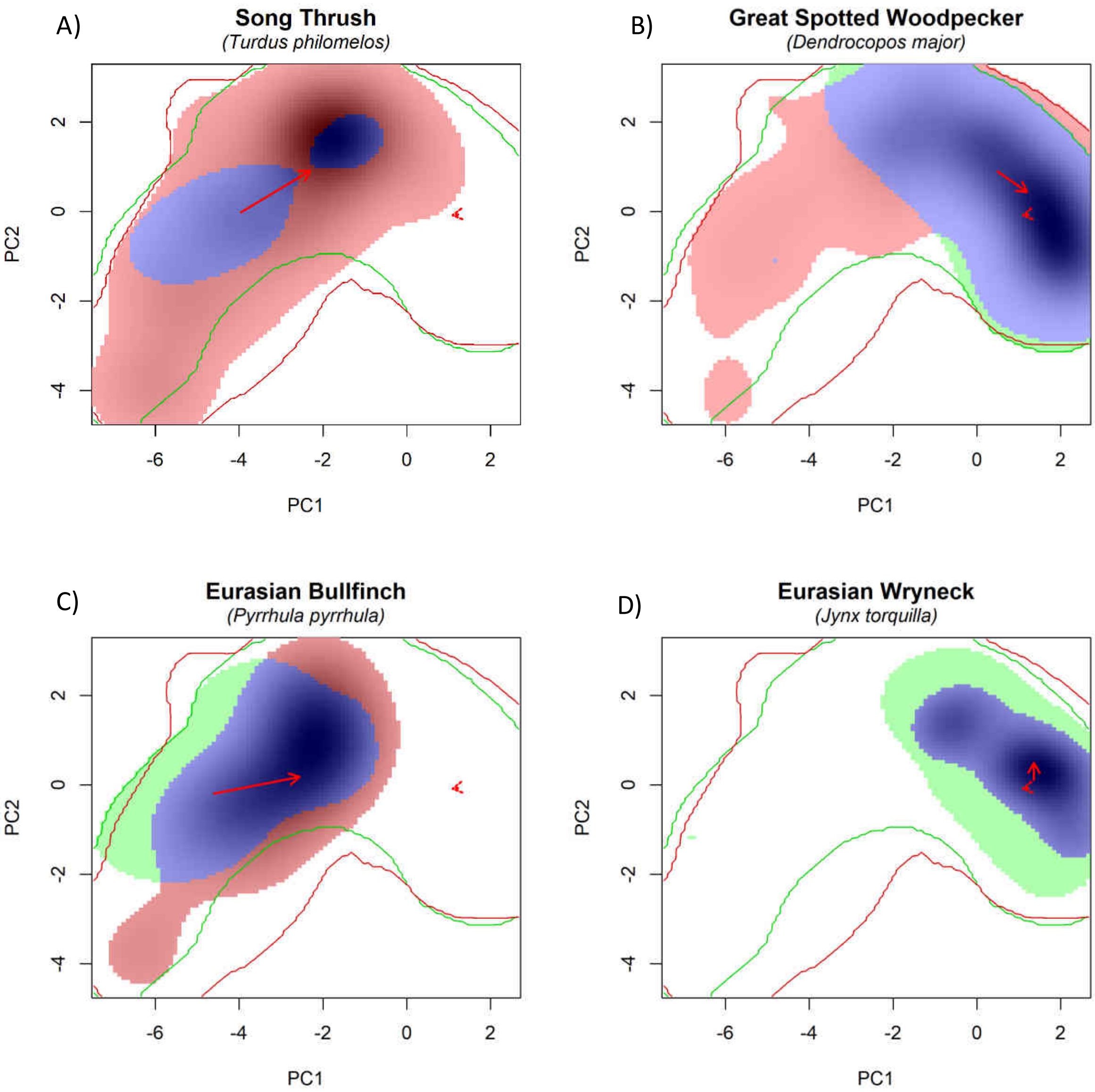

Figure 4.3. Examples of niche comparison between T_1 (1992-95-96) and T_2 (2015-16-17) projected in the E-space for four species. A) Song Thrush; B) Great Spotted Woodpecker; C) Eurasian Bullfinch; D) Eurasian Wryneck. In each graph, the red area represents the E-space exclusively occupied in T_2, the green area the E-space exclusively occupied in T_1, and the blue area the E-space occupied in both T_1 and T_2. The color intensity of the filled area represents the density of occurrence of the species in T_2. Green and red solid lines represent the whole extent of the available E-space in T_1 and T_2, respectively. Arrows indicate the centroids' shift from T_1 to T_2 for the available E-space (dashed arrow, where we did not detect any shift) and for the occupied E-space (solid arrow).

Across the 71 species, the median value of niche overlap between T_1 and T_2, assessed through the Schoener's D index, was 0.60 (range = 0.14 - 0.81). Most species showed low or moderate values of the expansion index (median = 0.04, range = 0 - 0.66), but the Dunnock (*Prunella modularis*), the

Song Thrush, the Water Pipit (*Anthus spinoletta*), the Willow Tit (*Poecile montanus*), and the Eurasian Skylark (*Alauda arvensis*) experienced a large expansion (> 0.40). Similarly, the median of the unfilling index was 0.06 (range = 0 - 0.32), but the Mallard (*Anas platyrhyncos*), the Common Kestrel (*Falco tinnunculus*), the Common Quail, the Eurasian Wryneck, the Melodius Warbler (*Hippolais polyglotta*), the Marsh Tit (*Poecile palustris*) and the Carrion Crow (*Corvus corone*) showed higher unfilling values (> 0.25) (Figure 4.4 and S4.8 in Supplementary materials). The Schoener's D resulted negatively correlated with both the expansion (Kendall *tau* = −0.34, p-value < 0.001) and the unfilling (Kendall *tau* = −0.27, p-value = 0.001), and the expansion was negatively correlated with the unfilling (Kendall *tau* = −0.26, p-value = 0.001).

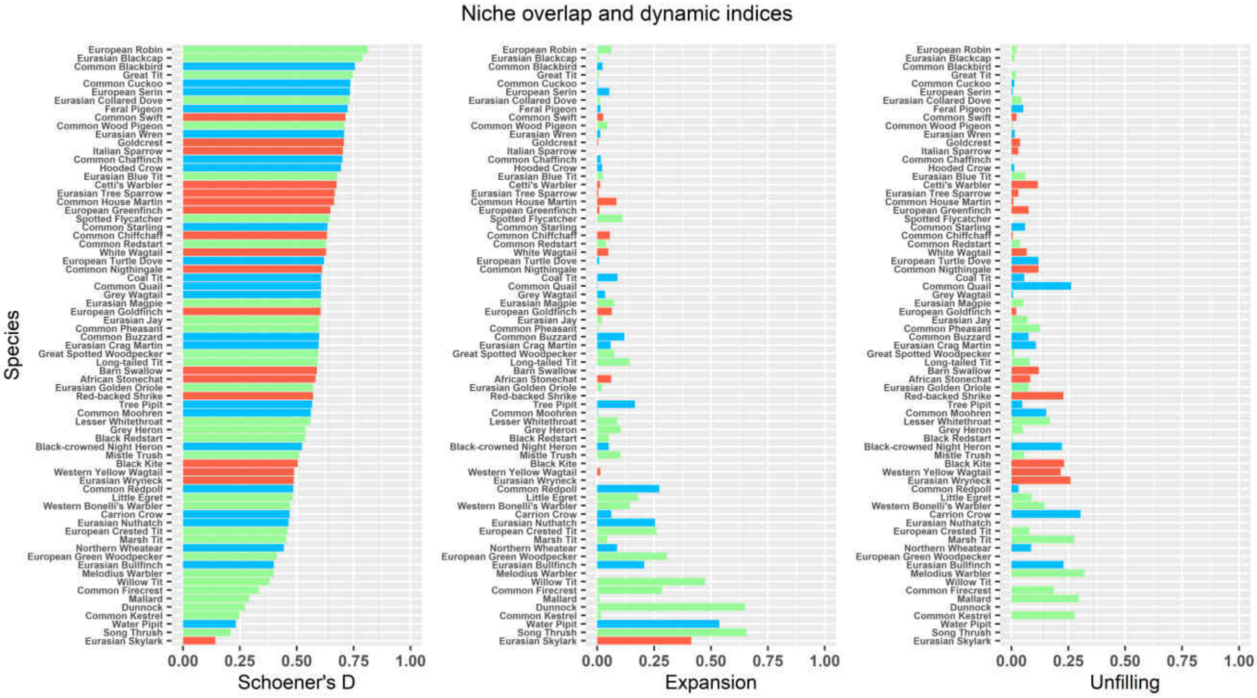

Figure 4.4. Niche overlap and dynamic indices between T_1 (1992-95-96) and T_2 (2015-16-17). The Schoener's D index (observed niche overlap), the expansion and unfilling (dynamic indices) are given for each species. The length of the bar is proportional to the value of the index. Species were reported with the common name (Gill et al., 2022) and listed in descending order in respect to the Schoener's D value. Bar colors reflect species trend: increasing populations, green; non-significant population trends, light blue; decreasing populations, red.

Niche equivalency and similarity tests were summarised in Table 4.1. Twenty-three of the 71 species showed a niche equivalency significantly smaller than expected by chance (equivalency test: p-value ≤ 0.05 for the niche divergence hypothesis), suggesting the existence of differences in niches between T_1 and T_2. On the other hand, seven species (Common Cuckoo, Eurasian Wren, European

Robin *Erithacus rubecula*, Common Blackbird *Turdus merula*, Lesser Whitethroat *Curruca curruca*, Eurasian Blackcap, Goldcrest *Regulus regulus*) significantly conserved their niche between the two periods (equivalency test: p-value ≤ 0.05 for the niche conservatism hypothesis). The similarity test did not accept the niche divergence hypothesis for any species (p-value > 0.05). However, the niche conservatism hypothesis was accepted for 56 species (p-value ≤ 0.05), showing that most species retained their own niche over time when both occurrence density grids were randomly shifted into the background environment.

Table 4.1. Schoener's D index and p-values for the equivalency (E) and similarity (S) test for niche divergence (D) and conservatism (C). Significant p-values (≤ 0.05) are marked in bold. Species are listed in taxonomic order with the common and scientific names according to Gill et al. (2022).

Species	Schoener's D	E (D)	E (C)	S (D)	S (C)
Black-crowned Night Heron (*Nycticorax nycticorax*)	0.52	**0.007**	0.994	0.968	**0.026**
Little Egret (*Egretta garzetta*)	0.48	**0.023**	0.977	0.947	**0.038**
Grey Heron (*Ardea cinerea*)	0.54	**0.003**	1.000	0.950	**0.035**
Mallard (*Anas platyrhynchos*)	0.29	**0.004**	0.996	0.812	0.211
Black Kite (*Milvus migrans*)	0.50	0.172	0.840	0.965	**0.042**
Common Buzzard (*Buteo buteo*)	0.60	0.297	0.690	0.990	**0.011**
Common Kestrel (*Falcon tinnunculus*)	0.25	**0.034**	0.970	0.762	0.229
Common Quail (*Coturnix coturnix*)	0.61	0.399	0.627	0.995	**0.012**
Common Pheasant (*Phasianus colchicus*)	0.60	**0.036**	0.979	0.968	**0.018**
Common Moohren (*Gallinula chloropus*)	0.56	**0.010**	0.995	0.968	**0.032**
Feral Pigeon (*Columba livia domestica*)	0.72	**0.033**	0.966	0.993	**0.010**
Common Wood Pigeon (*Columba palumbus*)	0.71	0.435	0.591	0.998	**0.009**
Eurasian Collared Dove(*Streptopelia decaocto*)	0.73	0.119	0.864	0.991	**0.008**
European Turtle Dove (*Streptopelia turtur*)	0.62	**0.033**	0.984	0.962	**0.028**
Common Cuckoo (*Cuculus canorus*)	0.74	0.999	**<0.001**	1.000	**0.002**
Common Swift (*Apus apus*)	0.71	0.933	0.061	0.995	**0.010**
Eurasian Wryneck (*Jinx torquilla*)	0.49	0.709	0.295	0.968	**0.048**
European Green Woodpecker (*Picus viridis*)	0.41	0.054	0.956	0.915	0.114
Great Spotted Woodpecker (*Dendrocopos major*)	0.59	0.444	0.589	0.961	**0.032**
Eurasian Skylark (*Alauda arvensis*)	0.14	**<0.001**	1.000	0.836	0.179
Eurasian Crag Martin (*Ptyonoprogne rupestris*)	0.60	0.531	0.487	0.942	**0.033**
Barn Swallow (*Hirundo rustica*)	0.59	**<0.001**	1.000	0.971	**0.021**
Common House Martin (*Delichon urbicum*)	0.66	0.454	0.535	0.996	**0.018**
Tree Pipit (*Anthus trivialis*)	0.57	0.842	0.168	0.976	**0.015**
Water Pipit (*Anthus spinoletta*)	0.23	0.181	0.821	0.905	0.101

Table 4.1 (cont.)

Western Yellow Wagtail (*Motacilla flava*)	0.49	**<0.001**	1.000	0.959	**0.036**
Grey Wagtail (*Motacilla cinerea*)	0.61	0.752	0.259	0.987	**0.008**
White Wagtail (*Motacilla alba*)	0.63	0.440	0.564	0.997	**0.006**
Eurasian Wren (*Troglodytes troglodytes*)	0.71	0.993	**0.003**	0.999	**0.002**
Dunnock (*Prunella modularis*)	0.27	**0.029**	0.982	0.884	0.101
European Robin (*Erithacus rubecula*)	0.81	1.000	**<0.001**	1.000	**<0.001**
Common Nigthingale (*Luscinia megarhynchos*)	0.61	**<0.001**	1.000	0.974	**0.031**
Black Redstart(*Phoenicurus ochruros*)	0.54	0.514	0.506	0.968	**0.027**
Common Redstart (*Phoenicurus phoenicurus*)	0.63	0.063	0.934	0.987	**0.012**
European Stonechat(*Saxicola rubicola*)	0.58	0.483	0.524	0.957	**0.028**
Northern Wheatear (*Oenanthe oenanthe*)	0.44	0.782	0.213	0.886	0.112
Common Blackbird (*Turdus merula*)	0.76	0.998	**0.002**	0.997	**0.002**
Song Thrush (*Turdus philomelos*)	0.21	**0.049**	0.946	0.908	0.105
Mistle Trush (*Turdus viscivorus*)	0.51	0.926	0.074	0.911	0.082
Cetti's Warbler (*Cettia cetti*)	0.68	0.812	0.200	0.988	**0.012**
Melodius Warbler (*Hippolais polyglotta*)	0.40	**0.046**	0.942	0.913	0.083
Lesser Whitethroat (*Curruca curruca*)	0.56	0.974	**0.025**	0.970	**0.029**
Eurasian Blackcap (*Sylvia atricapilla*)	0.79	1.000	**<0.001**	1.000	**<0.001**
Western Bonelli's Warbler (*Phylloscopus bonelli*)	0.47	0.253	0.754	0.881	0.118
Common Chiffchaff (*Phylloscopus collybita*)	0.63	0.410	0.595	0.988	**0.019**
Goldcrest (*Regulus regulus*)	0.71	0.979	**0.028**	0.998	**0.007**
Common Firecrest (*Regulus ignicapilla*)	0.33	0.190	0.833	0.832	0.175
Spotted Flycatcher (*Muscicapa striata*)	0.65	0.102	0.892	0.988	**0.014**
Long-tailed Tit (*Aegithalos caudatus*)	0.59	0.058	0.956	0.982	**0.013**
Marsh Tit (*Poecile palustris*)	0.45	**0.009**	0.994	0.955	**0.041**
Willow Tit (*Poecile montanus*)	0.38	0.207	0.738	0.963	0.057
European Crested Tit (*Lophophanes cristatus*)	0.46	0.526	0.499	0.873	0.168
Coal Tit (*Periparus ater*)	0.61	0.231	0.784	0.945	**0.046**
Eurasian Blue Tit (*Cyanistes caeruleus*)	0.68	0.092	0.890	0.995	**0.004**
Great Tit (*Parus major*)	0.75	0.415	0.536	0.995	**0.003**
Eurasian Nuthatch (*Sitta europea*)	0.46	0.099	0.909	0.938	**0.048**
Eurasian Golden Oriole (*Oriolus oriolus*)	0.57	0.055	0.937	0.970	**0.018**
Red-backed Shrike (*Lanius collurio*)	0.57	0.063	0.939	0.993	**0.014**
Eurasian Jay (*Garrulus glandarius*)	0.60	**0.036**	0.968	0.943	**0.050**
Eurasian Magpie(*Pica pica*)	0.61	**0.003**	0.999	0.974	**0.018**
Carrion Crow (*Corvus corone*)	0.47	0.582	0.425	0.958	**0.047**
Hooded Crow (*Corvus cornix*)	0.69	0.402	0.644	0.994	**0.010**
Common Starling (*Sturnus vulgaris*)	0.63	**<0.001**	1.000	0.993	**0.020**
Italian Sparrow (*Passer italiae*)	0.70	0.061	0.926	0.992	**0.009**

Table 4.1 (cont.)

Eurasian Tree Sparrow (*Passer montanus*)	0.67	**0.002**	1.000	0.988	**0.009**
Common Chaffinch (*Fringilla coelebs*)	0.70	0.931	0.069	0.999	**0.002**
European Serin (*Serinus serinus*)	0.73	0.313	0.691	0.991	**0.010**
European Greenfinch (*Chloris chloris*)	0.65	0.104	0.893	0.994	**0.007**
European Goldfinch (*Carduelis carduelis*)	0.60	**0.004**	0.996	0.992	**0.016**
Common Redpoll (*Acanthis flammea*)	0.48	0.613	0.374	0.979	**0.021**
Eurasian Bullfinch (*Pyrrhula pyrrhula*)	0.40	**0.035**	0.961	0.943	0.067

4.3.2. Relationship between niche temporal changes, population trends and species traits

Kendall correlation analysis (Figure 4.5) highlighted a negative association between the Schoener's D index and population trends (*tau* = −0.162), though it was only marginally significant (p-value = 0.053). A moderate significant positive correlation was underlined between population trends and the expansion index (*tau* = 0.239, p-value = 0.005), while we did not detect any association for the unfilling index (tau = −0.048, p-value = 0.571). The results were consistent even when trends close to the threshold of significance (p-value ≤ 0.10) were not set to zero value (Schoener's D: *tau* = −0.164, p-value = 0.049; expansion index: *tau* = 0.249, p-value = 0.003; unfilling index: *tau* = −0.070, p-value = 0.403).

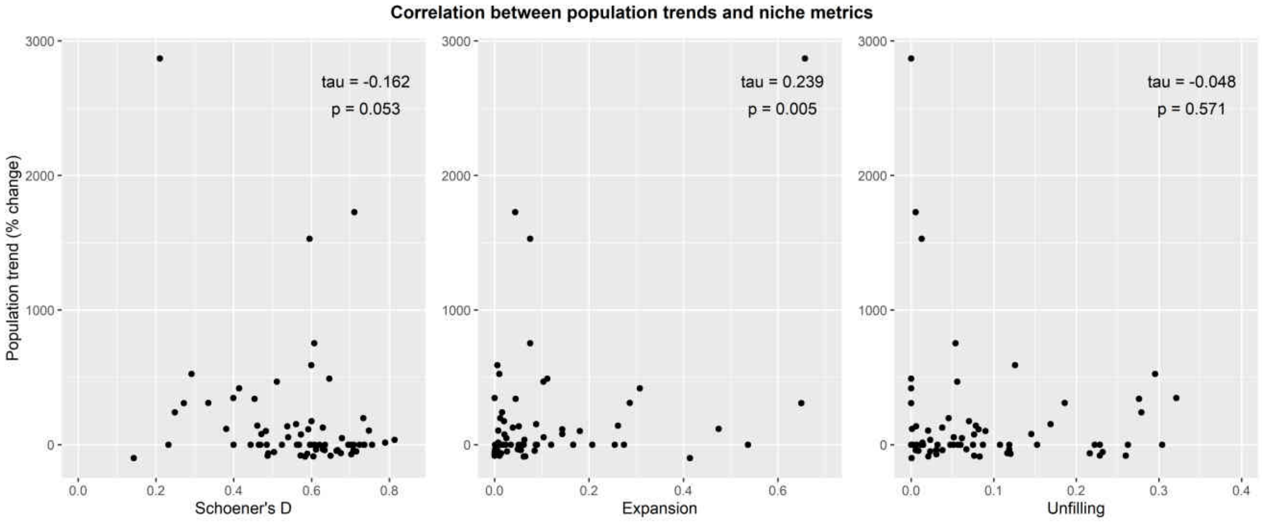

Figure 4.5. Kendall correlation between species population trends and niche metrics. Each dot represents a species (*n* = 71). Species population trends were reported as percentage of change (% change) of the population index from 1992 to 2019. Values of % change below zero indicate decreasing populations. Kendall's rank coefficient *tau* and the corresponding p-values (p) are shown in the upper right corner.

Regarding the relationship between niche metrics and continuous traits, PCA reordered them into four principal axes. Dim1 (40.5% of the total variance explained) represented a gradient in body size (positive correlation), Dim2 (19.4%) was related to most of the species specialisation indices (positive correlation), Dim3 (10.3%) to clutch size (positive correlation), and Dim4 (7.9%) was positively correlated with the number of broods per year. Dispersal ratio was negatively correlated with both Dim3 and Dim4, and positively correlated with Dim1 (S4.9 in Supplementary materials). Results revealed a weak relationship among the niche metrics and the four PCA dimensions (S4.9). Specifically, the unfilling index showed a slight positive correlation with Dim1 (0.23), i.e. body size, and Dim3 (0.19), i.e. clutch size, (Figure 4.6A), and a weak negative correlation with Dim4 (–0.17), thus demonstrating an association with species producing fewer broods (S4.10A-B in Supplementary materials). The expansion index resulted in a weak and negative correlation (−0.13) with Dim1, i.e. the higher the expansion, the smaller the body size (Figure 4.6A-B), and a weak and positive correlation (0.10) with Dim4, i.e. the higher the expansion, the higher is the number of broods (S4.10A-B). The dispersal ratio showed a weak negative association with the expansion index (Figure 4.6A and S4.10A) and a non-unidirectional relationship with the unfilling index (Figure 4.6A). The Schoener’s D highlighted a slight negative correlation (−0.12) with Dim3 (Figure 4.6A) and a slight positive correlation (0.10) with Dim2 (Figure 4.6B), the latter suggesting that specialist species tended to retain their niche more than generalist species.

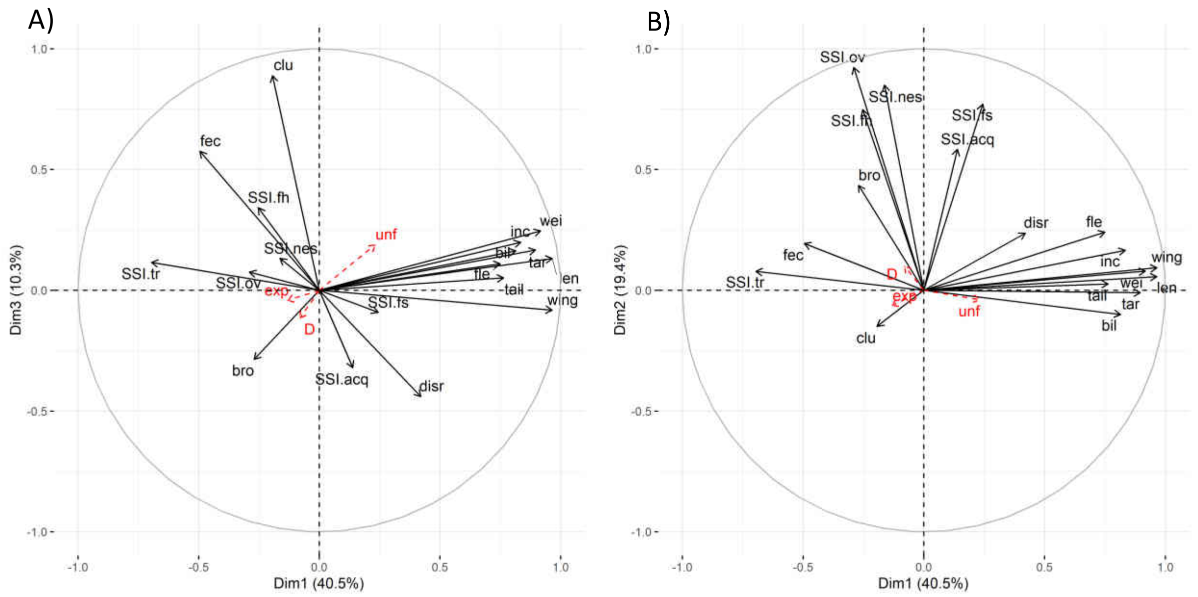

Figure 4.6. Relationship between niche metrics, life-history and ecological continuous traits. PCA biplot between the Schoener's D (D), unfilling (unf) and expansion (exp) niche metrics (red and dashed arrows) and the 18 continuous traits (solid black arrows) respect to Dim1 and Dim3 in A) and to Dim1 and Dim2 in B). Abbreviations' meaning for the continuous traits: len = body length; wing = wing length; tail = tail length; bil = bill length; tar = tarsus length; wei = body weight; clu = clutch size; bro = number of broods per breeding season; fec = annual fecundity; inc = incubation period; fle = fledging period; disr = dispersal ratio; SSI. = prefix for the specialisation indices; fh = foraging habitat; acq = acquisition behavior; nes = nesting habitat; fs = foraging substrate; tr = diet; ov = overall. See S4.2 for further details on species traits.

Regarding categorical traits, significant differences were detected for the unfilling index respect to migration strategy (Kruskal-Wallis χ^2 = 7.91, df = 2, p-value = 0.019), wherein Dunn's test highlighted a significant greater unfilling for long-distance compared to short-distance migrants (p-value = 0.020; Figure 4.7A). Moreover, all niche metrics showed differences with respect to the landscape type (unfilling index: Kruskal-Wallis χ^2 = 10.24, df = 3, p-value = 0.017; expansion index: Kruskal-Wallis χ^2 = 19.74, df = 3, p-value < 0.001; Schoener's D index: Kruskal-Wallis χ^2 = 13.48, df = 3, p-value = 0.004). Specifically, pairwise comparisons showed a greater unfilling for farmland birds compared to species inhabiting several types of landscapes (group "several", p-value = 0.014; Figure 4.7B), and a greater expansion for woodland birds and species inhabiting natural-open habitats compared to farmland species (p-value = 0.010 and p-value < 0.001, respectively; Figure 4.7C). Finally, species of natural-open habitats showed a lower niche overlap (Schoener's D) compared to both the group of “farmland” and “several” (p-value = 0.044 and p-value = 0.002, respectively; Figure 4.7D).

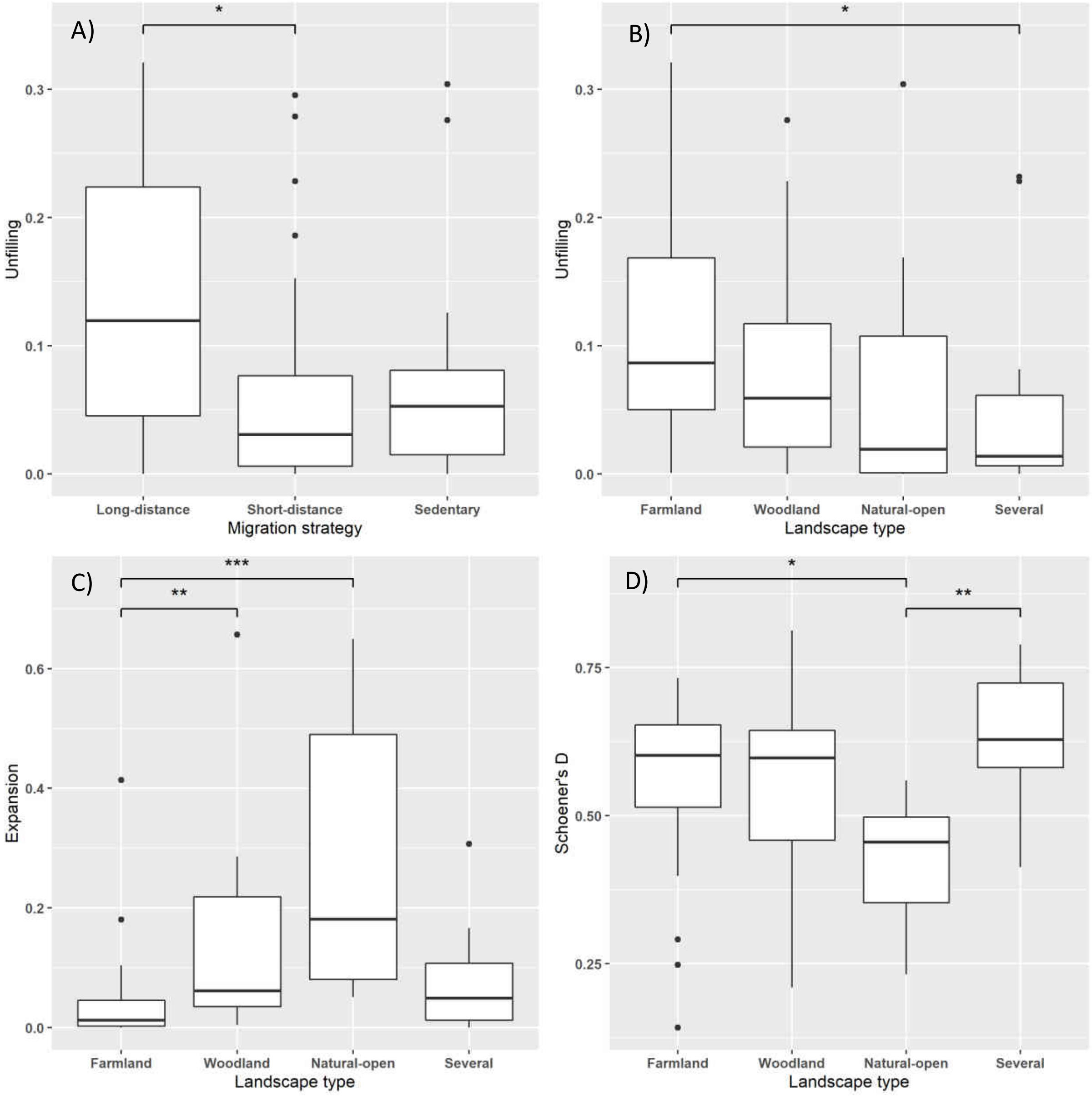

Figure 4.7. Box plots and significance level of Dunn’s test for pairwise comparisons for categorical traits for which Kruskal–Wallis test detected significant differences. A) Migration strategy and unfilling; number of species per group: long-distance = 20, short-distance = 29, sedentary = 22; Landscape type and B) unfilling, C) expansion, D) Schoener’s D (niche overlap); number of species per group: farmland = 28, woodland = 16, natural-open= 8; several = 19. Whiskers are 1.5 × IQR. Black dots represent outliers. Horizontal bars in the upper area indicate which group comparisons showed statistically significant differences. Asterisks represent the significance level: ≤ 0.001: ***, ≤ 0.01: **, ≤ 0.05: *. See S4.2 for further details on species traits.

4.4. Discussion

4.4.1. Niche quantification and temporal changes

Niche temporal changes of 71 common breeding birds in a wide region of northern Italy over 26 years revealed a high complexity of patterns across species. The equivalency tests supported the niche divergence hypothesis for 23 species (32%). This means that their niche occupancy in the E-space differed between T_1 and T_2, suggesting that these species changed their niche in relation to the accessible environmental conditions over time. Evidence for niche divergence requires two conditions (Broennimann & Guisan, 2008; Warren et al., 2008): (1) niche characteristics differ between ranges, and (2) these differences are greater than background environmental divergence. However, Rodríguez-Rodríguez et al. (2020) and Cuervo et al. (2021) argued that niches are already divergent when found less equivalent than expected by chance, i.e. significant equivalency test, and the niche conservatism hypothesis evaluated by the similarity test is not accepted. In our study, only seven species (Mallard, Common Kestrel, Eurasian Skylark, Dunnock, Song Thrush, Melodius Warbler, and Eurasian Bullfinch) satisfied this criterion, thus showing statistical evidence of niche divergence. For the other 16 of the 23 species, for which the equivalency test supported niche divergence (Table 4.1), we cannot confirm this hypothesis since the similarity test retained a larger niche similarity. We found strong evidence of niche conservatism (both the equivalency and the similarity tests supported the hypothesis) for the Common Cuckoo, the Eurasian Wren, the European Robin, the Common Blackbird, the Eurasian Blackcap, the Lesser Whitethroat, and the Goldcrest. The first five species occupied a large portion of the available E-space in both periods (S4.7), showing they were able to use a wide spectrum of climatic and habitat conditions. On one hand, it is possible they did not undergo great ecological pressures in the occupied E-space, on the other hand the environmental changes that occurred in the study area may have not significantly affected their niche because of a large range of environmental tolerance. Conversely, the Goldcrest is a forest specialist species and it is likely less prone to modify its habitat and climatic requirements even under ongoing environmental changes (it is actually the only woodland bird along with the Common Chiffchaff *Phylloscopus collybita* suffering from a population decline in the study area; Tirozzi et al., 2021 and *Chapter 3*). Regarding the Lesser Whitethroat, we underline that the species showed a Schoener’s D (0.56) just smaller than the overall median, and we did not exclude that the species rarity, especially in the first period (frequency of occurrence = 1%), could have affected the significance of the tests. Caution is in fact recommended when inference is conducted on rare species (Ralston et al., 2016).

The niche dynamic indices, expansion and unfilling provided useful additional information on niche temporal changes. Differently from the Schoener's D, they assess the niche overlap regardless of the density of occurrence. We observed that 27% and 31% of the species experienced a niche expansion and unfilling greater than 10% (values > 0.1), respectively. Moreover, as highlighted by the correlation analysis between the two indices, species showing an expansion tended to not experience a niche unfilling, and vice versa. Furthermore, our findings suggested that decreasing niche overlap (Schoener's D) is associated alternatively with niche expansion or unfilling, underlining the role of occupying new habitats, or losing original habitats, in determining differences in the observed niches.

We found an overall shift of the niche centroids towards greater values along PC1. This means a general tendency to experience higher thermal conditions, but the relationship between habitat and climate, often acting in a synergistic way (Peterson, 2003; Mantyka-Pringle, 2012; Oliver & Morecroft, 2014), should be considered. Our study area is characterised by an important altitudinal range (from 2 m to 4000 m a.s.l.), and habitat types, as well as anthropization intensity, are strictly associated with the elevational gradient and thus with temperatures. The characteristics of open and closed habitats differ according to the altitudinal range (e.g. open habitats are essentially wild in uplands while mainly anthropised in lowlands), and such differences must be taken into account to understand niche temporal changes. The general centroids' shift towards warmer climates can actually depend on several drivers that can be species-specific. Firstly, a species may undergo higher temperatures because of an increase of temperatures in the environment (we found an increase of the average temperature from 9.53 °C to 10.54 °C during the study period in the whole study area; data elaborated from the ECAD dataset; ECAD, 2021). Several studies underlined the ability of birds to track their climatic niche (e.g. Tingley et al., 2009; Tayleur et al., 2015), while lags may be observed especially under rapid environmental change on a short timescale (Devictor et al., 2008; La Sorte & Jetz, 2012; Sutton et al., 2015). In the presence of such lag-effects, or the absence of niche tracking for several reasons (e.g. species thermal physiological tolerances, species dispersal ability, habitat availability and landscape connectivity), raising temperatures might result in a passive shift of niche centroids towards warmer climates. Species responses to this phenomenon may be idiosyncratic and difficult to predict (La Sorte & Jetz, 2012), although some groups are expected to suffer more than others (e.g. mountain birds; Chamberlain et al., 2013; Pearce-Higgins et al., 2017; Scridel et al., 2018; Lehikoinen et al., 2019). Secondly, a species may move towards lower altitudes, and therefore to warmer climates, in response to fine-scale changes in the habitat structure and characteristics (including anthropogenic ones as forestry management, agricultural practices, intensity of grazing and mowing). For example, we found that the Song Thrush, the Common Firecrest (*Regulus ignicapilla*), and the Eurasian Bullfinch showed a shift in density of occurrence from high-altitude coniferous to middle and low-altitude mixed and broadleaved forests (S4.7). Fine-scale changes, not detectable in our study, can directly affect the species occurrence and habitat suitability within a specific type of habitat (Koma et al., 2021; Brambilla et al., 2020). In addition, modifications in habitat availability due to land uses changes might push a species to track the habitat component of its niche to find similar conditions. In our study, for example, the Mistle Thrush (*Turdus viscivorus*) moved its centroid towards high-altitude shrublands, maybe as response to an expansion of forests upwards and neo-colonization of wood at the expense of abandoned meadows in uplands (Piccardi & Celona, 2017). We also remark that some species may have extended their niche towards lower altitudes independently from environmental pressures, but as response of density-dependent factors (e.g. increasing populations; Ralston et al., 2017 and see Section 4.4.2) leading to colonise new environments. For example, the Black Redstart (*Phoenicurus ochruros*), a species originally associated with open-natural habitats, showed a meaningful increment in density of occurrence in closed habitats (mixed and broadleaved forests) and in lowland open habitats (where it colonised human buildings).

Despite we are confident of consistency of our results, we acknowledge that some limitations could affect species niche quantification. Specifically, we could not account for species detection probability because data did not include multiple surveys in the same site. Detection probability may represent an issue when comparing niche across species (Paniccia et al., 2018) However, intra-species niche comparisons are not supposed to be considerably affected by detection probability when comparing niche metrics of a species across different geographic areas (Liordos et al., 2021) or over time. In fact, in the case of a standardised sampling design, the species habitat-specific detection function is supposed to be constant over time (Newson et al., 2013), and its effect on niche comparison may be considered negligible. Moreover, our data collection and its aggregation into three-year time intervals further reduced the potential noise arising from imperfect detection (see Section 4.2.1). Measuring the effect of detection probability in niche modeling is certainly an issue that deserves attention in future research.

4.4.2. Relationship between niche temporal changes, population trends and species traits

The assessment of the relationship between niche metrics and population trends highlighted interesting patterns, partially confirming findings from Ralston et al. (2017). We found a positive correlation between population trends and niche expansion, while unfilling did not correlate with trends. Metapopulation theory predicts that in growing metapopulations with many individuals dispersing from local “source” populations, it is likely that local “sink” populations settled in suboptimal environments exist. On the contrary, in declining metapopulations it is probable that only the largest local populations persist in the most suitable environments, but not enough migrants are generated to colonise suboptimal environments and to support local “sink” populations (Pulliam, 1988; Hanski, 1998; Pulliam, 2000). However, we cannot exclude that a niche expansion due to stochastic phenomena, interspecific interactions with competitive exclusions, and/or fine-scale increase of habitat quality, could have pushed the species to extend the niche with a positive secondary effect on population size. In any case, some meaningful exceptions can be found for the positive relationship between niche expansion and population trends. We remark that the Eurasian Skylark, the bird undergoing the most negative population trend in Lombardy from 1992 to 2019 (Tirozzi, et al. 2021 and *Chapter 3*), showed one of the highest niche expansions during this time interval. In the first period (1992-1995-1996) the niche of the species was limited to open habitats in lowlands (mainly arable lands), while in the second period (2015-2016-2017) it extended in a new portion characterised by open habitats in uplands, though retaining the original core of the niche in lowlands. Changes of agricultural practices perhaps acted as ecological pressures for the species (Chamberlain & Siriwardena, 2000; Chamberlain et al., 2000; Eraud & Boutin, 2002; Koleček et al., 2015), and the fact that the Eurasian Skylark retained the original core area may be due to a partial lag-effect for which the species remains present in unsuitable environments that were previously suitable (Schurr et al., 2012). Additionally, we do not exclude that the two local populations that seem to emerge may undergo different ecological pressures leading to divergent population dynamics between the two areas. This example highlights the importance of integrating demographic responses with niche temporal changes, especially to implement conservation efforts and actions for threatened species.

Ralston et al. (2017) reported a significant relationship between niche unfilling and bird trends for the realised climatic niche in 46 birds breeding in North America. By also including habitat characteristics in our niche modeling, we did not find any association. Overlooking the fact that our study was carried out in a different biogeographic area and at very smaller spatial scale, increasing the complexity of the niche multidimensional space can reveal different patterns. Embracing this complexity can be the key to a better interpretation of the niche-trend relationship. Niche shifts in the occupied E-space, i.e. unfilling followed by expansion, could also mask the actual relationship between unfilling and population trends, but the negative correlation emerged between the unfilling and the expansion indices suggests excluding this hypothesis. We also found a negative correlation between the niche overlap and population trends very close to the significance threshold (p-value = 0.053). This finding might suggest that species tending to retain their niche more than others (in terms of niche occupancy within the E-space), may be more prone to demographic declines. This static response may represent a drawback when changes occur in the environment or in interspecific relationships, leading to population decline in a long-term perspective. Finally, dispersal limitation, depending on habitat configuration but also on species-specific characteristics, may play a crucial role in metapopulation and niche changes (Pulliam, 2000), and integrating this parameter in the modeling framework may improve our ability to understand this complex relation.

Regarding our last question, results highlighted a moderate relationship between niche temporal changes and species traits. Overall, the unfilling index was the most related with continuous traits. Findings suggested that birds with larger body size are more related with niche unfilling compared to smaller species. Large-bodied species have generally smaller population sizes, lower reproductive rates, and larger home or geographic range requirements than small-bodied species; moreover, they typically occupy higher trophic levels (Gaston & Blackburn, 1995). All of these characteristics make these species more prone to extinction (Henle et al., 2004; Wang et al., 2018), and understanding their niche changes could provide important insights to enhance conservation strategies.

Interesting findings also emerged for the relationship between unfilling and the reproduction-related traits (number of broods per year, average clutch size, fecundity). Niche unfilling grew with increasing clutch size (i.e. average number of eggs laid within a single brood) and with decreasing number of broods per year. It may suggest that species investing much effort in increasing the number of broods, rather than producing more eggs per brood, might be more adaptable to environmental changes and may be able to expand their niche. However, annual fecundity, the product of clutch size and number of broods (Jiguet et al., 2007), did not show a straightforward relationship with niche unfilling, and further studies should investigate the issue.

Dispersal ratio, a surrogate of species mobility and dispersal ability (Fischer & Lindenmayer, 2005; Li et al., 2018), showed that species with higher dispersal ability would not tend to expand the niche, but findings were inconclusive in respect to unfilling. We also have to consider that the dispersal ratio could be an inappropriate indicator of the dispersal ability (Dardanelli & bellis, 2021; Dondina et al., 2022), as well as that habitat configuration and landscape connectivity significantly affect the dispersal process (Dondina et al., 2018), leading to idiosyncratic responses between species. Regarding the degree of species specialisation (Dim2 of PCA), niche metrics were not linked with it, although a weak signal showed that specialist birds tend to retain their niche more than generalist ones. It supports the hypothesis that specialists require a narrow combination of environmental characteristics (Clavel et al., 2011), and they are less prone to modify their ecological needs in response to environmental change (Dondina et al., 2017).

Concerning the categorical ecological traits, neither nest type nor diet showed a relationship with niche metrics. Conversely, long-distance migrants, wintering in Sub-Saharan Africa, showed a higher niche unfilling compared to short-distance migrants, wintering in Europe or North Africa, and sedentary species, although statistically significant differences emerged only in the first comparison. Phenological mismatch (Saino et al., 2011; Taylor et al., 2016) may represent a putative driver for long-distance migrants. Despite the fact that species can attempt to adjust to advancement in spring phenophases through behavioral plasticity, for example, by a reduction in time between arrival and breeding (Newton, 2007) or anticipating the breeding ground arrival (Jonzén et al., 2006; Newson et al., 2016), these adjustments may remain insufficient to track phenological shift (Saino et al., 2011; Mayor et al., 2017; Burgess et al., 2018). Mismatches might lead, for example, to an asynchrony between food availability and species demand, generating spatially consistent directional selection on timing, which could promote rapid evolutionary change (Burgess et al., 2018). Moreover, prey availability may affect habitat suitability, as recently documented in raptors (Bangerter et al., 2021), leading to potential niche mismatch over time. Under climate and environmental changes, long-distance migrants may be outcompeted by sedentary species having similar niches, due to the residents' ability to better judge the onset of the breeding season (Wittwer et al., 2015). Such effects could affect long-distance migrants more than short-distance ones, which may be more capable of anticipating breeding ground conditions due to the proximity of their wintering areas to the breeding areas (Møller et al., 2008). In addition, niches could differ between wintering and breeding grounds (Schumm et al., 2021), with separate dynamics over time also due to different drivers acting in wintering and breeding areas (Howard et al., 2020). Exploring long-term niche dynamics throughout several phases of the annual cycle (breeding, migration, wintering) represents a key point to look at for future research.

We also found that species inhabiting natural-open landscapes (which are all birds inhabiting mountain areas) and woodland birds underwent a higher niche expansion in respect to farmland species. Overall, birds of natural-open habitats extended the niche along the open-closed habitat gradient, within the limit of their ecological requirements, as well as towards greater thermal conditions (see Section 4.4.1 for discussion on this point) and, as in the case of the Black Redstart, towards lowlands. Within woodland species, the direction of expansion showed a large interspecific variability. Some species extend the niche towards different type of forests (e.g. the Eurasian Bullfinch), other towards multiple directions of the available E-space (e.g. the Eurasian Nuthatch *Sitta europaea*) or along boundaries of the niche (e.g. the Common Chiffchaff). Forest species populations are increasing in Lombardy (Tirozzi et al., 2021 and *Chapter 3*). This can further support the hypothesis that population demography may act as a driver to affect niche expansion over time. On the contrary, farmland birds experienced a greater niche unfilling compared to species inhabiting several types of landscapes. Farmland birds are negatively influenced by intensification of agricultural practices (Newton, 2004). They could suffer fine-scale environmental changes (e.g. grazing intensity, mowing, use of pesticides, land consolidation) affecting habitat suitability, as well as a reduction of available habitats because of the reduction of agricultural lands that occurred in our study area over the considered period. Finally, the greater niche overlap of species inhabiting several types of landscapes and farmland birds compared to species of natural-open landscapes may reflect a larger environmental tolerance for the first group and more niche fidelity for the second group, leading, in the latter case, to an overall niche unfilling when environmental changes occurred.

4.5. Conclusions

Even though the study of long-term species niche dynamic could provide crucial information for investigating species responses to environmental changes, it is a poorly investigated topic in ecology. Our results provided evidence of the complexity of patterns in niche temporal changes across 71 birds breeding in a temperate region. Results supported niche divergence (equivalency test) for 32% of species, although two-thirds were not supported by the similarity test. We highlighted a general tendency to adjust the niche centroids towards warmer thermal conditions, which may depend on several drivers acting in an idiosyncratic way between species. Embracing different niche metrics, as well as tests for niche inference, is essential to understand niche changes.

To date, a totally overlooked aspect is the potential relationship between niche changes and population trends (but see Ralston et al., 2016, 2017) and species traits (but see Zurell et al., 2018; Schumm et al., 2021). We found a positive association between niche expansion and increasing populations, and a signal that species retaining their niche over time could be more prone to undergo population declines. Moreover, we found moderate evidence for a non-random association between niche changes and species traits, especially for body size, clutch size, number of broods per year, inhabited landscape type, and migration strategy.

We encourage the implementation of studies incorporating long-term population trends and niche dynamics with a focus on cause-effect relationship. Moreover, we highlight the importance of enhancing knowledge about the role of species traits in determining niche changes over time, but also working at the single-species level due to the specificity of responses. Implementing the modeling framework by including the potential variations of niche throughout several phases of annual cycle (breeding, migration, wintering), bionomic variables (biotic interactions and resource-consumer dynamics (Elton, 1927; Hutchinson, 1978), and dispersal dynamics represents a crucial point. We believe that this research roadmap could provide meaningful insights to improve conservation plans aimed at preserving threatened species and biodiversity.

Supplementary materials

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S4.1

Land-cover variables used in PCA (E-space). “DUSAF code” and “description” represent the classification according to the 3rd level of DUSAF digital map (ERSAF, 2018), while “Variable code” and “name” indicate the corresponding land covers used in the analyses after merging of some variables.

Land-cover variables			
DUSAF code	DUSAF description	Variable code	Variable name
111	Continuous urban matrix (e.g. dense residential areas)	C110	Continuous urban matrix
121	Industrial areas and large production plants		
122	Road and rail networks		
123	Harbours		
124	Airports		
131	Quarries		
132	Dumps		
133	Building sites		
134	Degraded areas		
141	Green urban areas		
142	Recreational areas		
112	Discontinuous urban matrix (e.g. farmsteads, scattered residential areas)	C112	Discontinuous urban matrix
211	Arable lands (e.g. maize, wheat, horticulture)	C211	Arable lands
213	Paddy fields	C213	Paddy fields
221	Vineyards	C220	Permanent orchard plantations
222	Orchards		
223	Olive groves		
224	Wood plantations	C224	Wood plantations
231	Meadows and pastures	C231	Meadows and pastures
311	Broadleaved forests	C311	Broadleaved forests
312	Coniferous forests	C312	Coniferous forests
313	Mixed forests	C313	Mixed forests
321	Grasslands	C321	Grasslands
322	Shrublands	C322	Shrublands
324	Shrub and grass vegetation under evolution	C324	Shrub and grass vegetation under evolution
331	Areas around waterbodies without vegetation	C330	Areas with sparse or absent vegetation
332	Debris deposits and rocks		
333	Rock areas with sparse vegetation		
334	Glaciers and perennial snow		
411	Wetland vegetation	C410	Wetland vegetation
511	Rivers and streams	C511	Rivers and streams
512	Natural and artificial lakes	C512	Natural and artificial lakes

S4.2

List of species traits and referencing literature.

Species traits		Abbreviation	References
Continuous			
Mean length of the body		len	Storchová & Hořák (2018)
Mean length of the wing		wing	Storchová & Hořák (2018)
Mean length of the tail		tail	Storchová & Hořák (2018)
Mean length of the bill		bil	Storchová & Hořák (2018)
Mean length of tarsus		tar	Storchová & Hořák (2018)
Mean weight in breeding season		wei	Storchová & Hořák (2018)
Mean clutch size		clu	Storchová & Hořák (2018)
Mean number of broods per breeding season		bro	Storchová & Hořák (2018); Tirozzi et al. (2022); *Chapter 3*
Annual fecundity (clu × bro)		fec	Jiguet et al. (2007)
Incubation period		inc	Storchová & Hořák (2018)
Fledging period		fle	Storchová & Hořák (2018)
Dispersal ratio (len/cube root[wei])		disr	Fischer & Lindenmayer (2005) Li et al. (2018)
Specialisation index for the foraging habitat		SSI.fh	Julliard et al. (2006); Pearman et al. (2014); Tirozzi et al. (2021); *Chapter 3*
Specialisation index for the acquisition behavior		SSI.acq	Julliard et al. (2006); Pearman et al. (2014); Tirozzi et al. (2021); *Chapter 3*
Specialisation index for the nesting habitat		SSI.nes	Julliard et al. (2006); Pearman et al. (2014); Tirozzi et al. (2021); *Chapter 3*
Specialisation index for the foraging substrate		SSI.fs	Julliard et al. (2006); Pearman et al. (2014); Tirozzi et al. (2021); *Chapter 3*
Specialisation index for the diet		SSI.tr	Julliard et al. (2006); Pearman et al. (2014); Tirozzi et al. (2021); *Chapter 3*
Overall specialisation index (mean[SSi.fh, SSi.acq, SSI.nes, SSI.fs, SSI.tr])		SSI.ov	Tirozzi et al. (2021); *Chapter 3*
Categorical			
Migration strategy		-	Tirozzi et al. (2021); *Chapter 3*
Groups	Long-distance migrants Short-distance migrants Sedentary		
Landscape type		-	Tirozzi et al. (2021); *Chapter 3*
Groups	Farmland Woodland Natural-open habitat Several		
Nest type		-	Storchová & Hořák (2018);
Groups	Elevated-nesters Ground-nesters Hole-nesters		Tirozzi et al. (2022); *Chapter 3*
Diet		-	Wilman et al. (2014);
Groups	Vertebrates Plant-eaters Invertebrates Omnivores		Tirozzi et al. (2022); *Chapter 3*

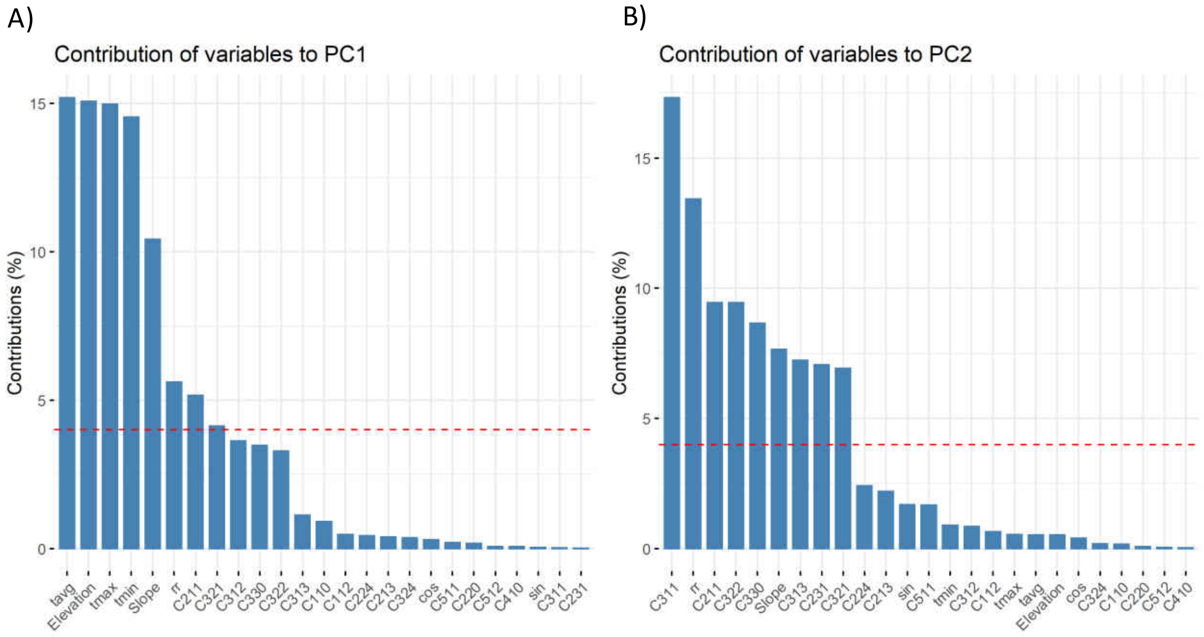
S4.3

Coordinates of each variable respect to the first two PCA-axes (E-space). See S4.1 and Section 4.2.2 in the main text for variables' abbreviations.

Variable	PC1	PC2
C110	0.23	0.05
C112	0.17	0.11
C211	0.56	−0.41
C213	0.15	−0.20
C220	0.10	0.04
C224	0.16	−0.21
C231	0.02	0.35
C311	−0.04	0.56
C312	−0.47	−0.12
C313	−0.26	0.36
C321	−0.50	−0.35
C322	−0.45	−0.41
C324	−0.15	0.06
C330	−0.46	−0.39
C410	0.06	−0.03
C511	0.11	−0.17
C512	−0.06	−0.03
Elevation	−0.95	−0.10
sin	0.05	−0.17
cos	−0.13	0.08
Slope	−0.79	0.37
rr	−0.58	0.49
tmax	0.95	0.10
tavg	0.96	0.10
tmin	0.94	0.13

S4.4

Contribution of each variable (%) to PC1 A) and PC2 B) (E-space). The red-dashed line represents the expected average contribution. If the contribution of the variables were uniform, the expected value would be the reciprocal of the number of variables (4%).



S4.5

Niche breadth and centroid for each species along the PCA-axes (E-space) in T1 and T2. T_1 = 1992-95-96; T_2 = 2015-16-17; PC1 = PCA-axis 1; PC2 = PCA-axis 2. Species are presented with the common name (Gill et al., 2022) and following the taxonomic order.

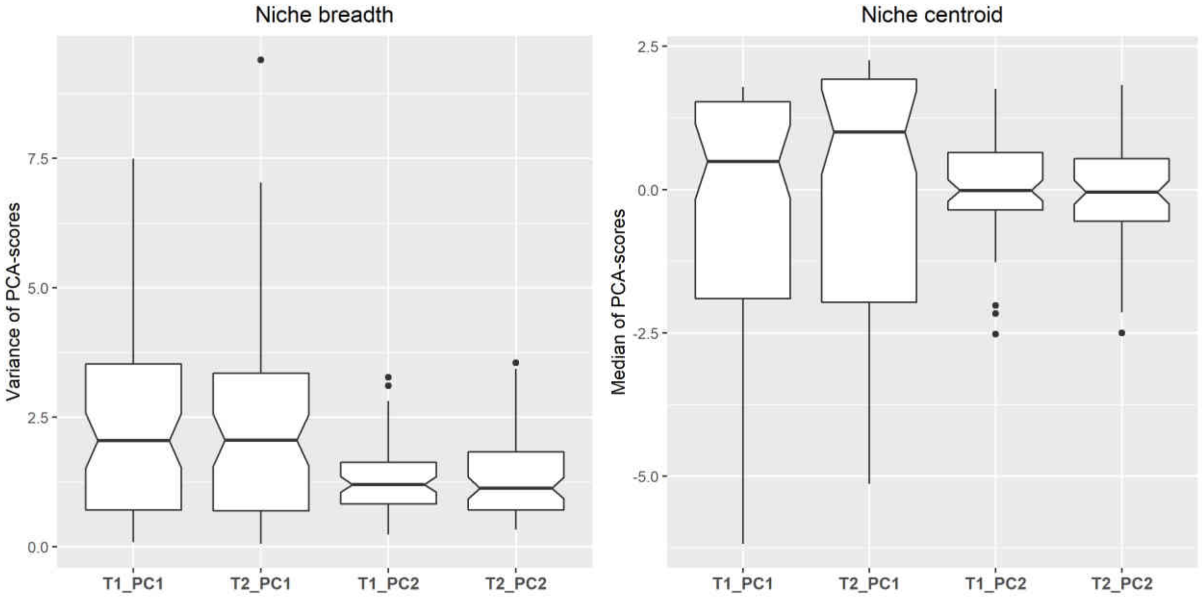
	Breadth				Centroid			
Species	T_1		T_2		T_1		T_2	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
Black-crowned Night Heron	0.18	0.40	0.06	0.33	1.59	−1.17	1.92	−0.94
Little Egret	0.09	0.33	0.12	0.38	1.53	−1.27	2.09	−1.03
Grey Heron	0.13	0.48	0.42	0.56	1.63	−1.06	2.03	−0.76
Mallard	1.26	1.69	0.41	0.68	1.35	−0.56	2.03	−0.85
Black Kite	1.49	1.12	1.47	1.36	0.15	0.70	0.50	1.18
Common Buzzard	2.05	1.20	2.39	1.44	−0.70	1.71	1.38	0.46
Common Kestrel	5.86	2.16	2.64	0.85	0.46	0.31	2.09	−0.67
Common Quail	0.42	0.57	0.16	0.59	1.63	−0.21	2.22	−0.91
Common Pheasant	0.58	1.26	0.39	0.75	1.56	−0.29	2.08	−0.73
Common Moohren	0.31	0.79	0.19	0.44	1.60	−0.66	2.02	−0.73
Feral Pigeon	0.38	0.75	0.36	0.63	1.62	−0.22	1.99	−0.20
Common Wood Pigeon	0.68	1.28	0.92	1.04	1.39	0.06	1.91	−0.22
Eurasian Collared Dove	0.50	0.90	0.57	0.77	1.55	−0.26	1.99	−0.24
European Turtle Dove	0.82	1.04	0.47	0.82	1.43	−0.03	1.89	−0.43
Common Cuckoo	4.19	1.72	4.76	1.89	1.03	−0.07	−0.65	0.83
Common Swift	2.39	1.27	3.10	1.22	1.45	−0.16	1.85	−0.04
Eurasian Wryneck	2.08	1.12	1.26	0.81	1.35	0.11	1.36	0.49
European Green Woodpecker	1.87	0.78	3.22	1.44	−0.61	1.26	0.83	0.38
Great Spotted Woodpecker	2.09	2.44	3.82	1.49	0.49	0.90	1.20	0.43
Eurasian Skylark	0.69	0.47	9.40	0.84	1.77	−0.70	2.03	−0.98
Eurasian Crag Martin	3.76	2.60	4.17	2.05	−1.74	1.55	−1.50	0.47
Barn Swallow	1.43	1.19	0.63	0.70	1.54	−0.07	2.02	−0.26
Common House Martin	2.05	1.27	4.61	1.24	1.13	0.33	1.48	0.07
Tree Pipit	2.74	1.86	1.74	2.31	−3.77	0.01	−3.55	−0.31
Water Pipit	0.44	0.78	1.40	1.09	−5.63	−2.52	−4.86	−2.50
Western Yellow Wagtail	0.17	0.44	0.06	0.34	1.79	−0.72	2.26	−1.03
Grey Wagtail	7.49	1.96	4.72	2.25	−2.75	0.23	−2.22	0.25
White Wagtail	5.20	1.57	6.43	1.73	−0.02	0.59	−0.91	0.31
Eurasian Wren	6.29	2.35	3.76	2.41	−1.59	1.07	−1.97	1.07
Dunnock	0.44	0.80	1.82	2.91	−5.49	−1.07	−4.54	−1.28
European Robin	3.90	1.32	3.57	2.22	−1.90	1.52	−1.97	1.26
Common Nigthingale	0.68	1.05	0.37	0.70	1.60	−0.38	2.06	−0.62

S4.5 (cont.)

Black Redstart	6.09	3.11	7.03	2.72	–5.66	–2.02	–3.89	–0.36
Common Redstart	3.45	1.10	4.11	1.21	–1.02	1.47	–0.66	0.72
European Stonechat	0.86	0.72	1.17	0.72	1.73	–0.44	1.92	0.02
Northern Wheatear	1.92	2.13	1.09	1.22	–5.49	–2.52	–4.73	–2.14
Common Blackbird	3.68	1.39	5.31	1.47	1.34	–0.01	1.76	–0.16
Song Thrush	3.59	1.19	3.06	3.23	–3.95	–0.02	–2.30	0.91
Mistle Trush	4.30	3.27	2.27	3.44	–3.08	0.38	–4.22	–0.58
Cetti's Warbler	0.33	0.67	0.23	0.51	1.71	–0.53	1.87	–0.53
Melodius Warbler	1.12	1.47	0.34	0.78	1.27	0.11	1.89	–0.42
Lesser Whitethroat	2.89	2.73	1.59	2.09	–5.75	–0.80	–4.69	–1.89
Eurasian Blackcap	3.85	1.20	4.57	1.33	0.93	0.25	1.01	0.32
Western Bonelli's Warbler	3.21	1.14	2.26	1.77	–1.47	1.76	–1.46	1.60
Common Chiffchaff	4.40	1.77	3.61	2.94	–1.91	1.53	–2.11	0.89
Goldcrest	2.83	1.77	2.12	1.57	–3.11	0.58	–2.88	0.57
Common Firecrest	5.19	0.85	3.47	0.80	–4.48	–0.44	–1.71	0.89
Spotted Flycatcher	2.13	1.28	2.63	1.08	0.86	0.83	0.54	0.78
Long-tailed Tit	2.66	0.75	2.58	1.13	–0.84	1.63	0.63	0.95
Marsh Tit	2.20	0.95	1.62	0.45	–1.97	1.57	–1.23	1.83
Willow Tit	1.79	1.85	1.57	3.11	–4.96	–0.73	–5.08	–1.60
European Crested Tit	3.47	2.05	3.19	3.55	–3.30	0.26	–3.34	–0.22
Coal Tit	5.04	1.90	3.24	3.16	–3.41	0.49	–2.58	0.72
Eurasian Blue Tit	2.58	0.88	1.93	0.90	–0.77	1.48	–0.39	1.34
Great Tit	2.90	1.41	2.97	1.26	0.44	0.59	1.36	0.25
Eurasian Nuthatch	1.56	0.23	2.59	0.99	–0.31	1.62	–1.38	1.66
Eurasian Golden Oriole	0.61	1.05	0.39	0.89	1.52	–0.19	1.90	–0.30
Red-backed Shrike	2.46	1.43	2.42	0.76	0.59	0.44	0.83	0.51
Eurasian Jay	4.37	1.34	3.53	1.53	–1.24	1.17	–0.84	1.36
Eurasian Magpie	0.34	0.65	0.32	0.66	1.53	–0.26	2.07	–0.43
Carrion Crow	5.44	2.81	3.77	2.70	–1.89	1.42	–4.42	–0.47
Hooded Crow	2.49	1.29	2.94	1.19	1.45	–0.15	1.68	0.08
Common Starling	0.71	0.95	0.34	0.64	1.60	–0.26	2.01	–0.34
Italian Sparrow	1.30	1.20	1.33	0.81	1.55	–0.16	1.97	–0.19
Eurasian Tree Sparrow	0.72	0.81	0.76	0.62	1.61	–0.32	2.04	–0.46
Common Chaffinch	5.58	1.36	6.15	1.98	–0.41	0.89	–0.95	0.69
European Serin	1.13	0.72	2.06	0.63	1.27	0.41	1.47	0.23
European Greenfinch	1.05	1.06	1.25	0.60	1.45	0.02	1.86	0.09
European Goldfinch	1.25	1.28	2.70	0.71	1.54	–0.11	1.85	0.05
Common Redpoll	0.74	1.51	1.22	1.67	–6.18	–2.16	–5.13	–2.11
Eurasian Bullfinch	2.57	1.22	2.04	2.78	–4.60	–0.20	–2.56	0.17

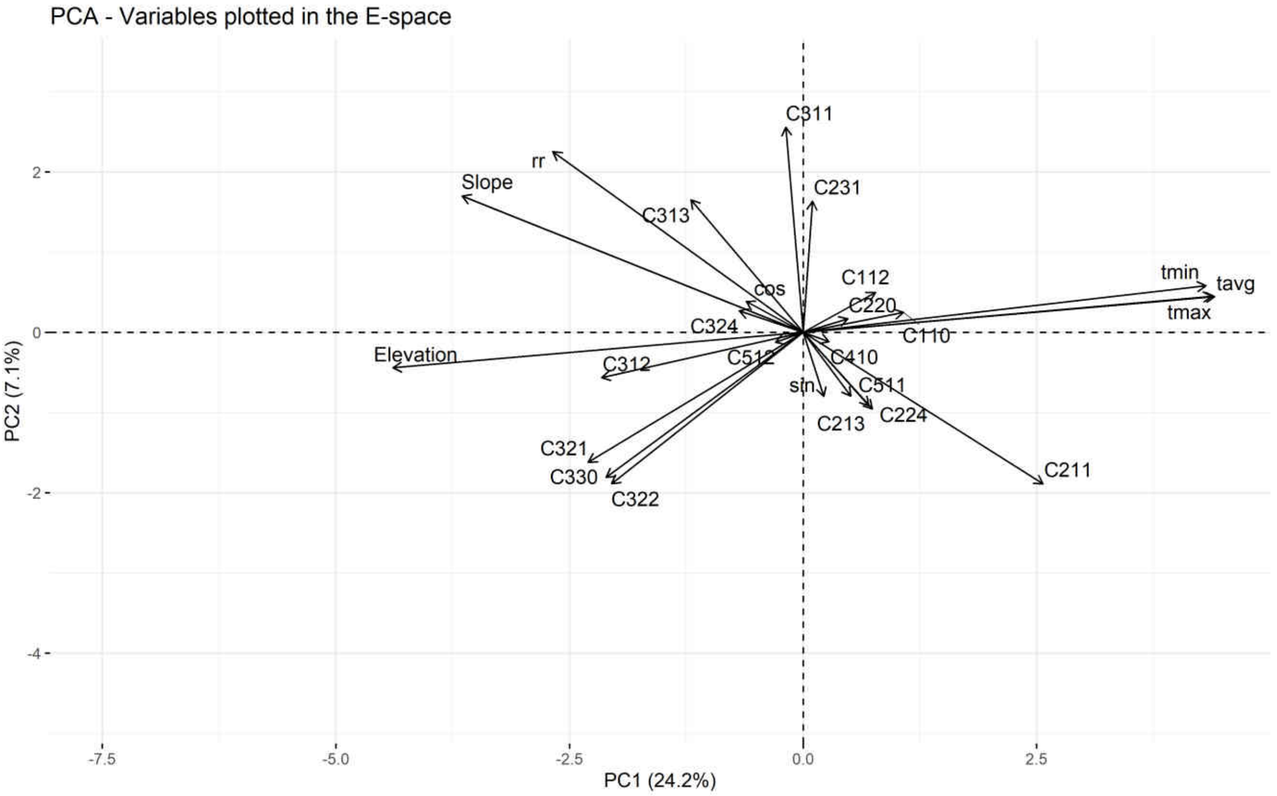
S4.6

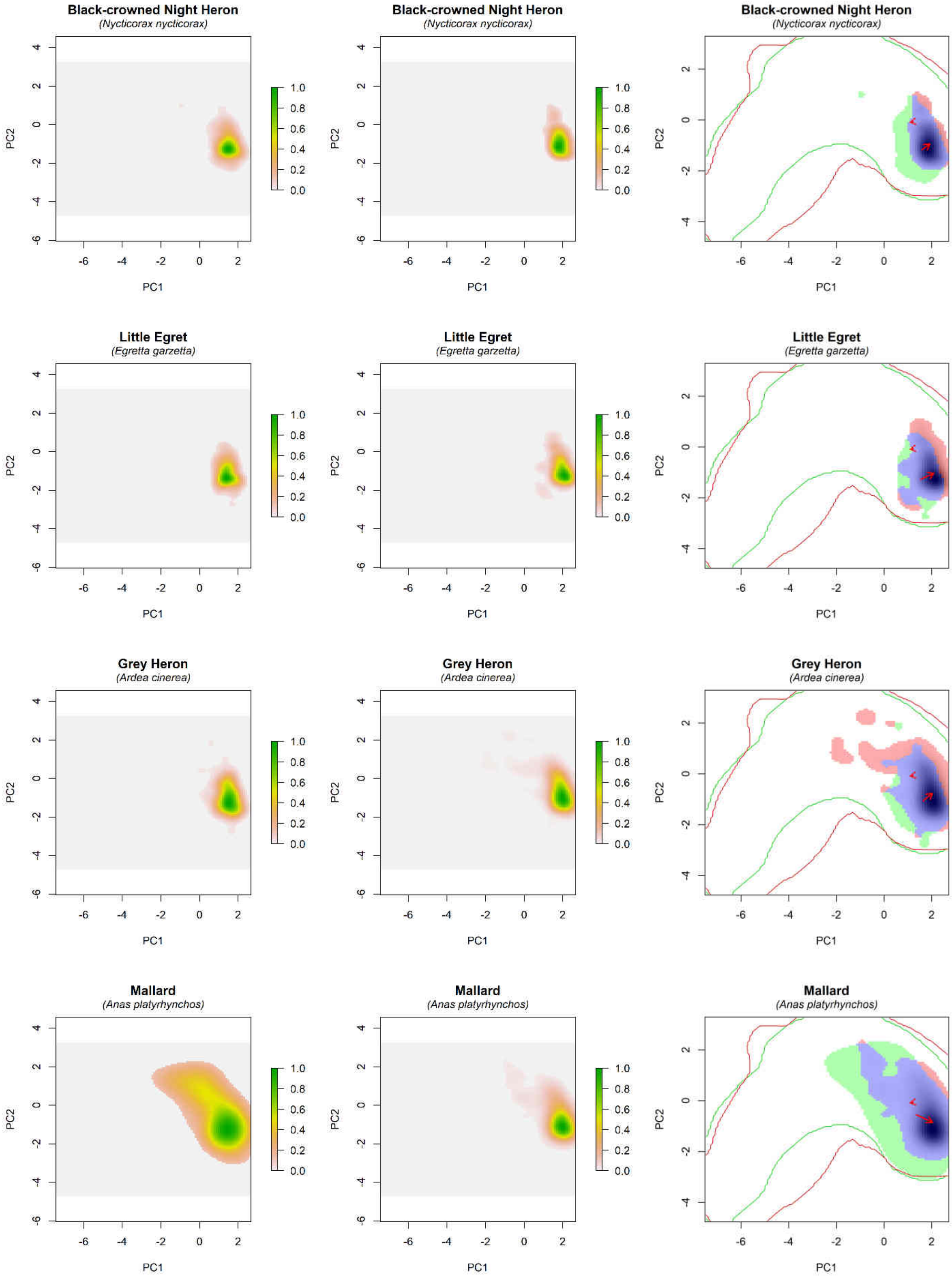
Notched box plots of niche breadth and centroid for each PCA-axis (E-space) in T_1 and T_2. From T_1 to T_2, the median of the niche breadth varied from 2.05 (range = 0.09 - 7.49) to 2.06 (range = 0.06 - 9.40) along PC1, and from 1.20 (range = 0.23 - 3.27) to 1.13 (range = 0.33 -3.55) along PC2. From T_1 to $T_{2,}$ the median of the niche centroid varied from 0.49 (range = −6.18 -1.79) to 1.01 (range = −5.13 -2.26) along PC1, and from −0.02 (range = −2.52 -1.76) to −0.04 (range = −2.50 -1.83) along PC2. In each box plot, the sample dimension is equal to the total number of the species (n = 71). Whiskers are 1.5 × IQR. Black dots represent outliers. T1 = 1992-95-96; T2 = 2015-16-17; PC1 = PCA-axis 1; PC2 = PCA-axis 2. Nothces give a roughly 95% confidence interval for medians. Wilcoxon rank sum test detected differences only for centroids' comparison along PC1 (niche breadth PC1: W = 2,550, p-value = 0.906; niche breadth PC2: W = 2,625, p-value = 0.671; niche centroid PC1: W = 1,991, p-value = 0.031; niche centroid PC2: W = 2,727, p-value = 0.401).

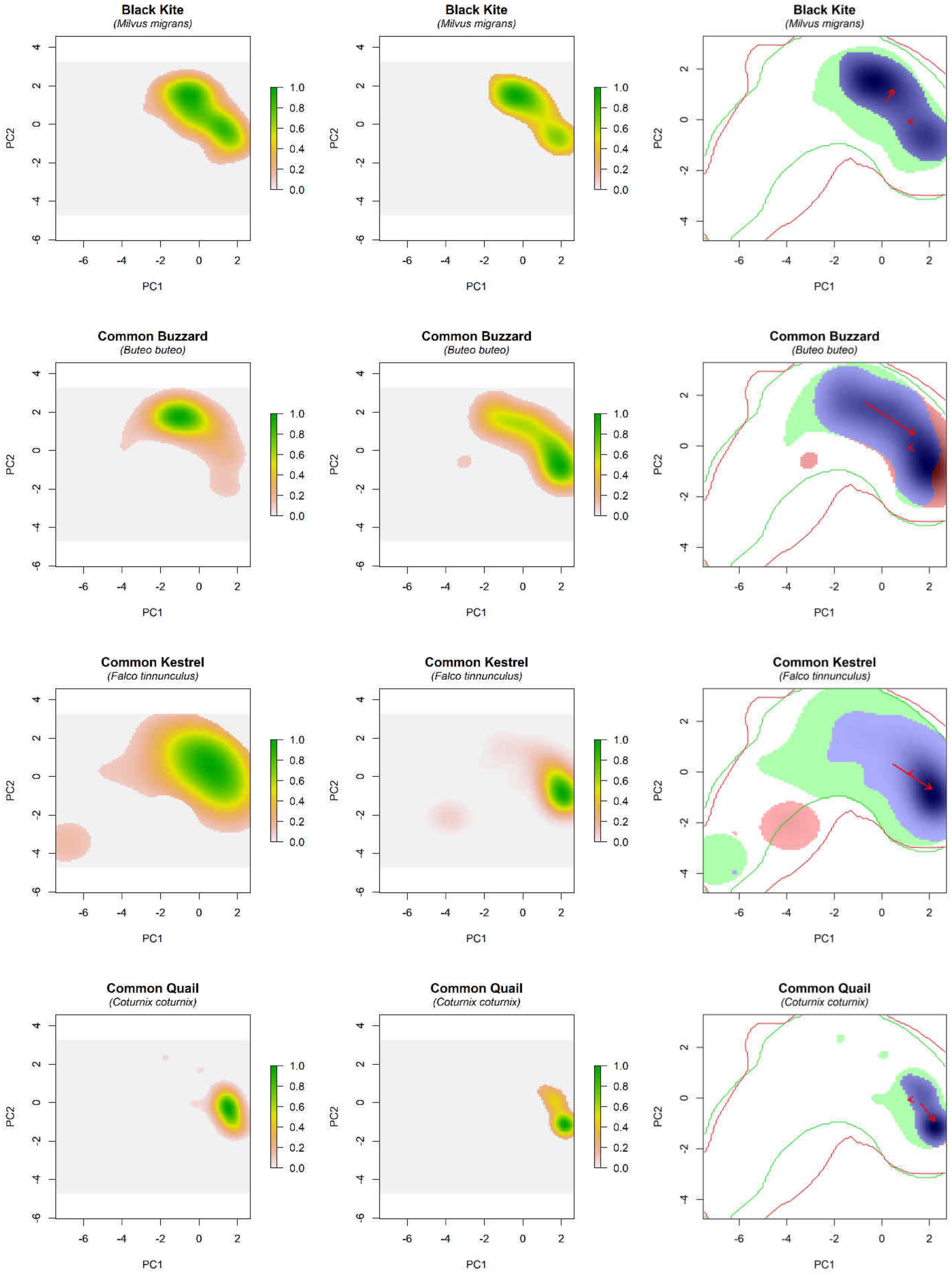


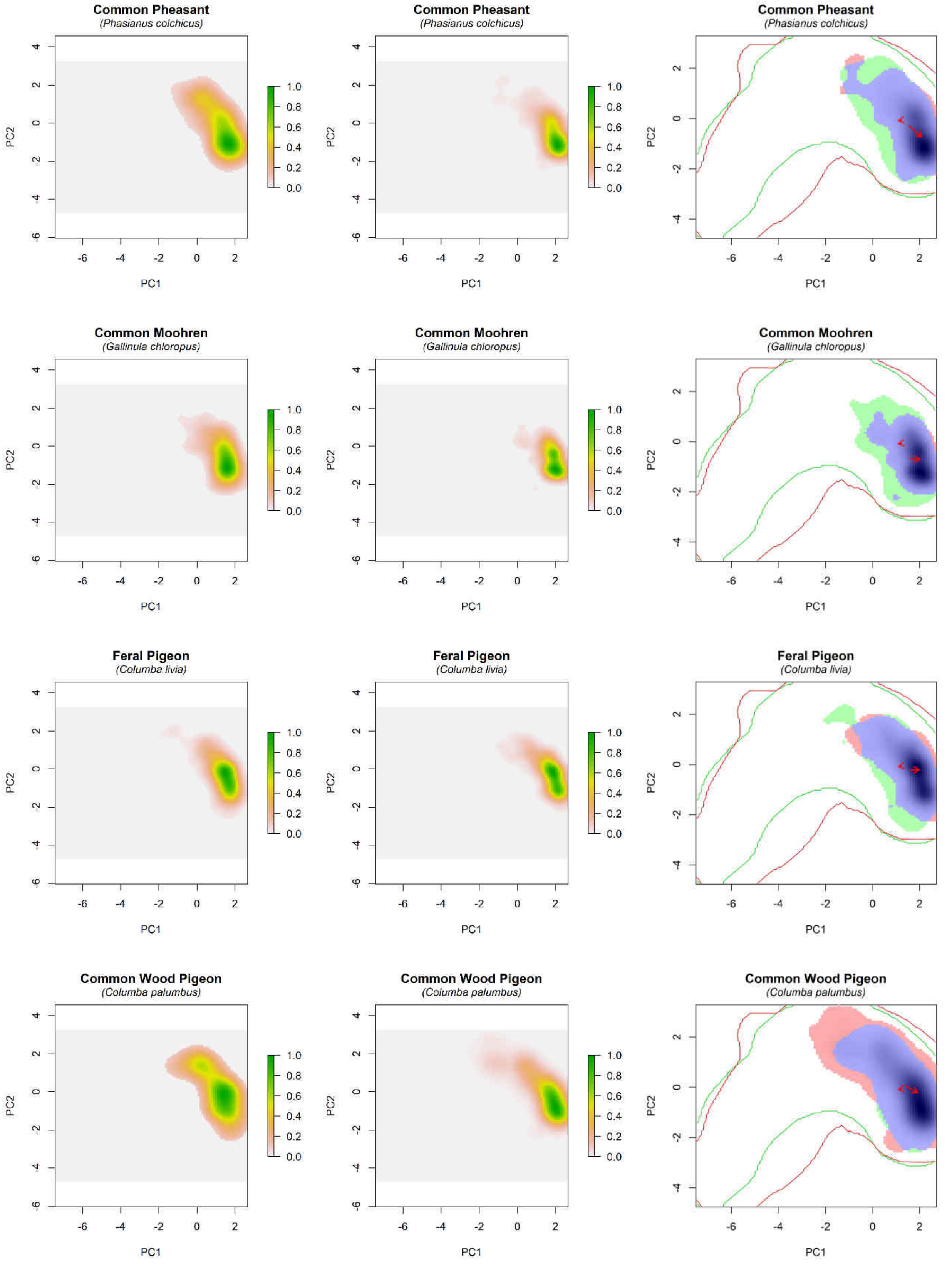
S4.7

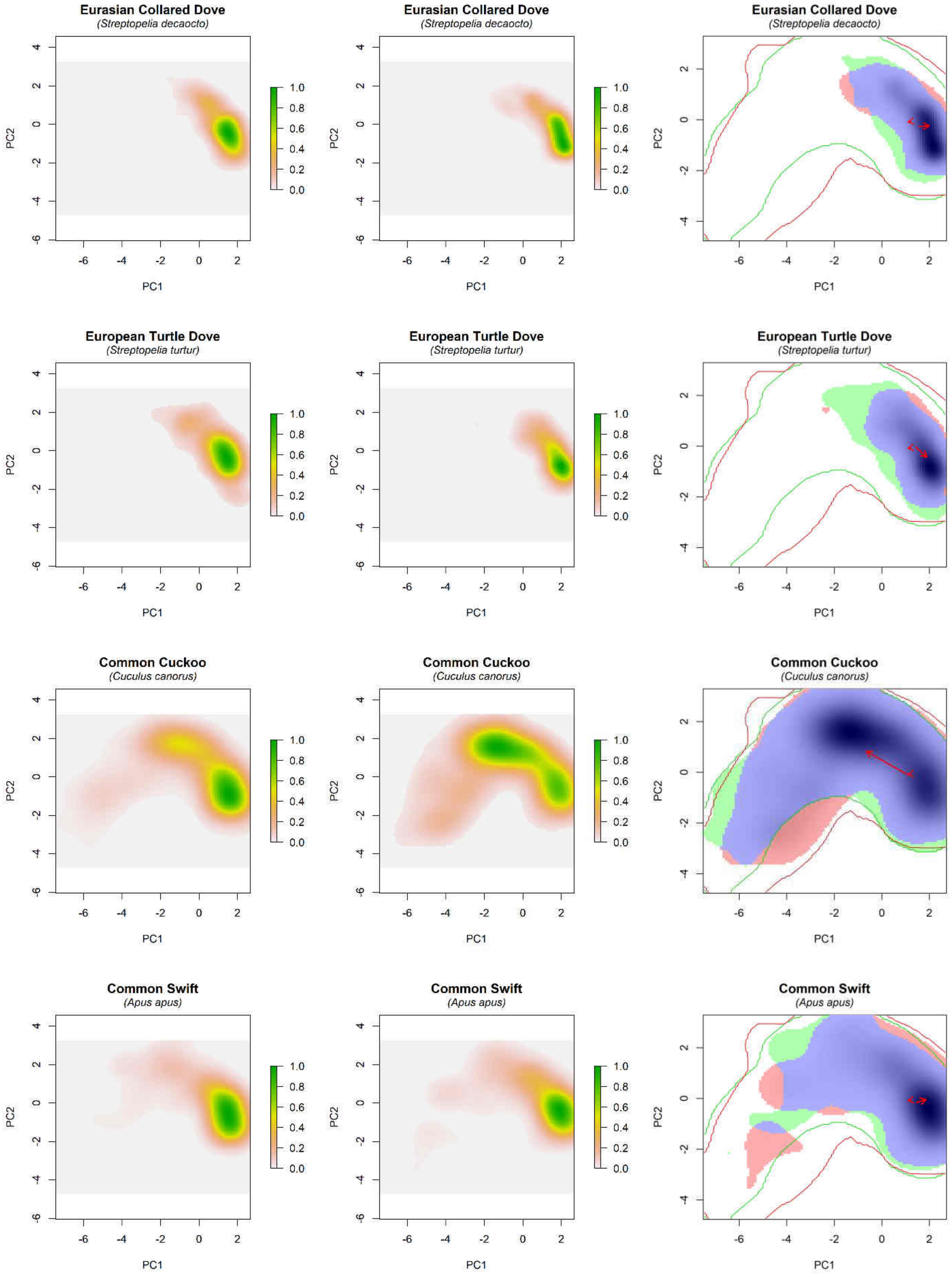
Niche quantification in the E-space for each species in T_1 (1992-95-96) and T_2 (2015-16-17) and niche changes between the two periods. The first plot represent the coordinates of the variables in the E-space to ease the interpretation of the niche respect to the PCA-axes. Niche in T_1 is shown in the left column, in T_2 in the middle column, and the overlap in the right column. In each row is represented a single species with its common and scientific name (Gill et al., 2022). In the graphs of niche in T_1 and T_2 separately, the density of occurrence of species is depicted through a colored gradient from light grey (0) to green (1). In the graphs representing niche changes between T_1 and T_2, the red area indicates the E-space exclusively occupied in T_2, the green area the E-space exclusively occupied in T_1, and the blue area the E-space occupied in both T_1 and T_2. Color intensity of the filled area represents the density of occurrence of species in T_2. The green and red solid lines represent the whole extent of the available E-space in T_1 and T_2, respectively. Arrows indicate the centroids' shift from T_1 to T_2 for the available E-space (dashed arrow) and for the occupied E-space (solid arrow).

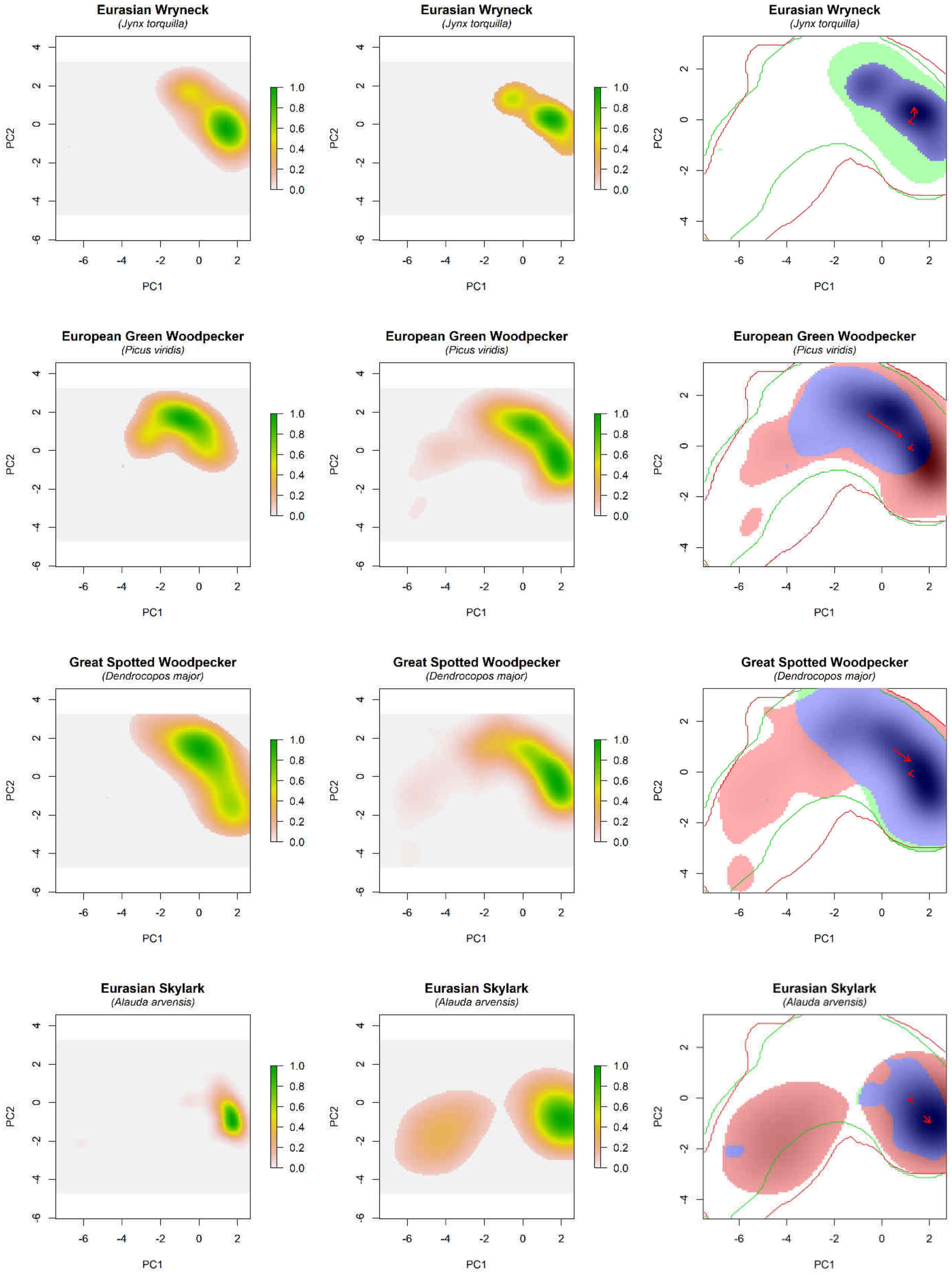


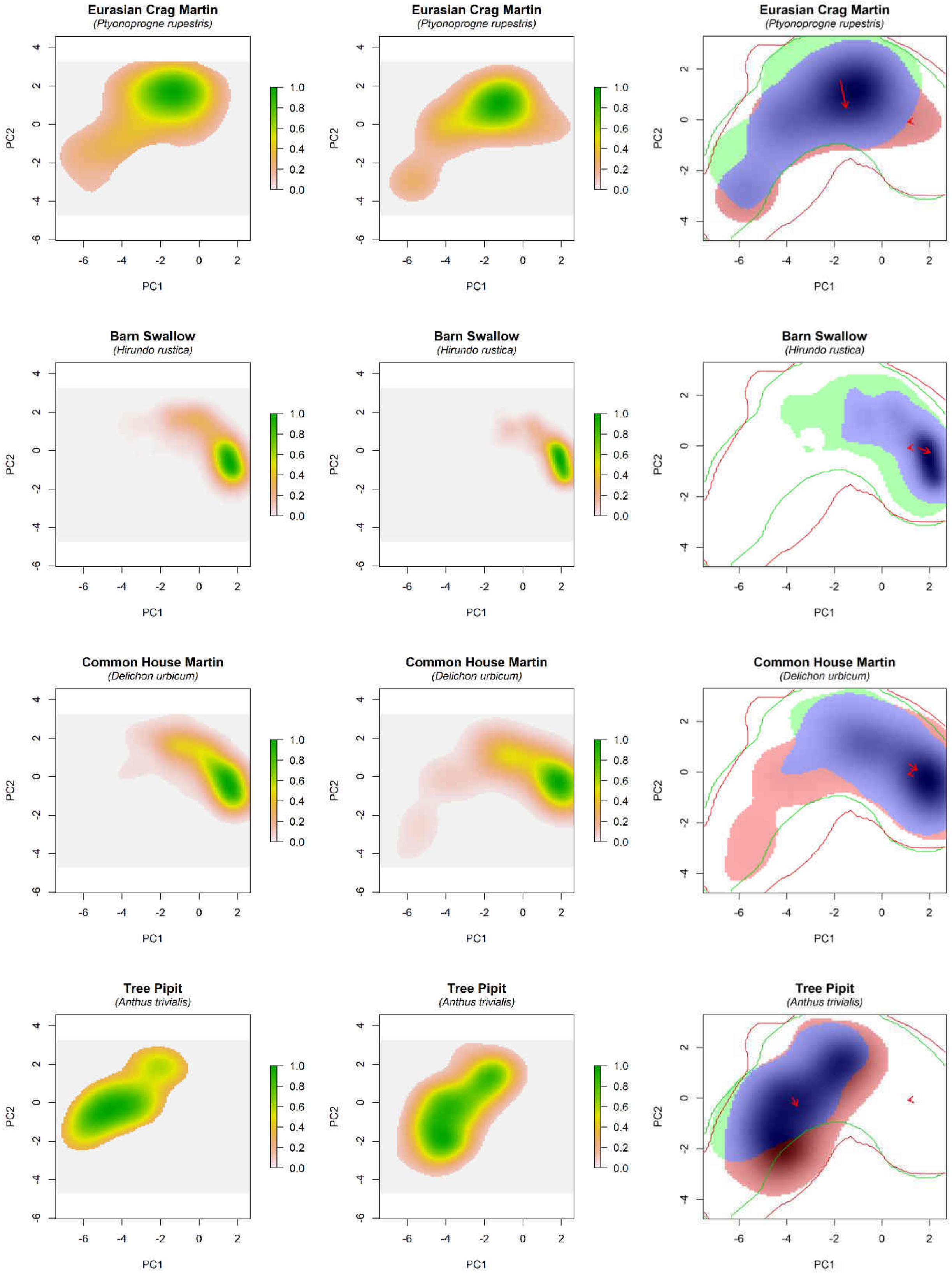

Black-crowned Night Heron
(Nycticorax nycticorax)
Black-crowned Night Heron
(Nycticorax nycticorax)
Black-crowned Night Heron
(Nycticorax nycticorax)
Little Egret
(Egretta garzetta)
Little Egret
(Egretta garzetta)
Little Egret
(Egretta garzetta)
Grey Heron
(Ardea cinerea)
Grey Heron
(Ardea cinerea)
Grey Heron
(Ardea cinerea)
Mallard
(Anas platyrhynchos)
Mallard
(Anas platyrhynchos)
Mallard
(Anas platyrhynchos)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

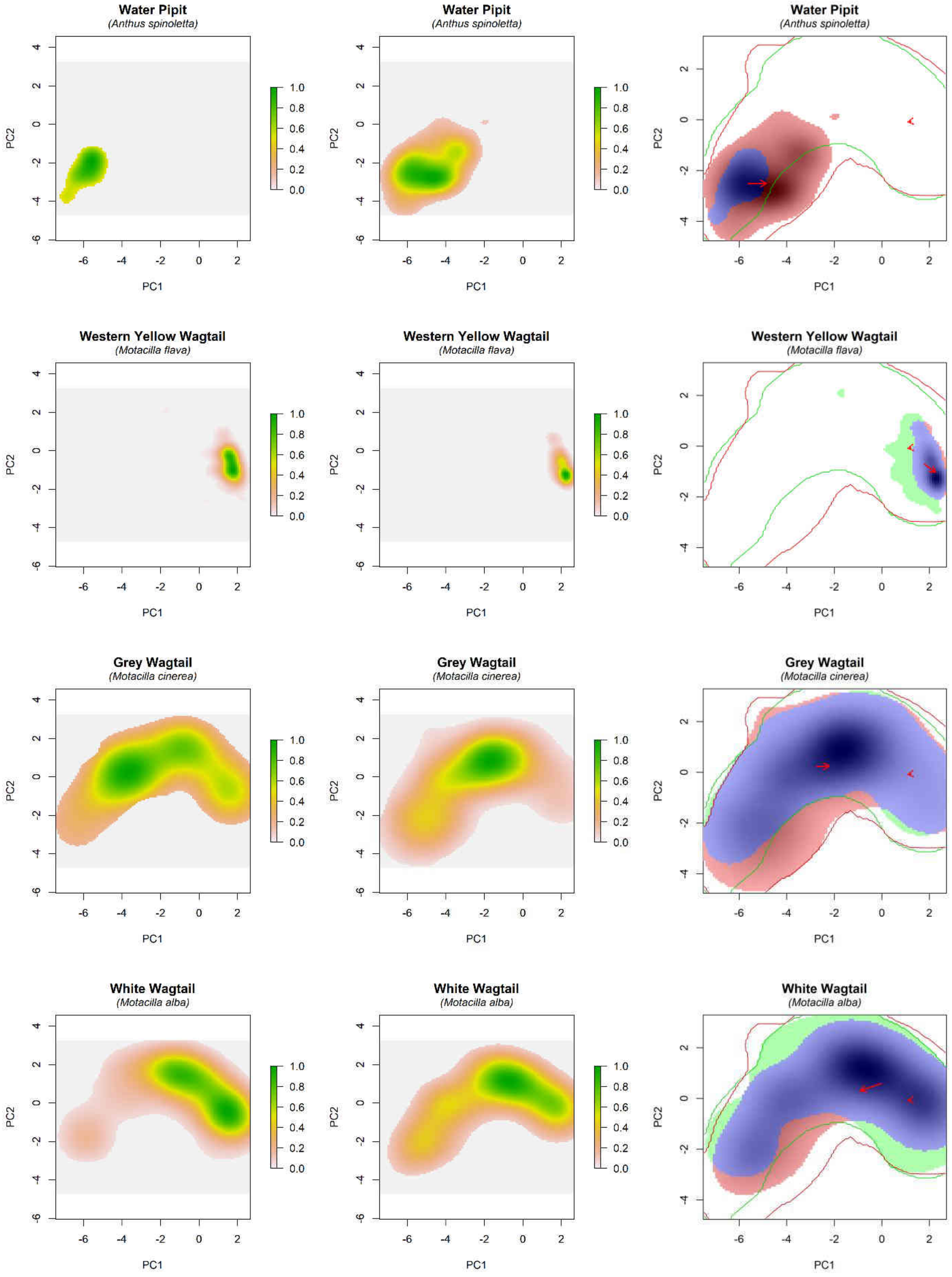

Black Kite
(Milvus migrans)
Black Kite
(Milvus migrans)
Black Kite
(Milvus migrans)
Common Buzzard
(Buteo buteo)
Common Buzzard
(Buteo buteo)
Common Buzzard
(Buteo buteo)
Common Kestrel
(Falco tinnunculus)
Common Kestrel
(Falco tinnunculus)
Common Kestrel
(Falco tinnunculus)
Common Quail
(Coturnix coturnix)
Common Quail
(Coturnix coturnix)
Common Quail
(Coturnix coturnix)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

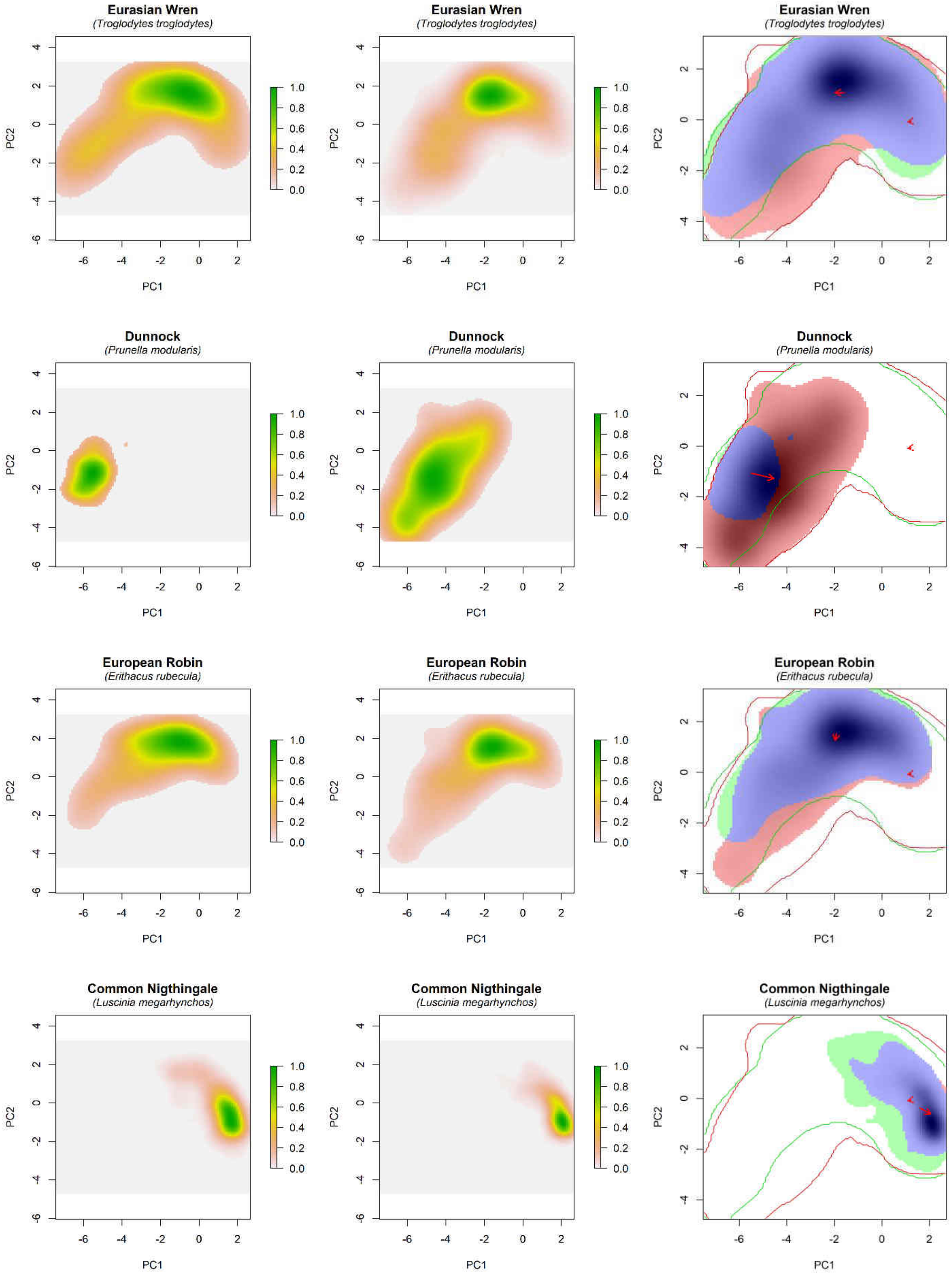

Common Pheasant
(Phasianus colchicus)
Common Moohren
(Gallinula chloropus)
Feral Pigeon
(Columba livia)
Common Wood Pigeon
(Columba palumbus)
PC1
PC2
-6
-4
-2
0
2
4
0.0
0.2
0.4
0.6
0.8
1.0

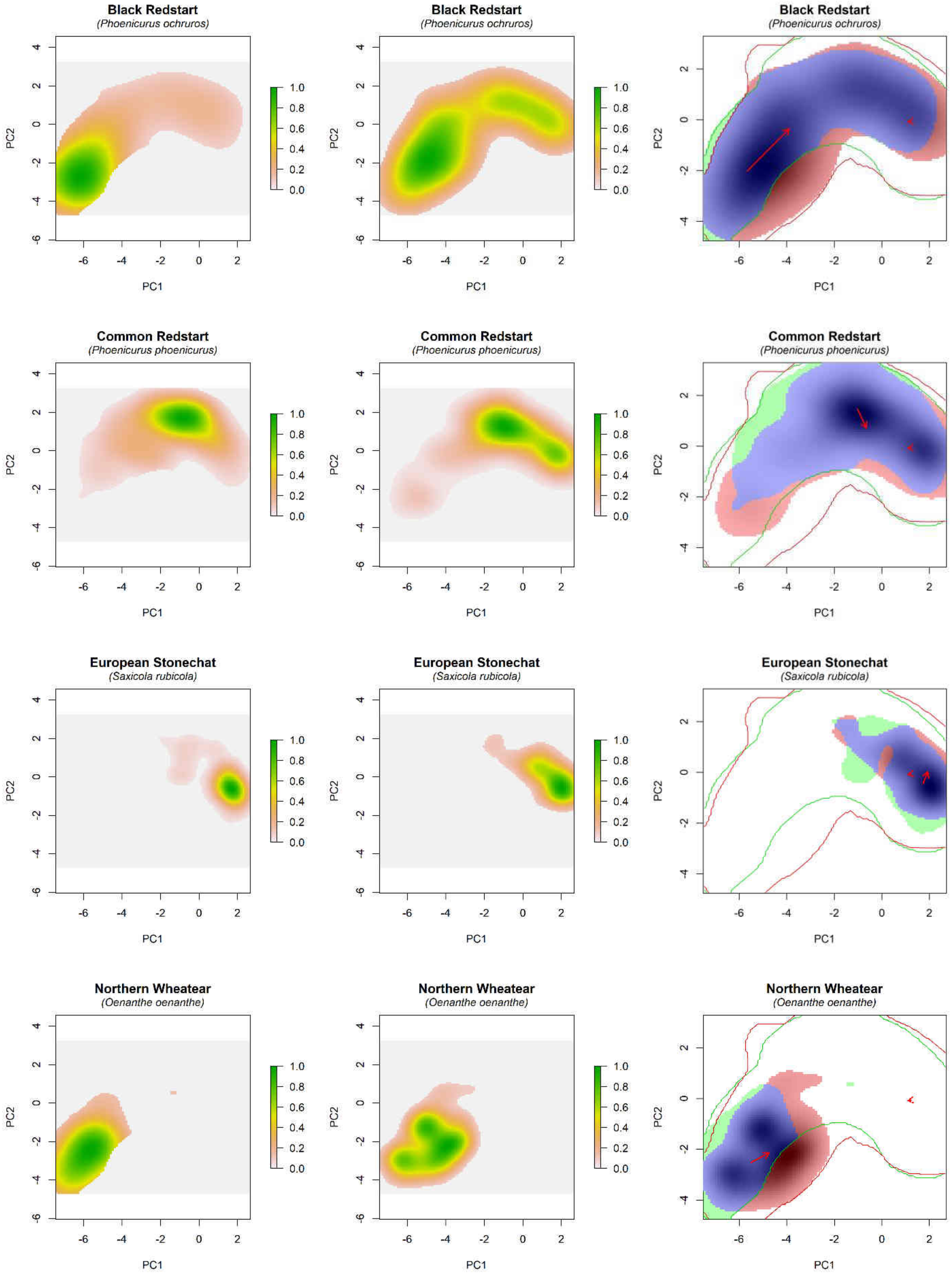

Eurasian Collared Dove
(Streptopelia decaocto)
Eurasian Collared Dove
(Streptopelia decaocto)
Eurasian Collared Dove
(Streptopelia decaocto)
European Turtle Dove
(Streptopelia turtur)
European Turtle Dove
(Streptopelia turtur)
European Turtle Dove
(Streptopelia turtur)
Common Cuckoo
(Cuculus canorus)
Common Cuckoo
(Cuculus canorus)
Common Cuckoo
(Cuculus canorus)
Common Swift
(Apus apus)
Common Swift
(Apus apus)
Common Swift
(Apus apus)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

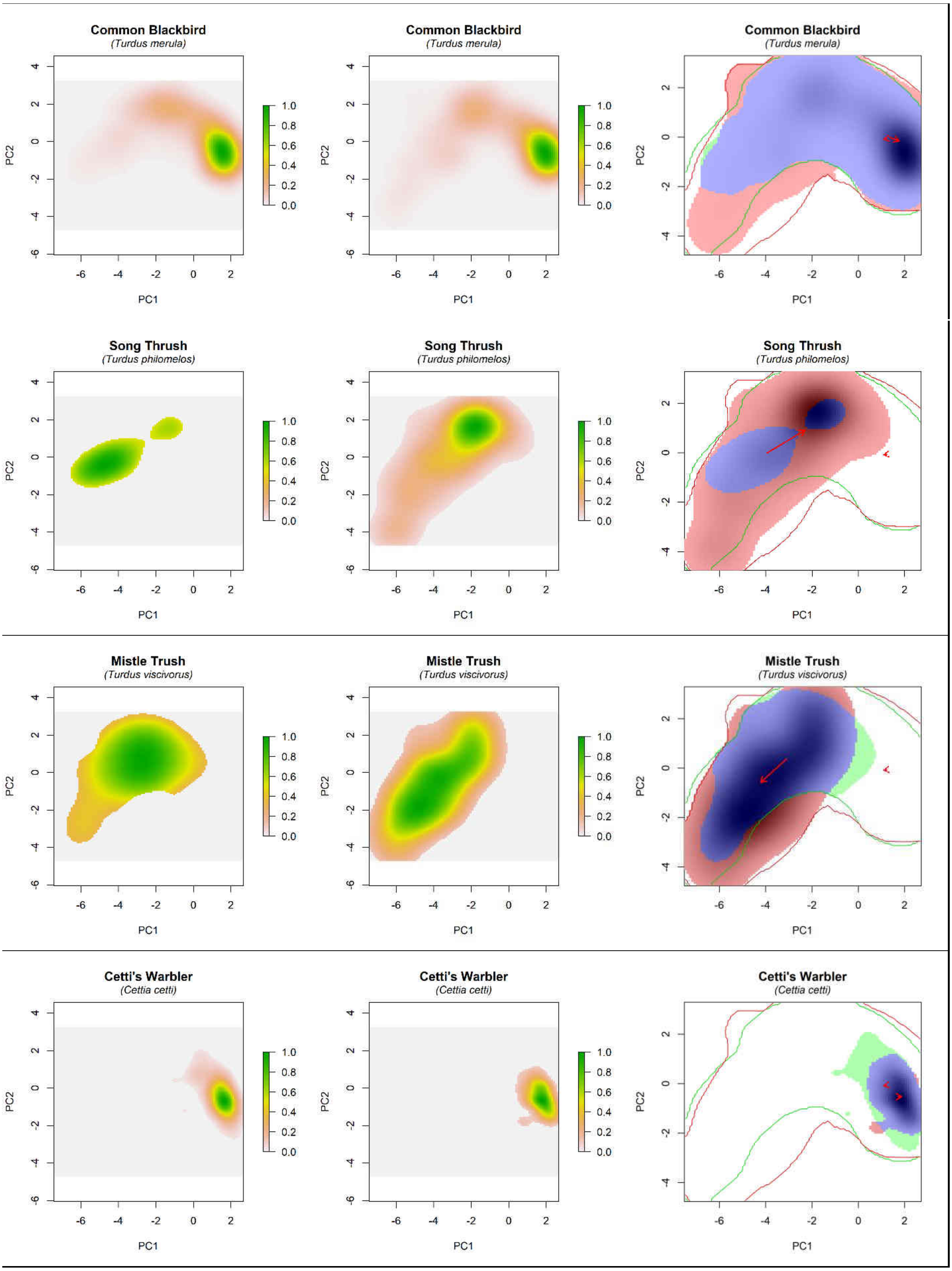

Eurasian Wryneck
(Jynx torquilla)
Eurasian Wryneck
(Jynx torquilla)
Eurasian Wryneck
(Jynx torquilla)
European Green Woodpecker
(Picus viridis)
European Green Woodpecker
(Picus viridis)
European Green Woodpecker
(Picus viridis)
Great Spotted Woodpecker
(Dendrocopos major)
Great Spotted Woodpecker
(Dendrocopos major)
Great Spotted Woodpecker
(Dendrocopos major)
Eurasian Skylark
(Alauda arvensis)
Eurasian Skylark
(Alauda arvensis)
Eurasian Skylark
(Alauda arvensis)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

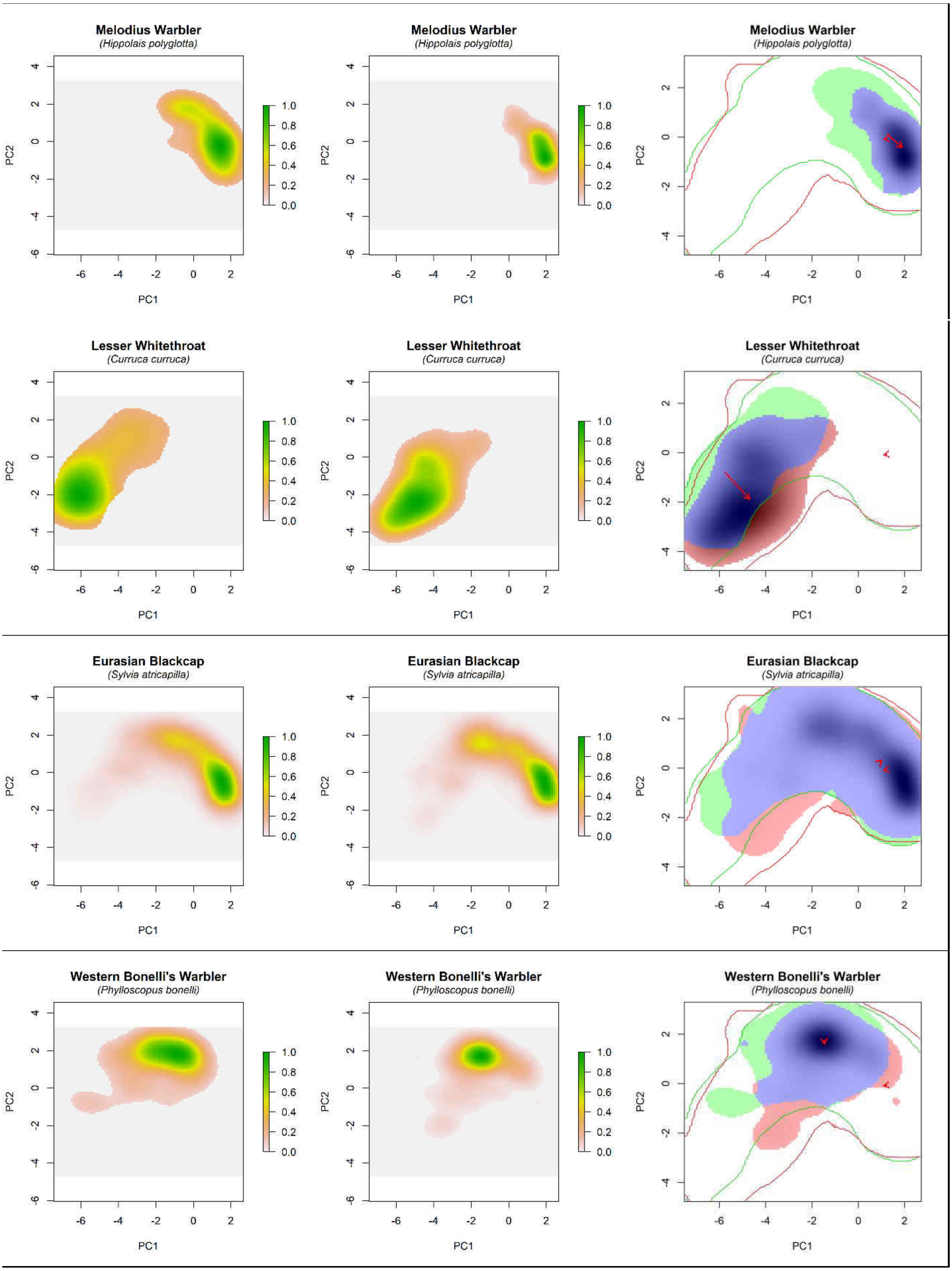

Eurasian Crag Martin
(Ptyonoprogne rupestris)
Barn Swallow
(Hirundo rustica)
Common House Martin
(Delichon urbicum)
Tree Pipit
(Anthus trivialis)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

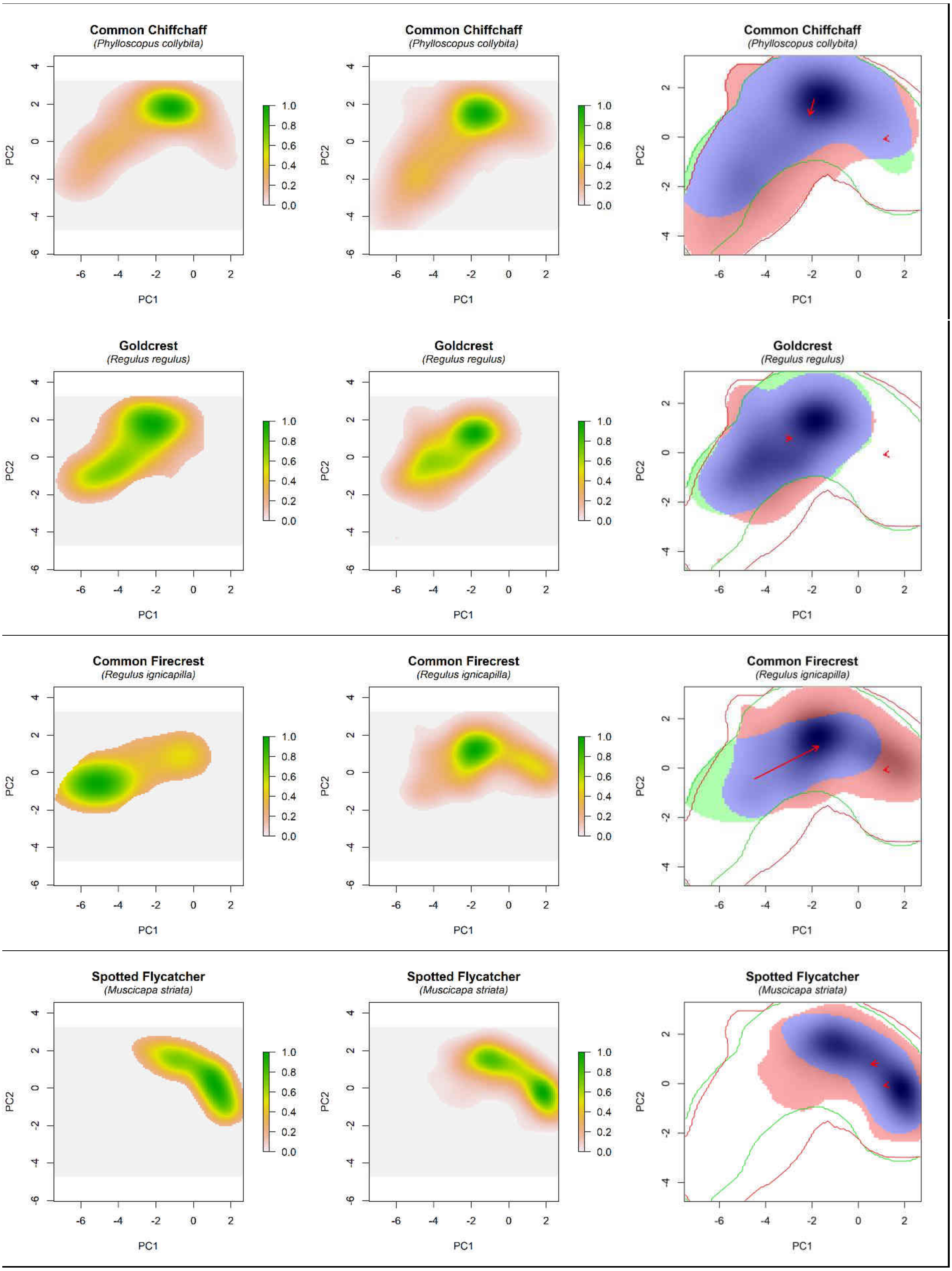

Water Pipit
(Anthus spinoletta)
Western Yellow Wagtail
(Motacilla flava)
Grey Wagtail
(Motacilla cinerea)
White Wagtail
(Motacilla alba)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

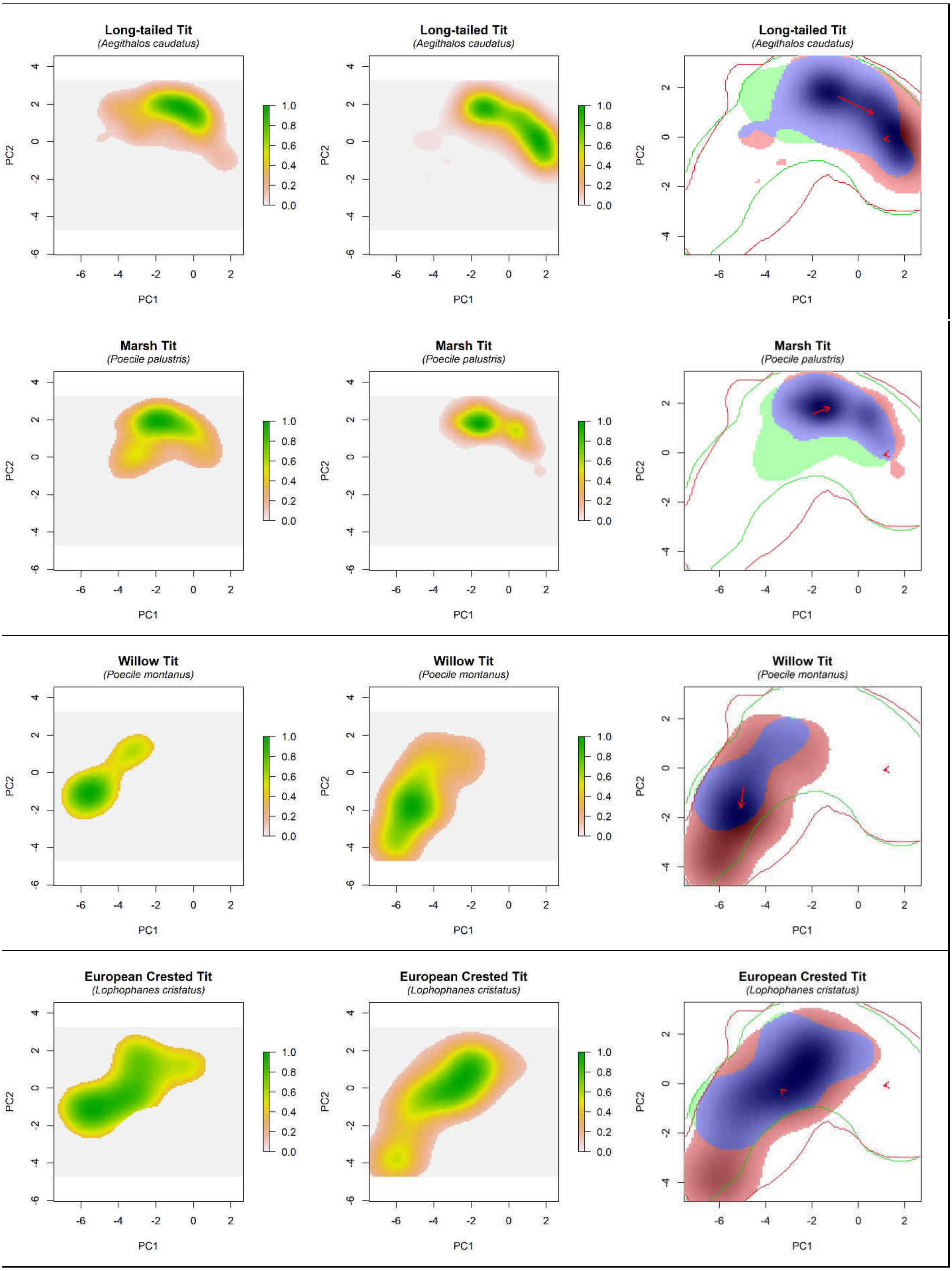

Eurasian Wren
(Troglodytes troglodytes)
Eurasian Wren
(Troglodytes troglodytes)
Eurasian Wren
(Troglodytes troglodytes)
Dunnock
(Prunella modularis)
Dunnock
(Prunella modularis)
Dunnock
(Prunella modularis)
European Robin
(Erithacus rubecula)
European Robin
(Erithacus rubecula)
European Robin
(Erithacus rubecula)
Common Nigthingale
(Luscinia megarhynchos)
Common Nigthingale
(Luscinia megarhynchos)
Common Nigthingale
(Luscinia megarhynchos)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

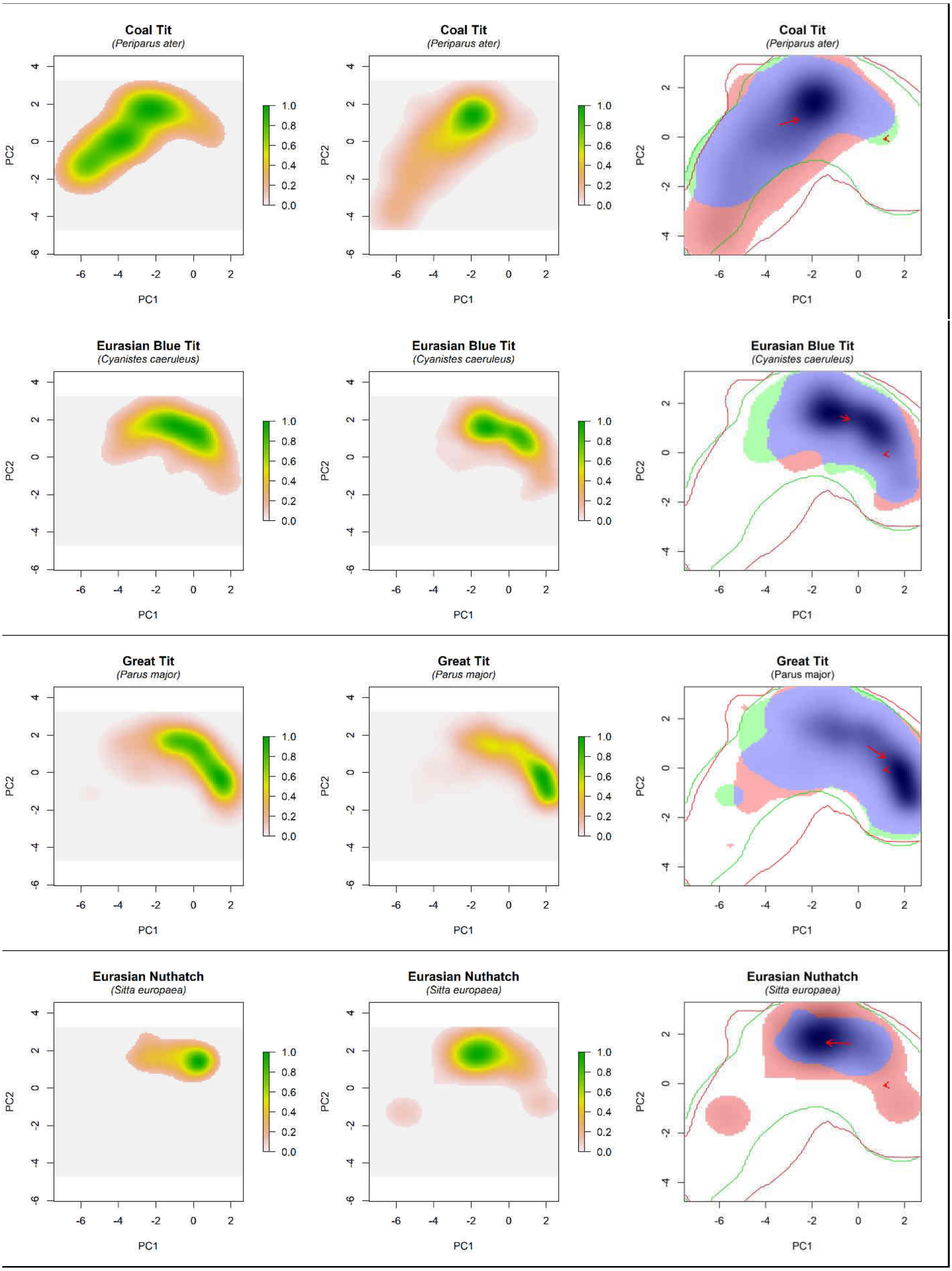

Black Redstart
(Phoenicurus ochruros)
Common Redstart
(Phoenicurus phoenicurus)
European Stonechat
(Saxicola rubicola)
Northern Wheatear
(Oenanthe oenanthe)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

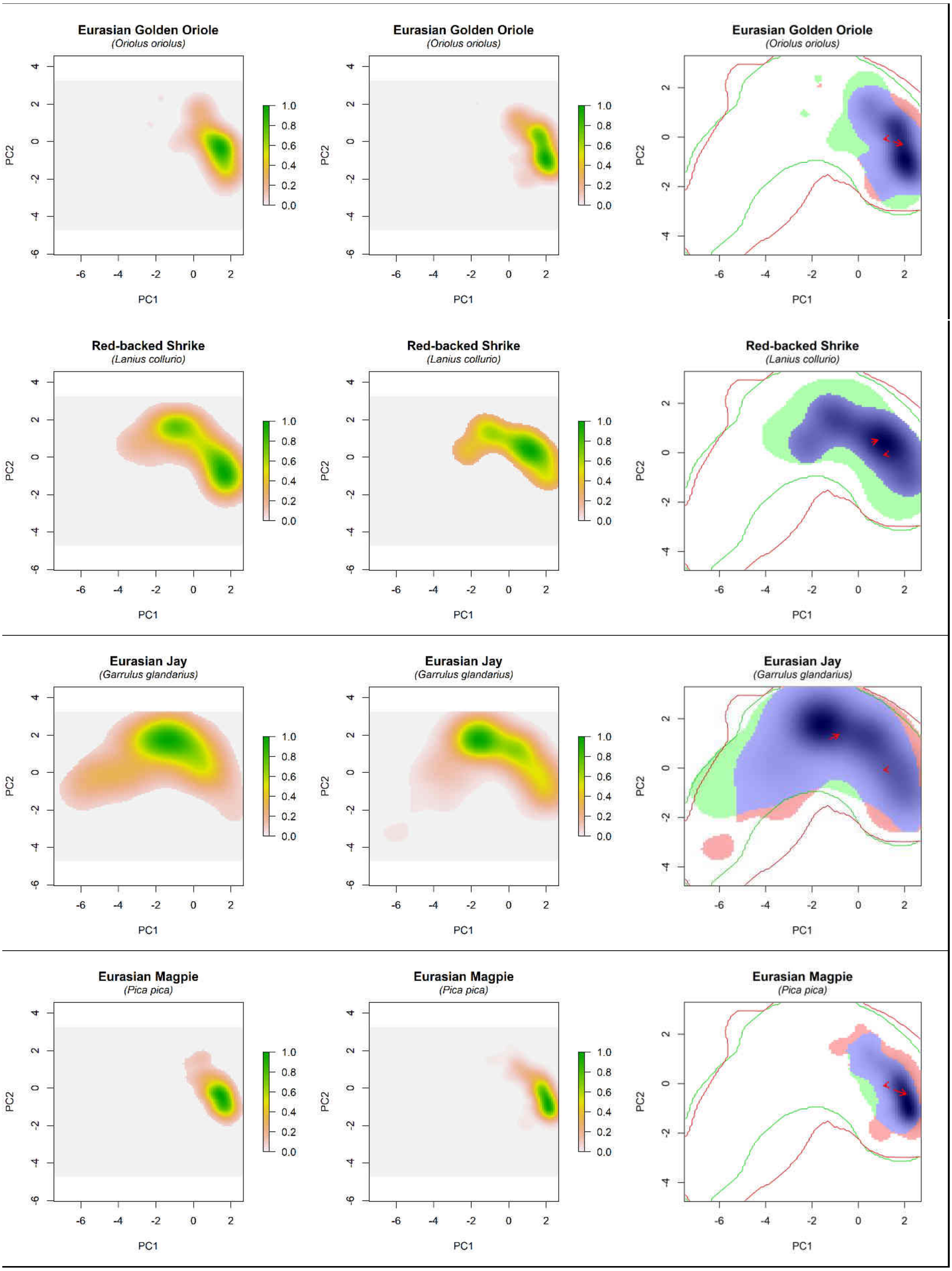

Common Blackbird
(Turdus merula)
Song Thrush
(Turdus philomelos)
Mistle Trush
(Turdus viscivorus)
Cetti's Warbler
(Cettia cetti)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

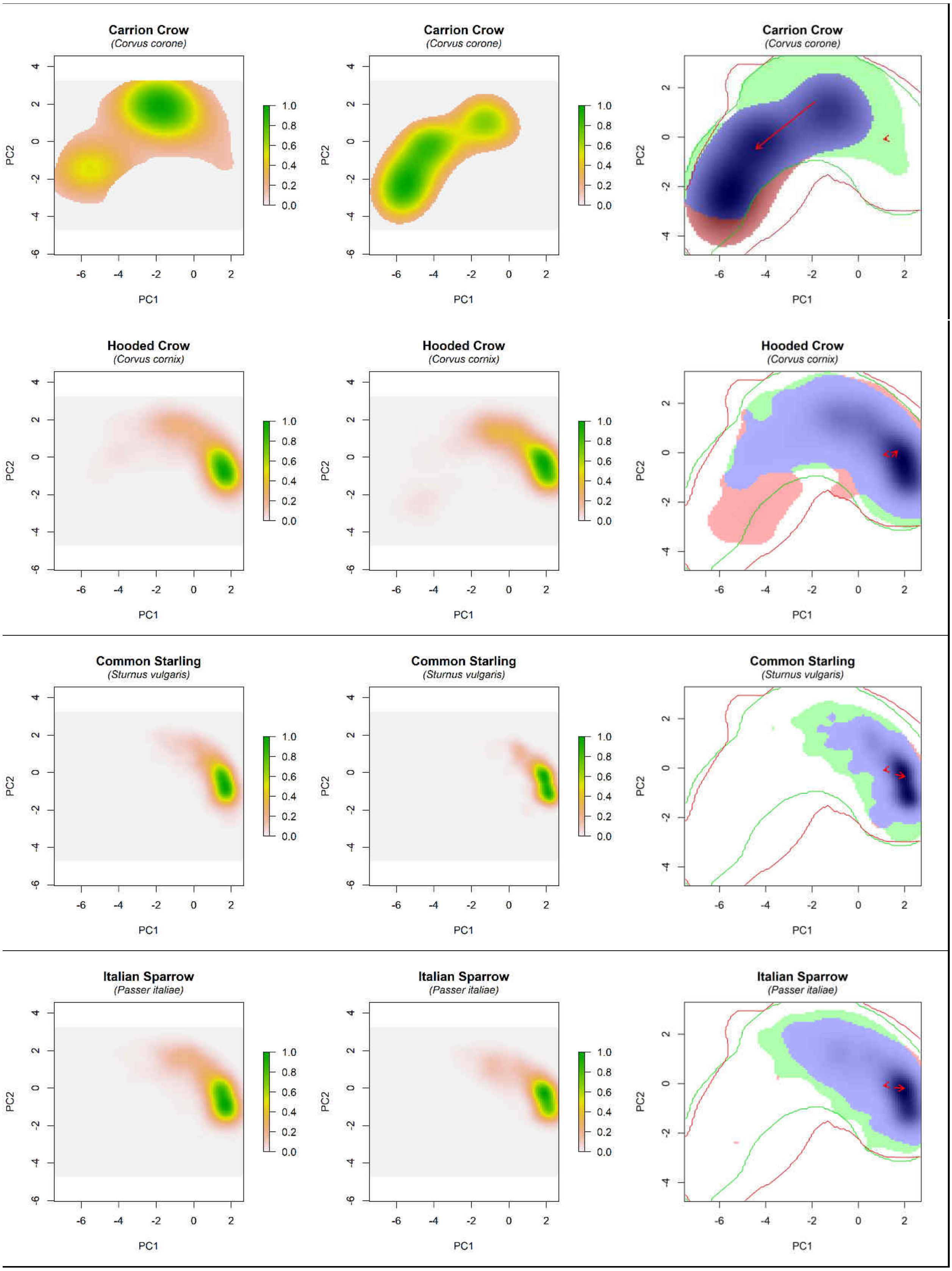

Melodius Warbler
(Hippolais polyglotta)
Melodius Warbler
(Hippolais polyglotta)
Melodius Warbler
(Hippolais polyglotta)
Lesser Whitethroat
(Curruca curruca)
Lesser Whitethroat
(Curruca curruca)
Lesser Whitethroat
(Curruca curruca)
Eurasian Blackcap
(Sylvia atricapilla)
Eurasian Blackcap
(Sylvia atricapilla)
Eurasian Blackcap
(Sylvia atricapilla)
Western Bonelli's Warbler
(Phylloscopus bonelli)
Western Bonelli's Warbler
(Phylloscopus bonelli)
Western Bonelli's Warbler
(Phylloscopus bonelli)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

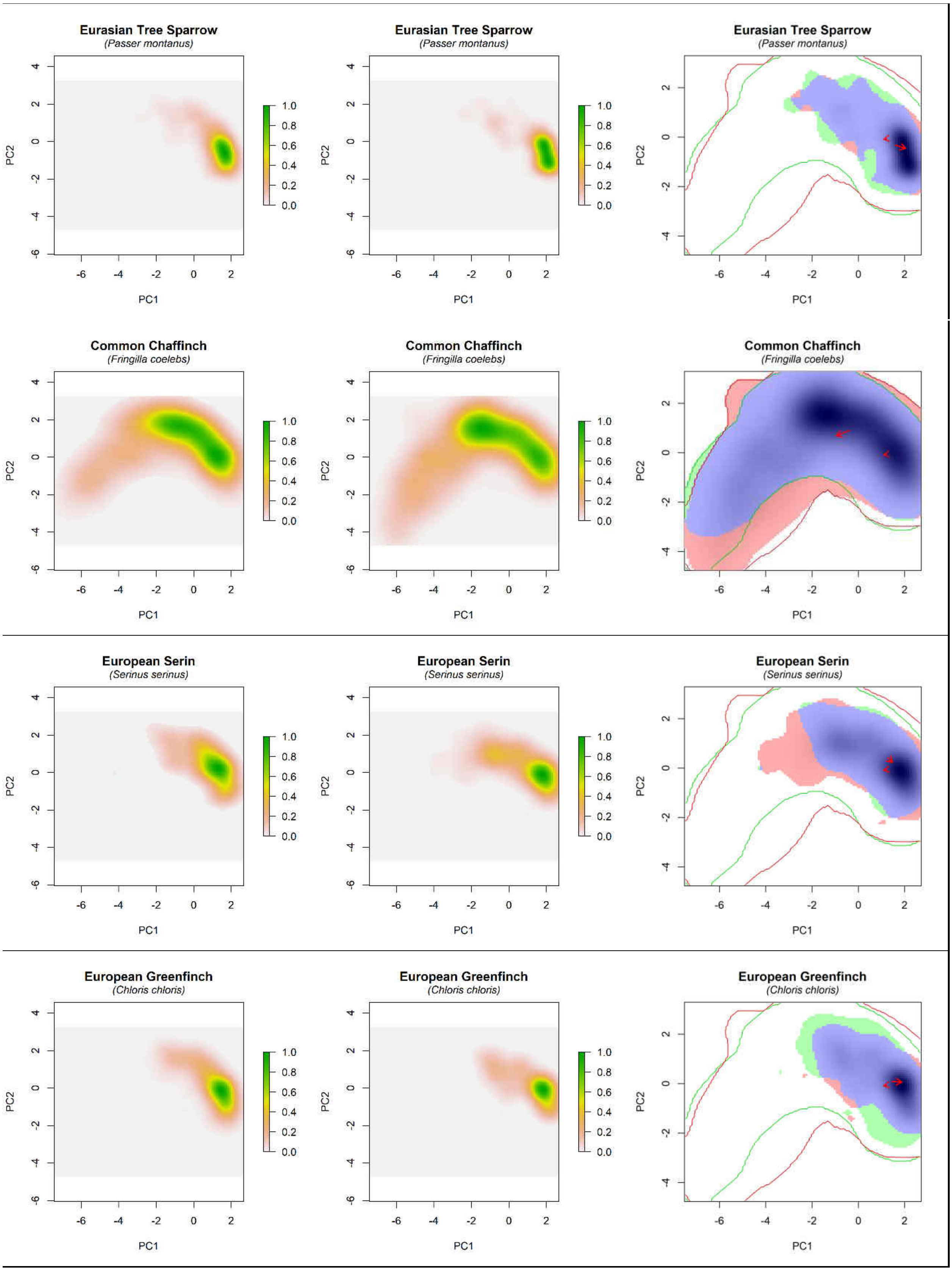

Common Chiffchaff
(Phylloscopus collybita)
Common Chiffchaff
(Phylloscopus collybita)
Common Chiffchaff
(Phylloscopus collybita)
Goldcrest
(Regulus regulus)
Goldcrest
(Regulus regulus)
Goldcrest
(Regulus regulus)
Common Firecrest
(Regulus ignicapilla)
Common Firecrest
(Regulus ignicapilla)
Common Firecrest
(Regulus ignicapilla)
Spotted Flycatcher
(Muscicapa striata)
Spotted Flycatcher
(Muscicapa striata)
Spotted Flycatcher
(Muscicapa striata)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

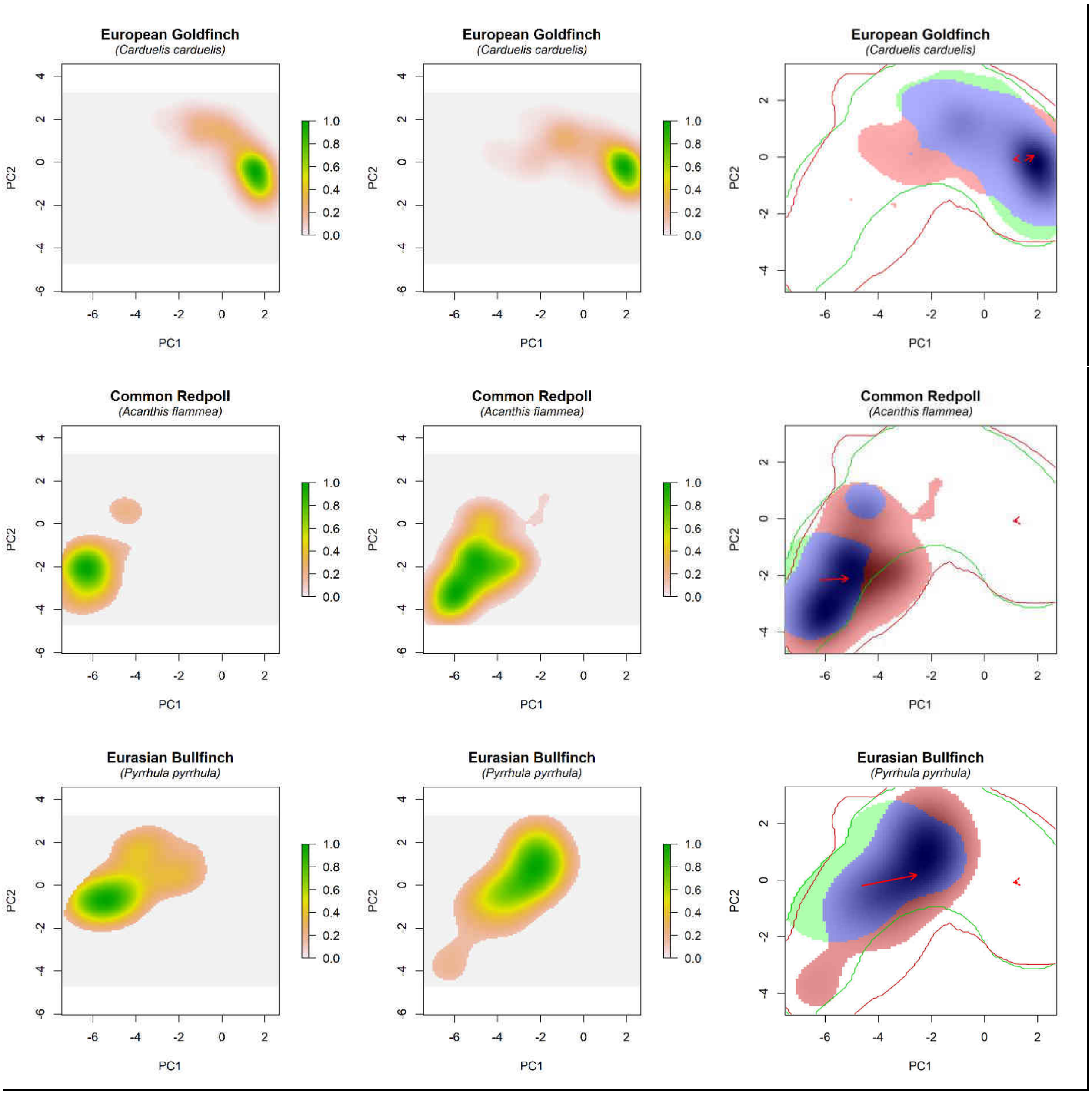

Long-tailed Tit
(Aegithalos caudatus)
Long-tailed Tit
(Aegithalos caudatus)
Long-tailed Tit
(Aegithalos caudatus)
Marsh Tit
(Poecile palustris)
Marsh Tit
(Poecile palustris)
Marsh Tit
(Poecile palustris)
Willow Tit
(Poecile montanus)
Willow Tit
(Poecile montanus)
Willow Tit
(Poecile montanus)
European Crested Tit
(Lophophanes cristatus)
European Crested Tit
(Lophophanes cristatus)
European Crested Tit
(Lophophanes cristatus)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0


Coal Tit
(Periparus ater)
Coal Tit
(Periparus ater)
Coal Tit
(Periparus ater)
Eurasian Blue Tit
(Cyanistes caeruleus)
Eurasian Blue Tit
(Cyanistes caeruleus)
Eurasian Blue Tit
(Cyanistes caeruleus)
Great Tit
(Parus major)
Great Tit
(Parus major)
Great Tit
(Parus major)
Eurasian Nuthatch
(Sitta europaea)
Eurasian Nuthatch
(Sitta europaea)
Eurasian Nuthatch
(Sitta europaea)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0


Eurasian Golden Oriole
(Oriolus oriolus)
Eurasian Golden Oriole
(Oriolus oriolus)
Eurasian Golden Oriole
(Oriolus oriolus)
Red-backed Shrike
(Lanius collurio)
Red-backed Shrike
(Lanius collurio)
Red-backed Shrike
(Lanius collurio)
Eurasian Jay
(Garrulus glandarius)
Eurasian Jay
(Garrulus glandarius)
Eurasian Jay
(Garrulus glandarius)
Eurasian Magpie
(Pica pica)
Eurasian Magpie
(Pica pica)
Eurasian Magpie
(Pica pica)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0


Carrion Crow
(Corvus corone)
Carrion Crow
(Corvus corone)
Carrion Crow
(Corvus corone)
Hooded Crow
(Corvus cornix)
Hooded Crow
(Corvus cornix)
Hooded Crow
(Corvus cornix)
Common Starling
(Sturnus vulgaris)
Common Starling
(Sturnus vulgaris)
Common Starling
(Sturnus vulgaris)
Italian Sparrow
(Passer italiae)
Italian Sparrow
(Passer italiae)
Italian Sparrow
(Passer italiae)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0


Eurasian Tree Sparrow
(Passer montanus)
Eurasian Tree Sparrow
(Passer montanus)
Eurasian Tree Sparrow
(Passer montanus)
Common Chaffinch
(Fringilla coelebs)
Common Chaffinch
(Fringilla coelebs)
Common Chaffinch
(Fringilla coelebs)
European Serin
(Serinus serinus)
European Serin
(Serinus serinus)
European Serin
(Serinus serinus)
European Greenfinch
(Chloris chloris)
European Greenfinch
(Chloris chloris)
European Greenfinch
(Chloris chloris)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0


European Goldfinch
(Carduelis carduelis)
Common Redpoll
(Acanthis flammea)
Eurasian Bullfinch
(Pyrrhula pyrrhula)
PC1
PC2
-6
-4
-2
0
2
4
1.0
0.8
0.6
0.4
0.2
0.0

S4.8

Schoener's D, expansion and unfilling index for each species. Species are presented with the common name (Gill et al., 2022) and following the taxonomic order.

Species	Schoener's D	Expansion	Unfilling
Black-crowned Night Heron	0.52	0.05	0.22
Little Egret	0.48	0.18	0.09
Grey Heron	0.54	0.10	0.05
Mallard	0.29	0.01	0.30
Black Kite	0.50	0.00	0.23
Common Buzzard	0.60	0.12	0.08
Common Kestrel	0.25	0.02	0.28
Common Quail	0.61	0.00	0.26
Common Pheasant	0.60	0.01	0.13
Common Moohren	0.56	0.00	0.15
Feral Pigeon	0.72	0.01	0.05
Common Wood Pigeon	0.71	0.04	0.01
Eurasian Collared Dove	0.73	0.01	0.05
European Turtle Dove	0.62	0.01	0.12
Common Cuckoo	0.74	0.00	0.01
Common Swift	0.71	0.03	0.02
Eurasian Wryneck	0.49	0.00	0.26
European Green Woodpecker	0.41	0.31	0.00
Great Spotted Woodpecker	0.59	0.07	0.01
Eurasian Skylark	0.14	0.41	0.00
Eurasian Crag Martin	0.60	0.06	0.11
Barn Swallow	0.59	0.00	0.12
Common House Martin	0.66	0.08	0.01
Tree Pipit	0.57	0.17	0.05
Water Pipit	0.23	0.54	0.00
Western Yellow Wagtail	0.49	0.01	0.22
Grey Wagtail	0.61	0.03	0.01
White Wagtail	0.63	0.05	0.07
Eurasian Wren	0.71	0.01	0.01
Dunnock	0.27	0.65	0.00
European Robin	0.81	0.06	0.02
Common Nigthingale	0.61	0.00	0.12
Black Redstart	0.54	0.05	0.01
Common Redstart	0.63	0.04	0.04
European Stonechat	0.58	0.06	0.08

S4.8. (cont.)

Northern Wheatear	0.44	0.09	0.09
Common Blackbird	0.76	0.02	0.00
Song Thrush	0.21	0.66	0.00
Mistle Trush	0.51	0.10	0.06
Cetti's Warbler	0.68	0.01	0.12
Melodius Warbler	0.40	0.00	0.32
Lesser Whitethroat	0.56	0.09	0.17
Eurasian Blackcap	0.79	0.01	0.01
Western Bonelli's Warbler	0.47	0.14	0.15
Common Chiffchaff	0.63	0.06	0.01
Goldcrest	0.71	0.00	0.04
Common Firecrest	0.33	0.29	0.19
Spotted Flycatcher	0.65	0.11	0.00
Long-tailed Tit	0.59	0.14	0.08
Marsh Tit	0.45	0.04	0.28
Willow Tit	0.38	0.47	0.00
European Crested Tit	0.46	0.26	0.08
Coal Tit	0.61	0.09	0.06
Eurasian Blue Tit	0.68	0.02	0.06
Great Tit	0.75	0.01	0.02
Eurasian Nuthatch	0.46	0.25	0.00
Eurasian Golden Oriole	0.57	0.02	0.08
Red-backed Shrike	0.57	0.00	0.23
Eurasian Jay	0.60	0.02	0.07
Eurasian Magpie	0.61	0.08	0.05
Carrion Crow	0.47	0.06	0.30
Hooded Crow	0.69	0.02	0.01
Common Starling	0.63	0.00	0.06
Italian Sparrow	0.70	0.00	0.03
Eurasian Tree Sparrow	0.67	0.01	0.03
Common Chaffinch	0.70	0.02	0.00
European Serin	0.73	0.05	0.01
European Greenfinch	0.65	0.01	0.08
European Goldfinch	0.60	0.06	0.02
Common Redpoll	0.48	0.27	0.03
Eurasian Bullfinch	0.40	0.21	0.23

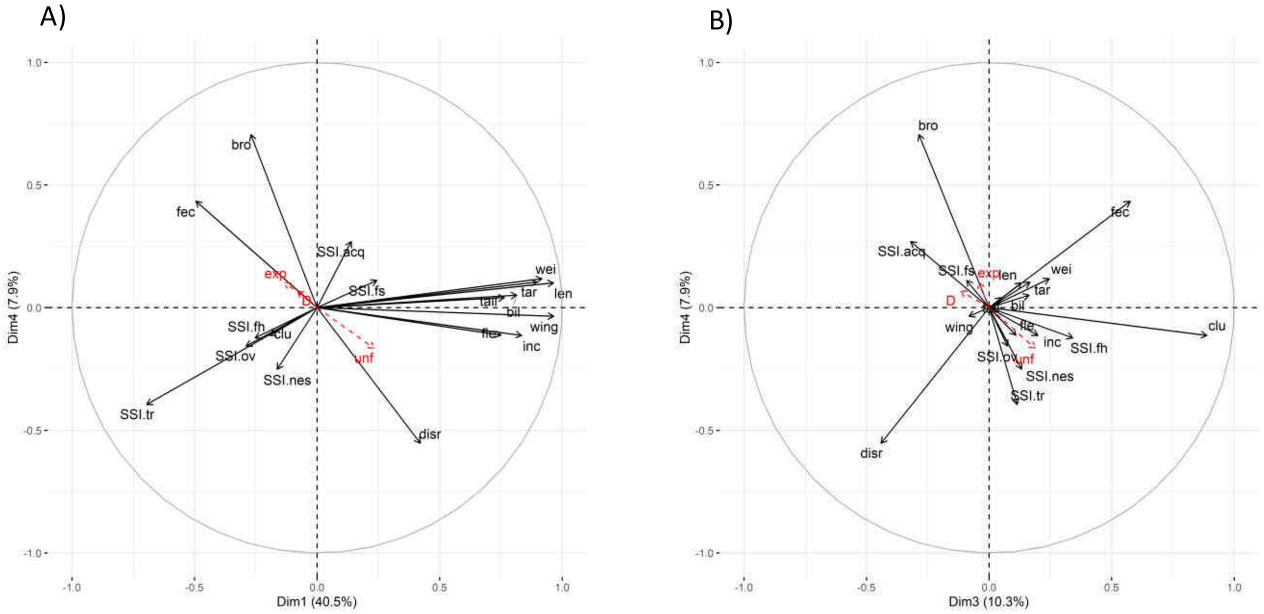
S4.9

Coordinates for the 18 continuous species traits and for niche metrics respect to the four retained PCA-axes (trait space). See S4.2 for traits' abbreviations.

Traits	Dim1	Dim2	Dim3	Dim4
len	0.97	0.06	0.13	0.10
wing	0.97	0.09	−0.08	−0.04
tail	0.76	0.03	0.05	0.04
bil	0.81	−0.10	0.16	0.05
tar	0.90	−0.01	0.17	0.10
wei	0.92	0.08	0.25	0.12
clu	−0.19	−0.15	0.89	−0.11
bro	−0.27	0.43	−0.29	0.71
fec	−0.49	0.19	0.58	0.43
inc	0.83	0.17	0.20	−0.11
fle	0.75	0.24	0.11	−0.11
disr	0.42	0.24	−0.44	−0.55
SSI.fh	−0.25	0.75	0.34	−0.12
SSI.acq	0.14	0.58	−0.32	0.27
SSI.nes	−0.16	0.85	0.13	−0.25
SSI.fs	0.24	0.77	−0.09	0.11
SSI.tr	−0.70	0.08	0.11	−0.39
SSI.ov	−0.29	0.92	0.08	−0.16
Niche metrics	**Dim1**	**Dim2**	**Dim3**	**Dim4**
Schoener's D	−0.08	0.10	−0.12	0.07
Expansion	−0.13	−0.06	−0.04	0.10
Unfilling	0.23	−0.04	0.19	−0.17

S4.10

Biplots between niche metrics and PCA-axes (trait space). A) Dim1-Dim4. B) Dim3-Dim4. For traits' abbreviations see S4.2. Dashed red arrows indicate the intensity of correlation for the niche metrics in the PCA space. D = Schoener's D; exp = expansion index; unf = unfilling index.



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Chapter 5

Extreme climatic events have widespread effects on UK breeding bird populations

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Submitted manuscript

Abstract

Climate change remains one of the most important challenges for biodiversity conservation. Most research effort had been focused on ecological and biological effects of long-term average change in climate, but recent studies highlighted that extreme climatic events can also lead to widespread and mainly negative effects across all taxa and ecological levels. Here, using generalised additive models (GAMs), we assessed the effects of extreme climatic events on relative abundance for 100 resident bird species over large spatial and temporal scales using the UK Breeding Bird Survey, spanning over 25 years, and identified the most sensitive species to extreme climatic events. We used five climatic indices computed at 1-km spatial resolution as proxies of extreme climatic events during the winter or breeding season, then we spatially linked such indices to bird counts with both one and two-year time lags, obtaining 12 climatic variables overall. Results demonstrated widespread and significant effects of extreme climatic events on bird relative abundances, with both common one-year and two-year lagged effects. Winter frost days, summer days during the breeding season and the simple precipitation intensity index during the breeding season showed broad negative effects, while the diurnal temperature range in both seasons and dry days during the breeding season showed more diversified effects across species, with a prevalence of positive effects. A large proportion of species responded to extreme climatic events with changes in local relative abundance, suggesting the use of such species for future studies in this research field. Extreme climatic events could exacerbate biological responses of avian populations placing new challenges for their conservation but also for biodiversity and ecological processes in general. Understanding both direct and indirect mechanisms through which extreme climatic events can affect wild populations, as well as effects arising from interactions with other factors (e.g. land-use changes) should be a primary goal for a conservation perspective.

5.1. Introduction

Climate change has been recognised as one of the major threats for biodiversity and species conservation (Bellard et al., 2012; Urban et al., 2015; Wiens, 2016; Martay et al., 2017; Manes et al., 2021). Biological responses can include several related outcomes (Maxwell et al., 2019), such as shift in distribution (Parmesan et al., 1999; Hickling et al., 2006; Chen et al., 2011; Auer & King, 2014), changes in population size (Cruz-Mcdonnell et al., 2016; Stephens et al., 2016), variations in phenology (Thackeray et al., 2016), behaviour (Saino et al., 2011), and fitness (Sanz et al., 2003). Most research effort had been focused on ecological and biological effects of long-term average change in climate, but in the last two decades extreme climatic events (e.g. extreme temperatures, heavy rainfall, prolonged drought; hereafter ECEs) have attracted increasing concern among ecologists (Bailey & van de Pol, 2016). Indeed, some studies pointed out that ECEs can lead to greater biological consequences compared to changes in climatic means (Maron et al., 2015; Bailey & van de Pol, 2016; Gardner et al., 2017; Harris et al., 2018; Marcelino et al., 2020), with widespread negative effects across all taxa and ecological levels (Maxwell et al., 2019). ECEs are expected to increase in frequency in the near future (IPCC, 2013), stressing the importance of assessing their impact on ecological systems and biodiversity. However, defining ECEs and evaluating the effects on biological systems is still a challenge for ecologists (Bailey & van de Pol, 2016). Using climatic indices as measure of ECEs has been shown to be informative to assess biological responses in wild populations (Morrison et al., 2016; Cady et al., 2019). Some of these indices are the result of the work of joint scientific committees, such as the Expert Team on Climate Change and Detection and Indices (etccdi.pacificclimate.org/index.shtml), or the European Climate Assessment & Dataset project (https://www.ecad.eu). Furthermore, species might display a temporal delay in biological responses to climate change (Thompson & Ollason, 2001; Janke et al., 2017; Saunders et al., 2021), and overlooking such delays could mask the real effect size of ECEs. The assessment of the effects of ECEs at large spatial scale over long time is a key challenge. Moreover, investigating multi-species responses is crucial to evaluate the impacts of ECEs on communities (Palmer et al., 2017), and to shed light on the main climatic drivers affecting populations and thus providing instructions for effective conservation policies. In this context, birds represent a suitable model taxon for investigating the effects of ECEs (Cohen et al., 2020), other than to be useful for planning environmental policies aimed at the conservation of biodiversity (Morelli et al., 2021; Oettel & Lapin, 2021; Santangeli & Girardello, 2021; Virkkala et al., 2022). They are sensitive to climate change (Pautasso, 2012; Chamberlain et al., 2016) and could be affected by ECEs in several ways.

ECEs can alter the viability of local populations (Fromant et al., 2021; McKechnie et al., 2021), provoke phenotypic selection (Acker et al., 2021), influence reproductive success (Cruz-McDonnell et al., 2016; Colón et al., 2017) or population growth (Morrison et al., 2016), and affect species' distribution (Cohen et al., 2020; Lavoie et al., 2021). Furthermore, the existence of large-scale long-term monitoring programs for birds (e.g. the North American Breeding Bird Survey [Sauer et al., 2017]; the PanEuropean Common Breeding Monitoring Survey [PECBMS, 2022]) represents an important source of structured data to assess responses over large spatial and temporal scales.

Using the UK Breeding Bird Survey (BBS; Harris et al., 2022), the national long-term monitoring program of common breeding birds in the United Kingdom (western Europe, 59°-50° N, 8°O-2°E), we performed a multi-species analysis aimed at: i) assessing the effect of ECEs (both one and two-years lagged effects) on relative abundance of bird populations (i.e. counts), ii) evaluating whether responses to ECEs are similar across species, and iii) identifying the most sensitive species to ECEs.

5.2. Materials and methods

5.2.1. Bird data

Bird data were derived from the UK BBS, which employs a stratified random sampling protocol where 1-km squares (fixed sampling units) are surveyed following a line-transect method (Gregory et al., 2004) along two 1-km transects. Squares are visited twice per year, once in the early breeding season (April to early-May) and again in the late breading season (late-May to June). For this study, we used the maximum of the two seasonal counts as a measure of relative abundance (Morrison et al., 2016). We used data collected from 1994 to 2019, excluding those obtained in 2001 when an outbreak of foot-and-mouth disease restricted access to many areas (Risely et al., 2013). Since the survey began in 1994, the number of squares surveyed has increased from 1,570 to more than 4,000 in 2019 (n = 69,163, mean = 2,767, standard deviation = 741).

We restricted the analyses to species having full or partial resident populations in the UK (McInerny et al., 2018) with a frequency of occurrence ≥ 2.5% throughout the study area and the entire time series.

Resident birds, spending the whole life cycle (both winter and breeding season) in the same region, are supposed to be influenced by local environmental conditions throughout the full year, although limited movements may occur in local populations from winter to breeding season, and resident birds could be indirectly affected by climatic conditions in non-breeding areas. We excluded gulls (genus *Larus* and the Black-headed Gull *Chroicocephalus ridibundus*) from the analyses because of the presence of an unknown number of non-breeding, migratory and off-duty individuals breeding at colonies many km from the BBS squares during the time of survey and over the whole study area. Data for the Feral Pigeon (*Columba livia*) only included domestic populations established in the wild, excluding the Rock Dove (*Columba livia*) populations. Furthermore, we warn some limitations in BBS sampling method for nocturnal species included in the analyses (the Tawny Owl *Strix aluco* and the Western Barn Owl *Tyto alba*), as well as the fact that counts for the Great Cormorant (*Phalacrocorax carbo*), the Grey Heron (*Ardea cinerea*), and the Little Egret (*Egretta garzetta*) may contain a proportion of individuals away from breeding sites. Finally, counts for the Eurasian Oystercatcher (*Haematopus ostralegus*), the Northern Lapwing (*Vanellus vanellus*), the Eurasian Curlew (*Numenius arquata*), the Common Snipe (*Gallinago gallinago*), the Common Redshank (*Tringa totanus*), and the European Golden Plover (*Pluvialis apricaria*) may include individuals from non-breeding flocks.

5.2.2. Extreme climatic events (ECEs)

As proxies of ECEs we used five climatic indices, four of which belong to the suite of 27 core indices developed by the Expert Team on Climate Change Detection and Indices (Karl et al., 1999; Peterson, 2001; see Table 5.1 for definitions). Three indices (summer days: SU; frost days: FD; daily temperature range: DTR) are temperature-based (T-based), while two (simple precipitation intensity index: SDII; dry days: DD) are rainfall-based (R-based). We computed these indices over two distinct periods: winter season (1st December-28/29th February) and breeding season (1st April-31th July) (Oedekoven et al., 2017). Specifically, SU, SDII, DD were calculated over the breeding season, while FD was calculated over the winter. DTR was computed separately over both the breeding and the winter seasons. Bird data in the year *t* were associated with the index of the preceding winter or breeding season in the year *t-1*, and to those of the two-previous year *t-2* to investigate potential lagged effects.

Table 5.1. Climatic indices used as proxies of ECEs. TN = daily minimum temperature; TX = daily maximum temperature; RR = daily amount of precipitation. W = winter, B = breeding.

Index	Index Name	Definition	Unit	Season	Source
FD0	Frost days	Count of days when TN < 0 °C	Day	W	Klein et al., 2009; ETCCDI, 2022
SU25	Summer days	Count of day when TX > 25 °C	Day	B	Klein et al., 2009; ETCCDI, 2022
DTR	Daily temperature range	Mean difference between daily TX and TN	°C	W; B	ETCCDI, 2022
SDII	Simple precipitation intensity index	Amount of precipitation (RR) on wet days (RR ≥ 1)	mm/day	B	Brunetti et al., 2001; ETCCDI, 2022
DD	Dry days	Count of days when RR < 1	Day	B	Reig-Gracia et al., 2021

Climatic indices (see Figure 5.1 as example for SDII) were computed starting from daily maximum and minimum temperature (TX and TN, respectively) and daily precipitation (RR) at 1 × 1 km gridded resolution using climatic data compiled by MetOffice and available on CEDA archive as netCDF format (Hollis et al., 2021, downloadable at https://archive.ceda.ac.uk/). Indices were computed in R software (R Core Development Team, 2020) using the package *raster* (Hijmans, 2021), then spatially and temporally matched with bird data through ArcMap 10.7.1 (ESRI, 2019). Long-term trends between 1961 and 2018 for each index showed statistically significant increasing trends for both breeding and winter DTR and SU25, increasing but non-statistically significant trend for SDII, stable trajectory for DD, and a statistically significant decrease for FD0. However, assessment of trends for the indices during the period 1992-2018, i.e. years linked to bird data, showed stable trajectories for all of them (see S5.1A-F in Supplementary materials for details).

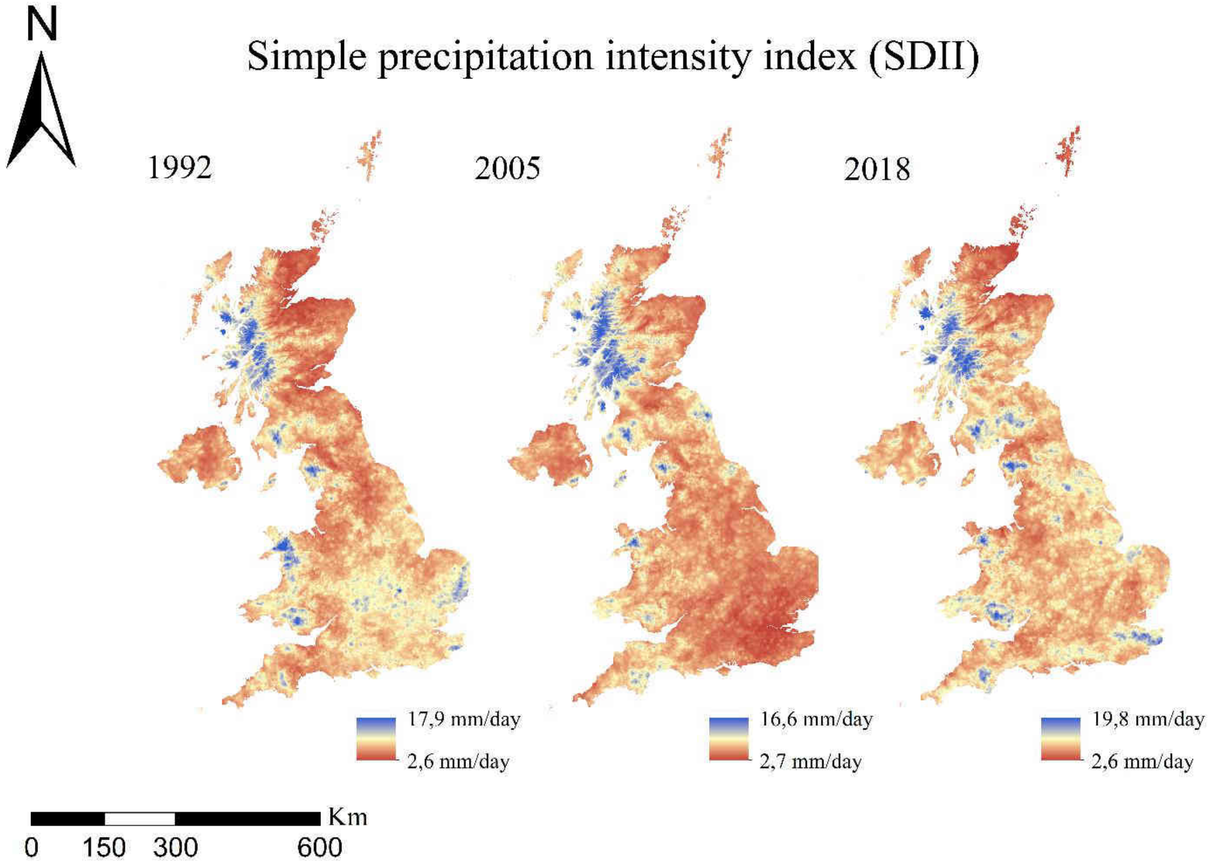


Figure 5.1. Simple precipitation intensity index (SDII; mm/day) for three distinct years across the UK.

5.2.3. Modelling framework and statistical analyses

We fitted generalised additive models (GAMs, Hasti & Tibshirani, 1986; Wood, 2017) using the package *mgcv* (Wood, 2021) in R (R Core Development Team, 2020). GAMs describe both linear and non-linear relationships between the response variable and predictors through a data-driven approach using splines (Wood, 2017). To control for potential confounding effects that can affect species abundance, we included elevation (m), habitat cover (%; nine classes), and a space-time smooth resulting from the interaction among northing, easting and year of survey that also accounted for potential spatial and temporal autocorrelation in the observed counts (Harrison et al., 2014; Oedekoven et al., 2017) (see S5.2 in Supplementary materials for details on covariates). For each species, to account for overdispersion in count data (i.e. the variance is larger than the mean, Zuur et al., 2009), we fitted two models assuming either a Poisson or a negative binomial distribution for the count data and using the Akaike Information Criterion (AIC; Burnham and Anderson, 2002) to select the best model (Virgili et al., 2017; Tirozzi et al., 2022a and *Chapter 2*).

The model can be expressed as:

$$\log(E[Y_i]) = f_s(northing, easting, year) + f_s(elev) + \sum_{h=1}^{k} f_s\,(Hab_h) + \sum_{c=1}^{n} f_s(C_c)$$

where $\log(E[Y_i])$ is the expected count for the species *i* on the predictors log-scale, f_s are smooth functions, *Hab* represents the habitat cover for each habitat *h*, and *C* each climatic variables *c* of interest (12 climatic variables overall). Before running the models, we checked for collinearity among explanatory variables (absolute value for Pearson coefficient > 0.7; Dormann et al., 2013; see S5.3 in Supplementary materials). Furthermore, the smooth estimation procedure in *mgcv* guarantees the reliability of results even in presence of concurvity (Wood, 2008). For all the explanatory variables, we used the thin plate regression spline as method of smoothing (Wood, 2003, 2017) and penalised the smoothing process through the shrinkage method in order to avoid overfitting and exclude non-significant variables by decreasing the level of the estimated degrees of freedom close to zero (Wood, 2017). To guarantee a reasonable ecological interpretation, we set the degree of freedoms (edf) at three, for each variable. The space-time smooth was handled as a full tensor product applying the shrinkage and setting the edf for each interacting variable at three (i.e. overall edf = 27). We used the restricted maximum likelihood (REML) as the smoothing parameter estimation method (Wood, 2011, 2017). Smoothed effects of the climatic indices on log-counts were classified in the following categories: n.s. = non-significant effect (p-value > 0.05; Wood, 2017); positive = monotonic and increasing functions also including asymptotic functions; negative = monotonic decreasing functions also including asymptotic functions; decreasing-increasing = functions showing a decrease first and then an increase (e.g. parabola with upward concavity); increasing-decreasing = functions showing an increase first and then a decrease (e.g. parabola with downward concavity). Effects for smooth functions with p-value ≤ 0.05 were assessed through a visual inspection and by computing their first derivative using the function *derivatives* in the R package *gratia* (Simpson, 2022). Moreover, uncertainty around the estimated smooths and the uncertainty around the first derivatives were considered to better characterise the relationship. We specified, “high uncertainty” when the confidence interval around the first derivative included zero over the whole function’s domain, and “moderate uncertainty” when the confidence interval around the first derivative included zero for a subset of the domain (see S5.4 in Supplementary materials). Furthermore, we identified the species that most responded to ECEs (considering the whole set of 12 indices, *t-1* and *t-2* separately, winter T-based, breeding T-based, and R-based) as those significantly affected (p-value of the smooth ≤ 0.05) by at least two-thirds of the indices on the total. For these species, the prevalent type of relationship for each group of indices was assigned to a specific category among the four aforementioned ones (positive, negative, decreasing-increasing, increasing-decreasing) when at least 50% of all statistically significant effects were included in the specific category. In cases of equal split for the type of relationship (i.e. 50% of the effects shared between two categories), both of them were assigned.

5.3. Results

We analysed 100 bird species overall. For all of them, based on AIC, negative binomial GAMs outperformed Poisson GAMs, revealing the presence of overdispersion in count data for all the species (estimated overdispersion parameter θ in negative binomial GAMs: mean = 0.568, range = 0.002 - 3.323) (see S5.5 in Supplementary materials). The explained deviance (median = 32.61%) ranged from 4.33% for the Eurasian Sparrowhawk (*Accipiter nisus*) to 88.42% for the Rose-ringed Parakeet (*Psittacula krameri*) (see S5.6 in Supplementary materials). All species were affected (p-value of the estimated smooth ≤ 0.05) by one climatic variable at least (median number of statistically significant effects of the climatic variables for each species = 8, range = 1 - 12). In the case of statistically significant effects, negative effects (e.g. Figure 5.2A) prevailed for frost days (FD0), summer days (SU25), and the simple precipitation intensity index (SDII), while positive effects (e.g. Figure 5.2B) were mainly found for the diurnal temperature range (DTR) in both seasons and dry days (DD) (Figure 5.3, S5.7 in Supplementary materials). Decreasing-increasing effects (e.g. Figure 5.2C) were rarer, while increasing-decreasing effects (e.g. Figure 5.2D) were mainly detected for DTR (in both seasons) and DD (Figure 5.3, S5.7).

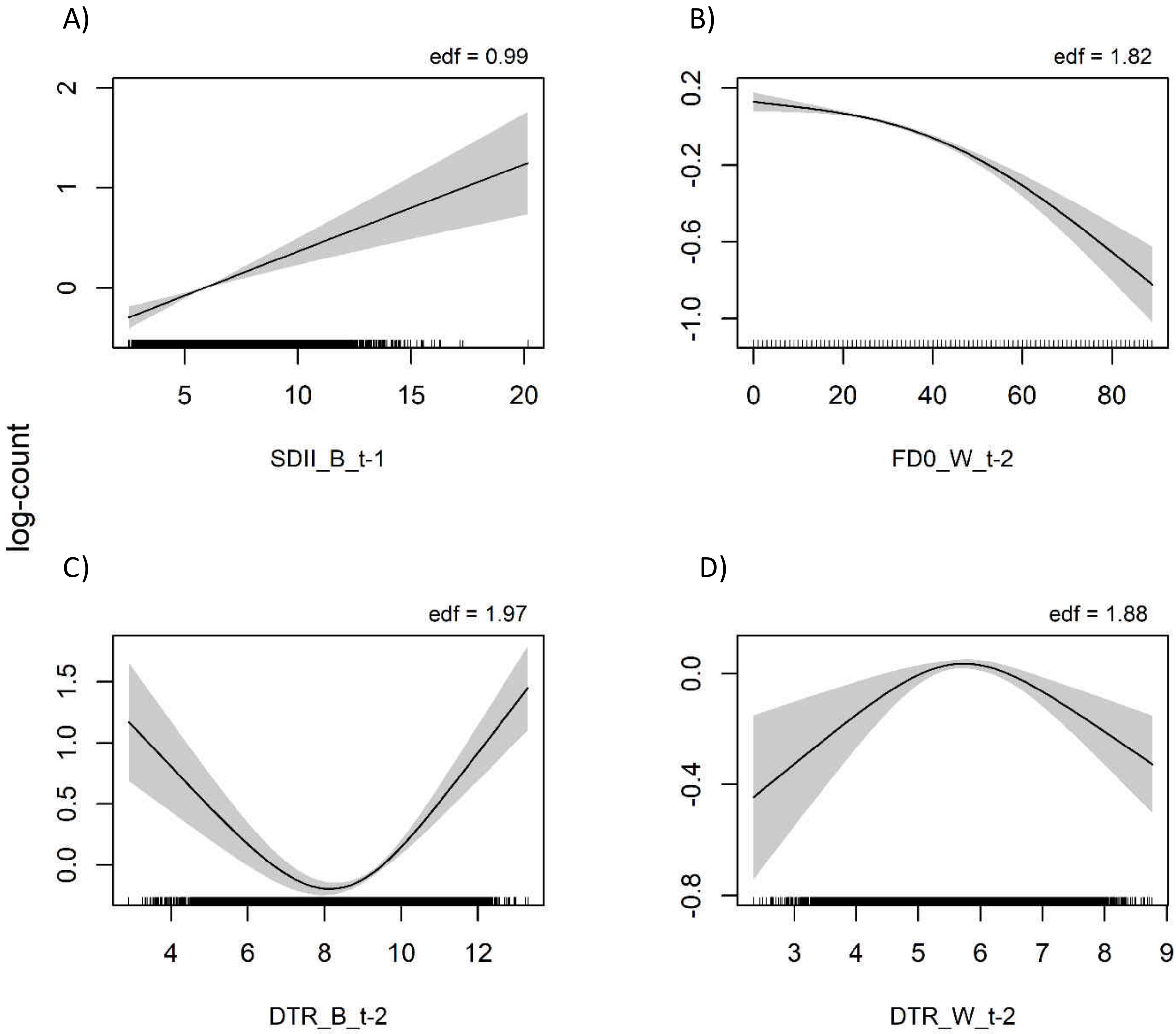


Figure 5.2. Examples of the four types of response curves in relation to the climatic indices. Partial effects plots describe the relationship between log-count (y-axis) and climatic indices net of the effects of the other explanatory variables included in the model. Edf (p-value < 0.001 in the showed cases) represents the estimated degree of freedom of the smooth function. Rugs on the x-axis represent the distribution of values of the explanatory variable. The grey area represents the 95% confidence interval for the regression line. A positive effect of the simple precipitation intensity index (SDII) is shown for the Eurasian Siskin (*Spinus spinus*) in A), a negative effect of frost days (FD0) for the White Wagtail (*Motacilla alba*) in B), a decreasing-increasing effect of the diurnal temperature range (DTR) for the Northern Raven (*Corvus corax*) in C), and an increasing-decreasing effect of DTR for the Eurasian Bullfinch (*Pyrrhula pyrrhula*) in D). After the acronym of the climatic index, "B" indicates the breading season, "W" the winter season, "t-1" and "t-2" the year used for the association between the climatic index and bird counts.

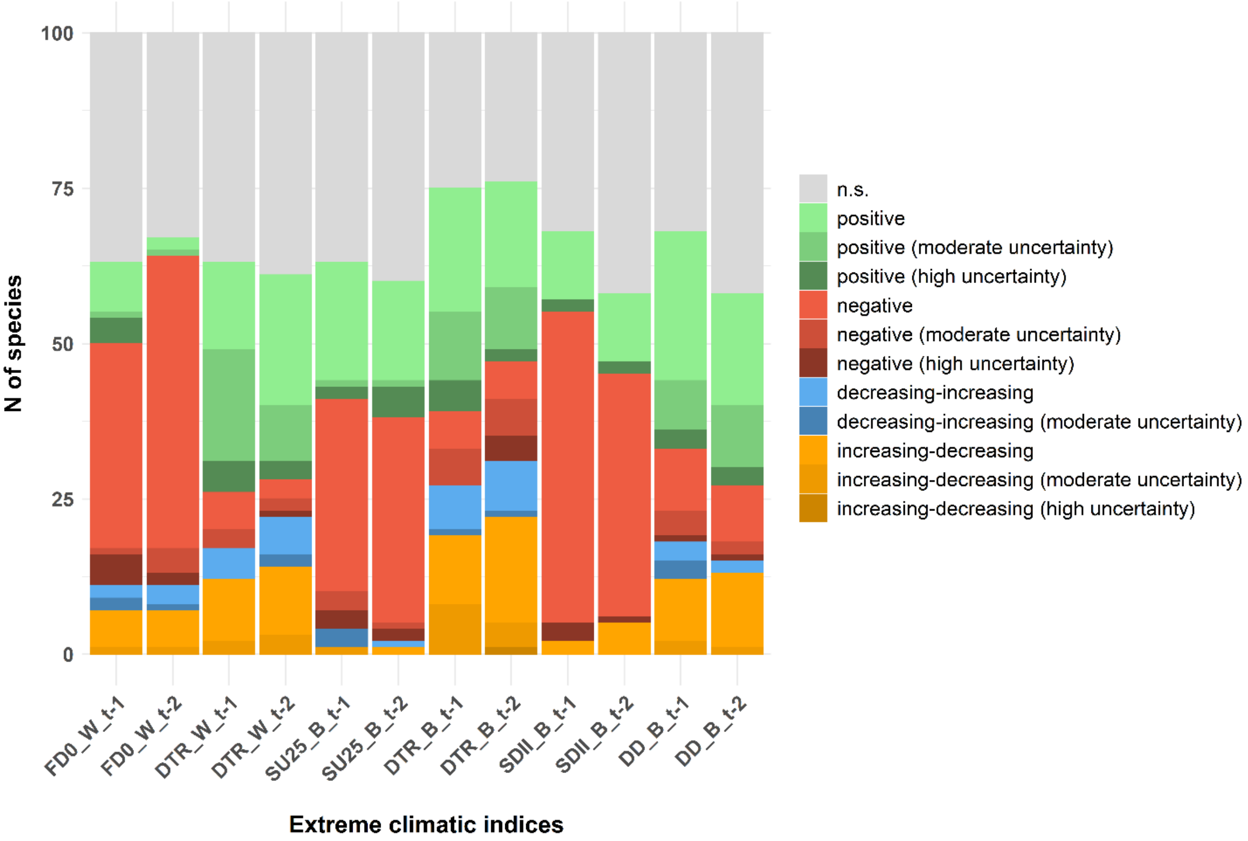


Figure 5.3. Bar chart showing the repartition of the type of effects for the climatic indices across the 100 species under study. FD0 =frost days, DTR = diurnal temperature range, SU25 = summer days, SDII = simple precipitation intensity index, DD = dry days. W = winter season, B = breading season; t-1 and t-2 indicate the year used for the association between the climatic indices and the bird counts. See Table 5.1 for details on the climatic indices. N.s. (in grey) indicates that the effect was not statistically significant. Statistically significant effects are classified into four main categories (positive: green, negative: red, decreasing-increasing: blue, increasing-decreasing: orange, see Section 5.2.3 for the explanation), and within the categories the proportion of species showing a significant degree of uncertainty (from moderate to high) are reported (see Section 5.2.3 and S5.4 for details).

Extreme climatic indices widely influenced (p-value ≤ 0.05) the expected counts (log-scale) both at time *t-1* and *t-2* (number of species affected at *t-1*: median = 65.5, range = 63 - 75; *t*-2: median: 60.5, range = 58 - 76). Two-year lagged effects (indices at time *t-2*) affected a similar number of species compared to the indices of the previous year *t-1*, except for SDII and DD where a lesser number of significant effects were detected (58 species for both indices in *t-2* while 68 in *t-1*) (Figure 5.3). FD0 showed negative effects for a greater number of species in *t-2* compared to *t-1* (53 vs 39, respectively), while the opposite was found for SDII (40 for *t-2* and 53 for *t-1*). For most of species, the response curve for the same climatic index was quite similar when comparing *t-1* and *t-2*, but there were several exceptions (S5.7). In some cases, significant effects were found in *t-1* but not in *t-2* (e.g. summer days SU25 for the Willow Ptarmigan *Lagopus lagopus*), or vice versa (e.g. frost days FD0 for the Yellowhammer *Emberiza citrinella*) (S5.7). Less frequently, responses were different between the two periods and in any case with small differences (e.g. DTR in the breeding season for the European Robin *Erithacus rubecula,* S5.7).

Fifty-eight species were the most sensitive to extreme climatic events overall (i.e. species where at least two-thirds of the 12 indices affected the response; p-value ≤ 0.05). Among them, the prevalent relationship, for species for which at least a half of the total significant effects were assigned to a unique category, was positive for 14 species, and negative for 18 species (Table 5.2). Within the taxonomic orders with at least four species, all species of Columbiformes (Eurasian Collared Dove *Streptopelia decaocto*, Common Wood Pigeon *Columba palumbus*, Feral Pigeon *Columba livia*, Stock Dove *Columba oenas*), half of the species of Accipitriformes and Charadriiformes, 74% of species belonged to Passeriformes showed to be sensitive to all indices. Conversely, Strigiformes did not result to be particularly sensitive to ECEs overall, and only the Short-eared Owl (*Asio flammeus*) and the Tawny Owl were largely and negatively influenced by T-based climatic indices in the breeding season (Table 5.2). When considering indices in relation to one (*t-1*) or two-year (*t-2*) lagged effects separately, we found 68 sensitive species in the "most sensitive" category (defined as above) for *t-1* and 61 for *t-2*. In the first case, the prevalent relationship was positive for 26 species, negative for 31 species and decreasing-increasing in two ones. Similarly, the prevalent relationship in *t-2* was positive for 20 species, negative for 29 species, and increasing-decreasing in six ones (Table 5.2). Fifty-three species were in the "most sensitive" category for winter T-based indices, with 22 prevalent positive responses, 29 negative, three decreasing-increasing, and six increasing-decreasing. 61 species were in the "most sensitive" category for breeding T-based indices, with 31 positive relationships, 30 negative, three decreasing-increasing, and seven increasing-decreasing. Fifty-five species were in the "most sensitive" category for R-based indices, with 24 positive prevalent relationships, 40 negative, one decreasing-increasing, and seven increasing-decreasing (Table 5.2). Columbiformes showed high sensitivity to each group of indices (three out of four species showed significant responses to winter T-based indices, and all species to breeding T-based and R-based indices), and Anseriformes showed high sensitivity to R-based indices (six out of 11 species). Passeriformes, which in our study included 18 different families and 46% of the analysed species, showed a high sensitivity to breeding T-based indices (80% of them showed significant responses to two-thirds of the indices belonging to this group). Additionally, they also showed considerable responses to breeding R-based and winter T-based indices (63% of the species for both cases). Among these most sensitive species, 45% of the responses were negative in case of winter T-based indices (Table 5.2).

Table 5.2. Number of statistically significant effects of ECEs and type of relationship for the 100 species analysed. Species are listed with the common name, following the taxonomic order and according to the International Ornithological Committee (IOC) World Bird List (Gill et al., 2022). In each column, the number of statistically significant effects is reported with a number, and the type of relationship is shown in parenthesis. “ECEs (tot)” includes all the 12 extreme climatic indices, “ECEs (t-1)” the 6 indices at time *t-1*, and “ECEs (t-2)” the 6 indices at time *t-2*. “T-based (W)” includes the 4 temperature-based indices during the winter season, “T-based (B)” the 4 temperature-based indices during the breading season, and “R-based (B)” the 4 rainfall-based indices during the breading season. For these last three indices, both time *t-1* and *t-2* were considered. The type of relationship has been reported when at least two-thirds of the indices in the group had affected the species abundance (p-value ≤ 0.05; marked in bold) and there was a prevalent type of relationship (i.e. ≥ 50% of the total significant effects was assigned to a unique category; see Section 5.2.3 for the applied criterion). When the type relationship was equally split between two categories, both of them were reported. N = negative, P = positive, ∪= decreasing-increasing, ∩= increasing-decreasing.

Species	Order	ECEs (tot)	ECEs (t-1)	ECEs (t-2)	T-based (W)	T-based (B)	R-based (B)
Little Grebe	Podicipediformes	5	**4 (P)**	1	2	1	2
Great Crested Grebe	Podicipediformes	5	3	2	**3 (N)**	2	0
Great Cormorant	Suliformes	6	3	3	2	1	**3 (N)**
Little Egret	Pelecaniformes	7	**4 (N)**	3	**3 (N)**	1	3
Grey Heron	Pelecaniformes	**11 (P)**	**6 (P)**	**5 (P)**	**4 (P,N)**	**4 (P)**	**3 (N)**
Mute Swan	Anseriformes	**9 (P)**	**4 (P,N)**	**5 (P)**	**3 (P)**	**3 (P)**	**3 (N)**
Greylag Goose	Anseriformes	**8**	**4**	**4 (N)**	2	**3 (∪)**	**3 (N)**
Canada Goose	Anseriformes	7	**4 (P,N)**	3	**3 (N)**	2	2
Egyptian Goose	Anseriformes	**8 (P)**	**4 (P)**	**4 (P,N)**	**3 (P)**	2	**3 (N)**
Common Shelduck	Anseriformes	7	**4 (∪)**	3	2	**3 (N)**	2
Mandarin Duck	Anseriformes	3	2	1	1	1	1
Gadwall	Anseriformes	5	3	2	1	2	2
Eurasian Teal	Anseriformes	3	3	0	1	1	1
Mallard	Anseriformes	**9**	**4 (P,N)**	**5**	**4 (P,N)**	2	**3 (N)**
Tufted Duck	Anseriformes	6	3	3	2	1	**3 (N)**
Common Merganser	Anseriformes	**8 (P)**	3	**5**	2	**3 (P)**	**3 (P)**
Red Kite	Accipitriformes	**11**	**6**	**5**	**4 (P)**	**4 (P,∪)**	**3 (N)**
Western Marsh Harrier	Accipitriformes	3	1	2	0	**3**	0
Hen Harrier	Accipitriformes	3	1	2	2	1	0

Table 5.2 (cont.)

Northern Goshawk	Accipitriformes	5	2	3	2	2	1
Eurasian Sparrowhawk	Accipitriformes	**8 (N)**	**4 (N)**	**4 (N)**	2	2	**4 (P,N)**
Common Buzzard	Accipitriformes	**8**	**4 (P)**	**4 (N)**	**3 (∩)**	**4 (P,N)**	1
Common Kestrel	Falconiformes	6	3	3	1	2	**3 (N)**
Merlin	Falconiformes	5	**4 (N)**	1	**3 (N)**	1	1
Peregrine Falcon	Falconiformes	5	**4 (P)**	1	1	2	2
Willow Ptarmigan	Galiiformes	**8 (N)**	**5 (N)**	3	2	**3 (∩)**	**3 (N)**
Black Grouse	Galiiformes	3	3	0	1	1	1
Red-legged Partridge	Galiiformes	7	3	**4**	**3 (P)**	2	2
Grey Partridge	Galiiformes	5	3	2	1	1	**3 (P)**
Common Pheasant	Galiiformes	**9**	**5**	**4 (∩)**	1	**4 (P,N)**	**4 (∩)**
Indian Peafowl	Galiiformes	2	1	1	0	2	0
Common Moorhen	Gruiformes	**10 (P)**	**6 (P,N)**	**4 (P)**	**3 (P)**	**3**	**4 (P,N)**
Eurasian Coot	Gruiformes	**10 (P)**	**6**	**4 (P)**	**4 (N)**	**3 (P)**	**3 (P)**
Eurasian Oystercatcher	Charadriiformes	**9 (N)**	**4 (N,∪)**	**5 (N)**	**3 (∪)**	**3 (N)**	**3 (N)**
Common Ringed Plover	Charadriiformes	4	1	3	1	2	1
European Golden Plover	Charadriiformes	7	3	**4 (N)**	**3**	2	2
Northern Lapwing	Charadriiformes	7	3	**4 (N)**	2	1	**4 (N,∩)**
Common Snipe	Charadriiformes	**8**	**4 (P)**	**4 (N)**	2	2	**4 (N,∩)**
Eurasian Woodcock	Charadriiformes	1	1	0	0	0	1
Eurasian Curlew	Charadriiformes	**8**	**5**	3	**3 (∪)**	**3 (∩)**	2
Common Redshank	Charadriiformes	**9**	**5**	**4 (N)**	**3 (∪)**	**4 (N)**	2
Feral Pigeon	Columbiformes	**11**	**5 (N)**	**6**	**3**	**4 (P,N)**	**4 (P,N)**
Stock Dove	Columbiformes	**8 (N)**	**4 (P,N)**	**4 (N)**	2	**3 (N)**	**3 (N)**
Common Wood Pigeon	Columbiformes	**12**	**6**	**6 (P)**	**4 (P,∩)**	**4**	**4 (P,N)**
Eurasian Collared Dove	Columbiformes	**10 (N)**	**4 (P,N)**	**6 (N)**	**3 (P)**	**3 (N)**	**4 (P,N)**
Rose-ringed Parakeet	Psittaciformes	5	3	2	**3 (N)**	1	1
Western Barn Owl	Strigiformes	4	2	2	2	0	2
Little Owl	Strigiformes	4	1	3	2	2	0
Tawny Owl	Strigiformes	7	**4 (P,N)**	3	2	**4 (N)**	1
Short-eared Owl	Strigiformes	7	3	**4 (P,N)**	2	**3 (N)**	2
Common Kingfisher	Coraciiformes	**8 (P)**	**5 (P)**	3	**4 (P,N)**	**3 (P)**	1
European Green Woodpecker	Piciformes	**10 (N)**	**6 (N)**	**4 (N)**	**4 (N)**	**3 (P)**	**3 (N)**
Great Spotted Woodpecker	Piciformes	**10 (P)**	**5 (P)**	**5 (N)**	**4 (P)**	**3 (P)**	**3 (N)**
Lesser Spotted Woodpecker	Piciformes	2	1	1	0	1	1
Eurasian Skylark	Passeriformes	**11**	**6**	**5**	**4 (∩)**	**4 (N,∪)**	**3 (P)**
Meadow Pipit	Passeriformes	**12 (N)**	**6 (N)**	**6 (P,N)**	**4 (N)**	**4 (N)**	**4 (P)**
Grey Wagtail	Passeriformes	**10 (P)**	**5 (P)**	**5 (P)**	**4 (P,N)**	**3 (P)**	**3 (N)**
White Wagtail	Passeriformes	**10 (N)**	**5**	**5 (N)**	**3 (N)**	**4 (N)**	**3 (P)**
White-throated Dipper	Passeriformes	**9 (N)**	**4 (P,N)**	**5 (N)**	**4 (P,N)**	**3 (P)**	2
Eurasian Wren	Passeriformes	**12**	**6 (N)**	**6 (∩)**	**4 (P,N)**	**4 (∩)**	**4 (N,∩)**
Dunnock	Passeriformes	**10 (N)**	**5 (N)**	**5 (N)**	**4 (N)**	2	**4 (P,N)**
European Robin	Passeriformes	**12 (N)**	**6 (N)**	**6**	**4 (N)**	**4 (P)**	**4 (N)**
European Stonechat	Passeriformes	**10 (N)**	**5**	**5 (N)**	**3 (N)**	**4 (N)**	**3 (P)**
Common Blackbird	Passeriformes	**12 (N)**	**6 (N)**	**6 (N,∩)**	**4 (N)**	**4 (N)**	**4 (N,∩)**
Fieldfare	Passeriformes	**8 (P)**	**4 (P)**	**4 (P)**	**3 (P)**	**3 (P)**	2
Song Thrush	Passeriformes	**11**	**5 (N)**	**6 (∩)**	**3 (N)**	**4 (N)**	**4 (∩)**
Redwing	Passeriformes	6	3	3	1	1	**4 (P,N)**
Mistle Thrush	Passeriformes	7	3	**4 (P)**	**3 (N)**	**3 (P)**	1
Cetti's Warbler	Passeriformes	6	2	**4 (P,N)**	**3 (N)**	1	2
Goldcrest	Passeriformes	**10**	**5**	**5**	**4 (N)**	**4 (P)**	2
Long-tailed Tit	Passeriformes	7	3	**4 (P)**	**3 (P)**	2	2
Marsh Tit	Passeriformes	6	**4 (P)**	2	2	**3 (P)**	1
Willow Tit	Passeriformes	5	2	3	1	**3 (P)**	1
Coal Tit	Passeriformes	**10 (P)**	**6 (P)**	**4 (P)**	2	**4 (P,N)**	**4 (P)**

Table 5.2 (cont.)

Eurasian Blue Tit	Passeriformes	**10 (P)**	**6 (P)**	**4 (P,N)**	**4 (∩)**	**3 (P)**	**3 (N)**
Great Tit	Passeriformes	**11**	**5**	**6 (P)**	**4 (P)**	**4 (P)**	**3 (N)**
Eurasian Nuthatch	Passeriformes	**8**	**4 (P)**	**4 (N)**	1	**3 (P)**	**4 (N,∩)**
Eurasian Treecreeper	Passeriformes	**10 (P,N)**	**5 (N)**	**5 (P)**	**4 (P,N)**	**4 (P,N)**	2
Eurasian Jay	Passeriformes	**8 (P)**	**5**	3	2	**4 (P)**	2
Eurasian Magpie	Passeriformes	**11 (N)**	**5 (N)**	**6 (N)**	**4 (N)**	**4 (P)**	**3 (N)**
Western Jackdaw	Passeriformes	**11**	**6 (N)**	**5**	**4 (P)**	**3 (N)**	**4 (P,N)**
Rook	Passeriformes	**11**	**5**	**6 (P)**	**3 (P)**	**4 (N)**	**4 (P,N)**
Carrion Crow	Passeriformes	7	**4 (N)**	3	2	**4 (P,N)**	1
Hooded Crow	Passeriformes	**9 (N)**	**4 (N)**	**5**	2	**3 (N)**	**4 (∪)**
Northern Raven	Passeriformes	7	2	**5**	**3 (N)**	2	2
Common Starling	Passeriformes	**12**	**6 (P)**	**6 (∩)**	**4**	**4 (P,∩)**	**4 (N)**
House Sparrow	Passeriformes	**11**	**5**	**6 (N)**	**4 (P,N)**	**3 (∩)**	**4 (P,N)**
Eurasian Tree Sparrow	Passeriformes	**10**	**5**	**5**	2	**4 (N,∩)**	**4 (P,N)**
Common Chaffinch	Passeriformes	**8**	**4 (P)**	**4 (N)**	**3 (∩)**	**4 (P,N)**	1
European Greenfinch	Passeriformes	**12 (N)**	**6 (N)**	**6 (N)**	**4 (P,N)**	**4 (N)**	**4 (P,N)**
European Goldfinch	Passeriformes	**8**	**5**	3	2	**3 (∩)**	**3 (N)**
Eurasian Siskin	Passeriformes	**9**	**5 (N)**	**4 (P)**	1	**4 (P,N)**	**4 (P)**
Common Linnet	Passeriformes	**10 (N)**	**4 (N)**	**6 (N)**	2	**4 (N)**	**4 (P,N)**
Twite	Passeriformes	2	1	1	0	2	0
Lesser Redpoll	Passeriformes	7	**4 (N)**	3	1	**3 (N)**	**3 (N)**
Red Crossbill	Passeriformes	6	2	**4 (P)**	2	2	2
Eurasian Bullfinch	Passeriformes	**8**	**4 (P)**	**4 (∩)**	2	**4 (P,N)**	2
Yellowhammer	Passeriformes	**10**	**4**	**6 (N)**	**3 (∩)**	**4 (N)**	**3 (P)**
Common Reed Bunting	Passeriformes	**8**	**5**	3	**4 (N)**	2	2
Corn Bunting	Passeriformes	6	**4 (P,N)**	2	1	2	**3 (P)**

5.4. Discussion

Climate change remains one of the most important challenges for biodiversity conservation and understanding how extreme climatic events interact with wild populations is critical to plan adequate strategies and to predict future biodiversity changes (Roberts et al., 2019). Here we assessed the effects of extreme climatic events on relative abundance (counts of individuals at survey sites) for 100 resident bird species at large spatial and temporal scale using the UK BBS (> 69,000 sampled sites over 25 years), and identified the most sensitive species to extreme climatic events among resident birds. Defining suitable proxies representing extreme climatic conditions is pivotal but often controversial (Bailey & van de Pol, 2016). Our results supported evidence that climatic indices could be suitable to measure biological responses of populations to extreme climatic events. The flexible GAM framework allowed detection of both linear and non-linear response curves that may often characterise species responses to climatic variables (Pearce-Higgins & Crick, 2019). In several cases, response curves revealed the presence of threshold-like responses, the identification of which is crucial for assessing the effect of environmental pressures on biological system (Bailey & van de Pol, 2016).

5.4.1. Effects of extreme climatic events

Our findings demonstrated the existence of widespread effects of extreme climatic events on bird populations. Number of winter frost days (FD0), a measure of winter severity, showed a clear negative effect for most of the species. Winter severity can negatively affect the survival of individuals, with greater effects on first-year birds compared to adults (Robinson et al., 2004; Robinson, et al., 2007). We found a greater proportion of negative effects for the two-year lagged index FD0_W_t-2 compared to FD0_W_t-1. This might depend on the fact that roughly one-third of the analysed species reach the age of reproduction later than the first year (Storchová & Hořák, 2018), thus resulting in a delayed effect over time. Additionally, we cannot exclude that winter severity might indirectly influence population dynamics through bottom-up processes (e.g. food availability) that may act on older individuals as well. As the long-term trend for the number of frost days (S5.1A) has been negative in our study area, the negative contribution of winter severity could lessen in the future. Summer days (SU25), used as proxy of prolonged extreme hot temperatures during the breeding season, showed a large proportion of negative effects (36% and 37% of the total of the species in *t-1* and *t-2*, respectively). Some previous studies highlighted that hot temperatures in summer could negatively affect abundance in birds (Beale et al., 2006; Franks et al., 2017), although many species show overall positive responses between temperature and population groth rates (Pearce-Higgins et al., 2015). High temperatures during the breeding season or in summer could affect the reproductive success of adults through direct effects on the reproductive performance (Conrey et al., 2016; Cruz-McDonnell & Wolf, 2016; Pattinson et al., 2022), but also through bottom-up processes affecting the abundance or availability of food resources (Pearce-Higgins, 2010; Pearce-Higgins et al., 2010). However, we also found a consistent proportion of positive effects of summer days (22% in both *t-1* and *t-2*), which is consistent with this variable being likely to be correlated with mean temperature and therefore also measuring milder breeding seasons. For example, in our study the Red Kite (*Milvus milvus*) showed a positive response to the increasing number of summer days. Nägeli et al. (2022) highlighted that for this species brood loss during the nestling phase is linked to low temperatures, and the increase of spring temperature could actually favour the population growth and the altitudinal expansion of the species distribution. Similarly, abundance of some corvids (Corvidae) such as the Eurasian Magpie (*Pica pica*), the Carrion Crow (*Corvus corone*) and the Eurasian Jay (*Garrulus glandarius*), as well as the Common Starling (*Sturnus vulgaris*) and the Great Tit (*Parus major*) positively responded to summer days. These species are often present in urban environments, and the effects of hot temperatures could be influenced by habitat characteristics with dampened or reverse effects in urban areas (Pipoly et al., 2022). Differently from frost days and summer days, the daily temperature range (DTR) showed a smaller proportion of negative effects, especially during the winter season. DTR may be an important predictor for species distribution and occurrence in animals (Ribeiro et al., 2015; Sutton et al., 2022), but how wild animal populations respond to this climatic parameter remains barely investigated in ecological studies on climate change. In an experiment in laboratory conditions, Briga & Verhulst (2015) demonstrated that large DTR increased mortality in Zebra finches (*Taeniopygia* cf. *guttata*), with different patterns found in relation to foraging environment and thermal condition. However, in natural systems, species responses may be less predictable due to the complexity of the system. Our results revealed prevalent positive effects of DTR on bird relative abundance, and a significant proportion (12% - 22%) of an initial positive effect followed by a negative effect (increasing-decreasing response curve). These findings suggested that beyond a threshold (roughly 5°-6° Celsius in winter and 8°-10° Celsius in the breeding season, see S5.7), the positive effects disappeared and a further increase of DTR leads to clear negative responses in abundance, maybe linked to the increase of physiological stress (Briga & Verhulst, 2015). However, the degree of uncertainty of the response curve was greater for DTR compared to the other indices (Figure 5.3), and the ecological response around the limit values of the index needs to be assessed prudently. In relation to the effects of precipitation on bird abundance during the breeding season, our findings highlighted that the intensity of rainfall, measured by the simple precipitation intensity index (SDII), extensively and negatively influenced bird counts, while responses to drought, evaluated by the number of dry days (DD), varied across species. The precipitation intensity can affect birds in several ways. Rainfall intensity during nesting can affect nest survival in passerines (McDonald et al., 2013; Schroeder et al., 2022). Nests could be destroyed and the mortality rate of juveniles could increase dramatically in conditions of heavy rain. Precipitation combined with moderate temperatures may physiologically stress clutches, as nest material may remain wet long after the precipitation ceases. Moreover, wet plumage can increase heat loss (Wilson et al. 2004), reduce flight performance (Ortega-Jimenez & Dudley, 2012), resulting in increasing of energy expenditure (Hertel & Ballance 1999). Rainfall can also alter bird foraging behaviour (De Pascalis et al., 2022), as well as the perception of the surrounding environment (Yorzinski 2020), resulting in a variation of capabilities of bird predators to localise preys, but also in a reduction of birds to detect potential predators (Sergio, 2003; Whittingham et al. 2004). Such disruptions may result in reducing foraging efficiency, leading to negative effects on body mass (Cox et al., 2019) that can ultimately affect fitness (Moronisotto et al., 2020). On the other hand, several studies linked drought to negative consequences on reproductive success in birds (Robinson et al., 2004, 2012; Colón et al. 2017), survival of adults (Robinson et al., 2004), with strong negative effects at higher trophic levels (Prugh et al., 2018). Severe droughts can also act through indirect ways, for example by altering habitat conditions and structures where a species lives (Hinojosa-Huerta et al., 2013; Mastrantonis et al., 2019), or by favouring brood parasitism or nest predation in bird species (McCreedy & Van Riper, 2015; Colón et al., 2017). However, our findings did not show widespread negative effects of droughts on bird abundance, rather we found a prevalence of positive effects (35% and 31% of the species in *t-1* and in *t-2*, respectively). Palmer et al. (2017) highlighted that drought conditions might have weaker negative effects upon birds. In wetlands, for example, bird assemblages could be favoured by moderate drought conditions, especially those species feeding on aquatic and benthic fauna as consequence of the surfacing of new foraging areas leading to a temporary increase in size of feeding areas and food availability (Jitariu et al., 2022). In our study, wetland birds belonging to Anatidae, Rallidae, Scolopacidae, Haematopodidae, Charadriidae, Ardeidae, Podicipedidae, Phalacrocoracidae, Alcedinidae (27 species overall) were not affected by drought conditions (33% and 59% of non-significant effects, respectively in *t-1* and *t-2*), or showed positive responses in 26% of the cases in both *t-1* and *t-2*.

Our results also highlighted widespread two-year lagged effects. Bird population responses to climate change can show delays due to ecological and demographic processes (Jenouvrier, 2013). Lagged effects can act in several ways, for example through food webs (Trivelpiece et al., 2011), but also directly by affecting offspring recruitment (Sandwik et al., 2012; Saunders et al., 2021). Effects of climatic variables on a species can remain similar across years (or detected only in one year), as we found for most of the analysed species, although they can sometimes be different (Sandwik et al., 2012). Contrasting effects may be more difficult to be explained, and may depend on diverse processes involved. For example, we found contrasting effects of frost days in the Western Barn Owl *Tyto alba*, with a positive effect in the preceding winter and a negative effect in the two-year preceding winter (S5.7). Although harsh conditions in winters immediately preceding the breeding season can negatively affect reproductive parameters in the Western Barn Owl populations (Chausson et al., 2014), effects on individuals' survival could be more marked in adults than juveniles (Altwegg et al., 2006). This could partially explain the observed delayed effects, but also ecological processes such as effects of severe winters on availability of prey populations, especially represented by rodents (Bosè and Guidali, 2001), could play an important role. On the other hand, the opposite effect of one-year lag-effect highlights that other mechanisms could be involved, and responses to extreme climatic events are not simple to be predicted.

5.4.2. Species sensitivity

Our analyses also identified the most sensitive species to extreme climatic events. Species that responded to the whole set of 12 climatic variables (58%) belong to several and different avian taxonomic orders. It suggests extreme climatic events could widely affect avian populations independently from phylogenetic constraints. Many previous works had been focused on iconic or endangered birds (e.g. Conrey et al., 2016; Colón et al., 2017; Pardo et al., 2017; Cleeland et al., 2020), but little attention has been given to multi-species studies (but see Cohen et al., 2020, 2021). Assessing sensitivity and responses of multiple species to extreme climatic events, which are expected to be more and more common in the near future (IPCC, 2013), is crucial to identify trajectories of potential and future environmental changes and how they could act on biological and ecological systems. In this study, 18 species showed widespread negative responses to extreme climatic events, while 14 species showed broad positive responses. This means that such birds could be eligible sentinel species for studying extreme climatic events, and their sensitivity should be further assessed in future studies. Moreover, multi-species analyses can reveal overlooked patterns that are valuable for wildlife conservation. Despite that common or non-threatened species may currently need less conservation effort compared to threatened or rare ones, it does not mean that in the future such species may suffer from a significant decline due to increasingly recurring extreme weather conditions. Some common and widespread species such as the Common Blackbird (*Turdus merula*) and the European Robin, characterised by positive long-term population trends (Harris et al., 2022), were affected by broad negative responses to extreme climatic events which emphasises that also such species could be impacted by future climate change. Their short-term population trends 2010-2020 (Harris et al., 2020), for example, highlighted a reduction in population growth rate (European Robin) or a weak decline (Common Blackbird), that may also depend on climate-induced effects. On the other hand, some species could benefit from extreme climatic conditions (Maxwell et al., 2019), likely due to local adaptations, higher tolerances, ecological plasticity or greater resilience capacity (Renton et al., 2018; Cooper et al., 2020; Pipoly et al., 2022; Schoenjahn et al., 2022).

When considering the effects of climatic indices with one or two-year lagged effects separately, we found widespread effects across all taxonomic orders. Exceptions included Psittaciformes (1 species, the Rose-ringed Parakeet) and Suliformes (1 species, the Great Cormorant) in both *t-1* and *t-2*, while

Falconiformes (3 species), Podicipediformes (2 species), Coraciiformes (1 species, the Common Kingfisher *Alcedo atthis*) for two-year lagged effects. This suggests that not only long-lived species are prone to be affected by lagged effects of climate (Sandwik et al., 2005), but also short-lived species, such as most of Passeriformes under study, may be affected by extreme climatic events with time lags.

Columbiformes showed high sensitivity in responses to extreme climatic events. Previous studies stressed heat tolerance capacity for this group (Pollock et al., 2020), but tolerances can vary greatly within avian orders (McKechnie et al., 2017). For example, we found that the Eurasian Collared Dove and the Stock Dove were negatively affected by increasing number of summer days. The Feral Pigeon showed an opposite effect and the Common Wood Pigeon a different pattern again (S5.7).

The high sensitivity of Anseriformes to rainfall-based indices, which was mainly characterised by negative responses (Table 5.2), may be linked to their dependency on water. Such species depend on water habitat for feeding, nesting, rearing chicks, and increases of water surface can negatively affect their abundance (Canepuccia et al., 2007). The increase of rainfall intensity during restricted time intervals could cause unexpected rise of the water table during vulnerable phases of the life cycle (i.e. breeding season), leading to significant negative consequences likely involving offspring recruitment. Observed responses to SDII for this group (S5.7) seem to confirm such a negative pattern. Moreover, findings for some species (Mute Swan *Cygnus olor*, Tufted duck *Aythya fuligula*, Gadwall *Mareca strepera*) further enforce this evidence, showing positive responses to the increase of the number of dry days that could lead to a general reduction of water surface.

Finally, Passeriformes showed a high sensitivity to each of three groups of indices (winter T-based, breeding T-based, breeding R-based), especially to breeding T-based indices for which they reached 80% of significant responses. Being of small size, except for corvids, species of this taxon could largely suffer from hot thermal physiological stress induced by dehydration arising from greater evaporative cooling demands (Albright et al., 2017), but heat tolerance can also vary in relation to habitat characteristics (Freeman et al., 2022) that could explain the diversification in the observed type of responses. Very interestingly, 45% of responses to winter T-based indices across the 29 most sensitive species of Passeriformes was negative. Smaller species usually suffer from a greater risk of heat dissipation because of their relatively larger body surface area. In winter, keeping body temperature within the optimal range requires a higher metabolism that in small passerines may be reached by gaining lean body mass in fat to fuel overnight metabolism (Haftorn, 1992) or by physiological adaptations such as facultative hypothermia (McKechnie & Lovegrove, 2002).

However, both strategies have fitness costs, for example due to needs for increasing food supply in the first case or to higher predation risks in the second (Brodin et al., 2017). These factors likely make small birds more susceptible to severe temperatures or thermal stress in winter, resulting in a broad presence of negative responses to winter temperature-based indices as shown by our findings.

5.5. Conclusions

In this study, we assessed the effects of extreme climatic events on bird populations of 100 resident species at large spatial (United Kingdom) and temporal scales (25 years) using long-term monitoring data collected from the UK Breeding Bird Survey. Predicting long-term species responses to extreme climatic events at large spatial scale could represent a critical goal to predict population dynamics and species distributions. Findings highlighted widespread and significant effects of extreme climatic events on bird relative abundances, with both one-year and two-year lagged effects. Identifying suitable proxies to measure the magnitude of extreme climatic events in a biological perspective is crucial for future research. Indices used in this study, which are defined from a climatological point of view, were shown to be suitable for assessing biological responses. Winter frost days, summer days during the breeding season and the simple intensity precipitation index during the breeding season showed broad negative effects, while the diurnal temperature range in both seasons and dry days in the breeding season showed more diversified effects across species, with a prevalence of positive effects.

This work also identified several species that were more susceptible to effects of extreme climatic events and the direction of the responses, suggesting the use of such species for future studies in this research field. Extreme climatic events could exacerbate biological responses of avian populations placing new challenges for their conservation but also for biodiversity and ecological processes in general, because of the importance of birds in ecosystems and biological communities (Harris et al., 2020; Valkó et al., 2022). Embracing functional and ecological traits in further research could represent an added value for the modelling framework, as species traits able to capture the existence of shared ecological pressures in groups of species with similar characteristics (Tirozzi et al., 2021 and *Chapter 3*; Couet et al., 2022; Tirozzi et al., 2022b and *Chapter 4*).

Understanding both direct and indirect mechanisms through which extreme climatic events can affect wild populations should be a primary goal for a conservation perspective. For this purpose, specific studies need to focus on mechanistic processes involving species responses and climate change, analysing the effects on population demographic parameters, including bottom-up effects resulting from both species interactions and variation in resource availability (Pearce-Higgins et al., 2010). Furthermore, climate change can also interact with other factors, such as changes in land use and habitat loss, with synergistic actions whose effects on populations or biodiversity could be unexpected from individual analyses of these drivers. (Mantyka-Pringle et al., 2012; Bani et al., 2019; Newbold et al., 2019; Streib et al., 2022). Investigating the consequences of such interactions and disentangling their relative contribution would allow obtaining essential data for a better and more exhaustive understanding of species responses to a changing environment.

Supplemementary materials

List of content

S5.1. Long-term trends 1961-2018 and short-term trends 1992-2018 for FD0 in A), DTR_W in B), SU25 in C), DTR_B in D), SDII in E), DD in F) throughout the study area (UK).

S5.2. Covariates used in the models in addition to the climatic variables.

S5.3. Pearson correlation coefficients between each pair of explanatory variables.

S5.4. AIC comparison between the Poisson and the negative binomial GAMs.

S5.5. Explained deviance (%) for the negative binomial GAMs.

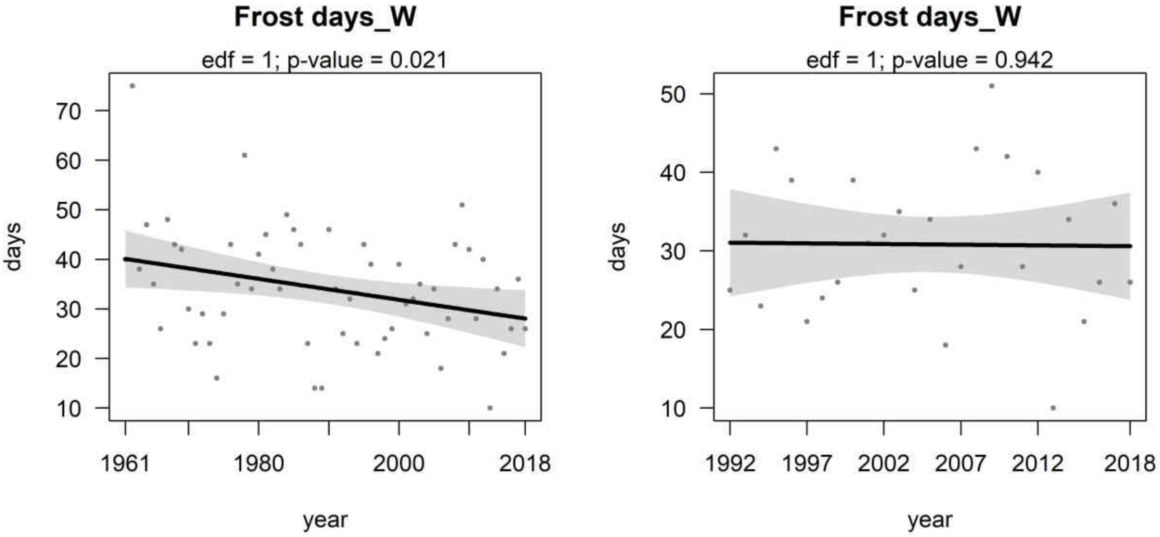
S5.6. Criterion used for the assignment of “high uncertainty” or “moderate uncertainty” in addition to the main categories describing the type of relationship between bird counts and the extreme climatic indices.

S5.7. Effects of extreme climatic indices on bird relative abundance (counts).

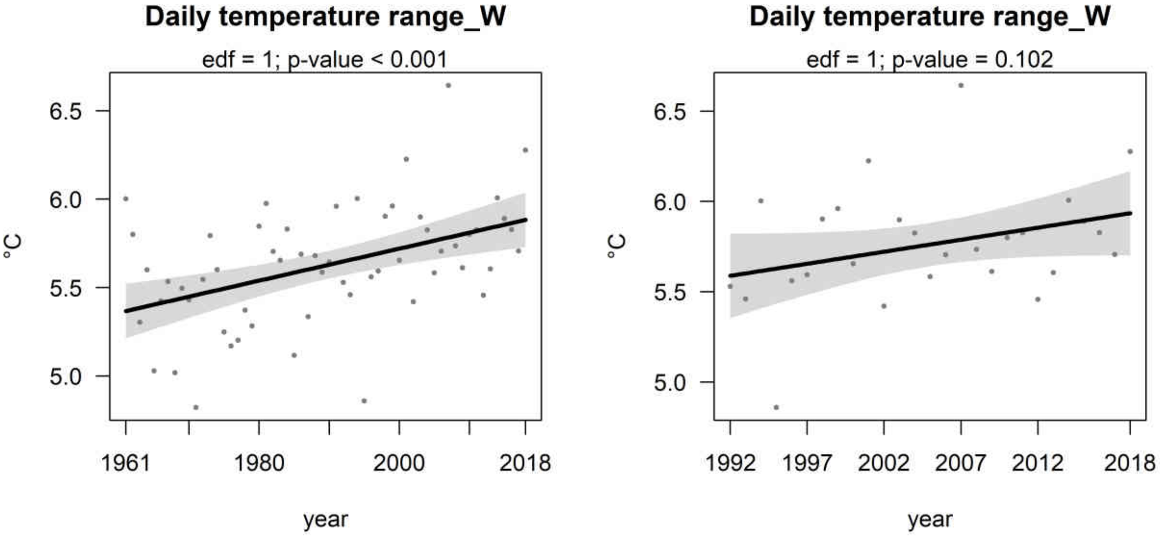
S5.1

Long-term trends 1961-2018 and short-term trends 1992-2018 for FD0_W in A), DTR_W in B), SU25_W in C), DTR_B in D), SDII_B in E), DD_B in F) throughout the study area (UK). W= winter season, B= breeding season. Trends were assessed by generalised additive models (GAMs), using the thin plate regression spline as method of smoothing and the restricted maximum likelihood (REML) to estimate the smoothing parameter. Annual median values throughout the whole of the UK at 1-km square resolution (1,305,000 values for each year) were used to assess trends. The estimated degree of the smooth function (edf) and the corresponding p-value are showed at the top of the graph.

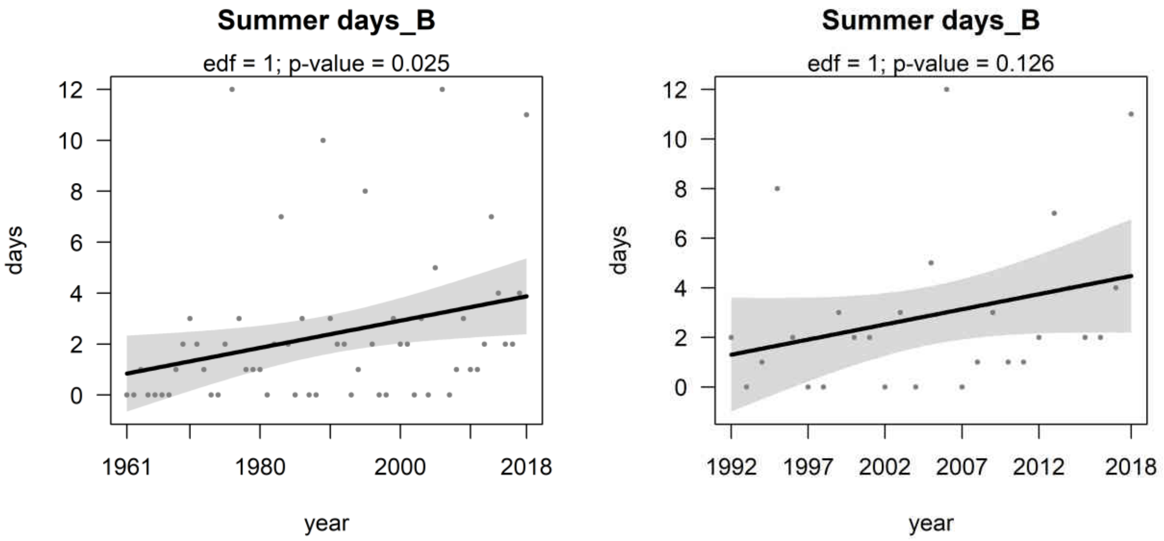
A) Winter frost days (FD0_W).



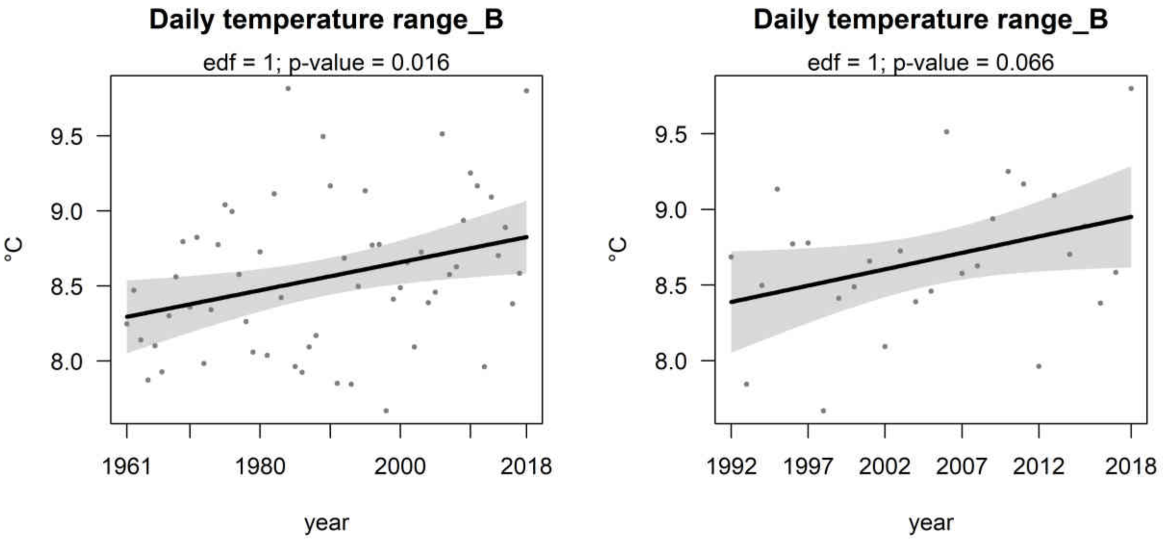
B) Winter daily temperature range (DTR_W)



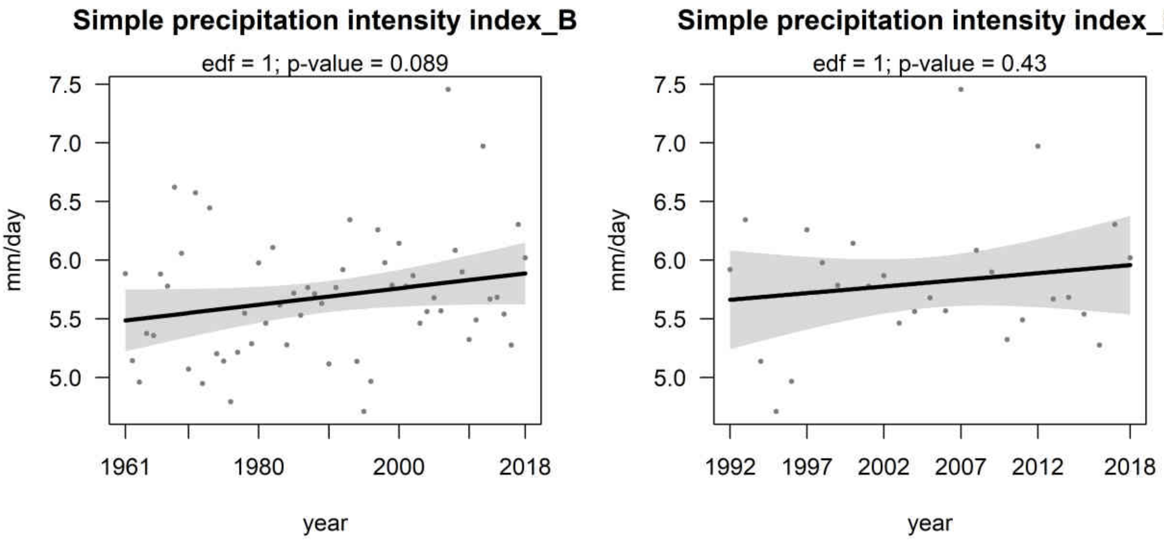
C) Breeding summer days (SU25_B).



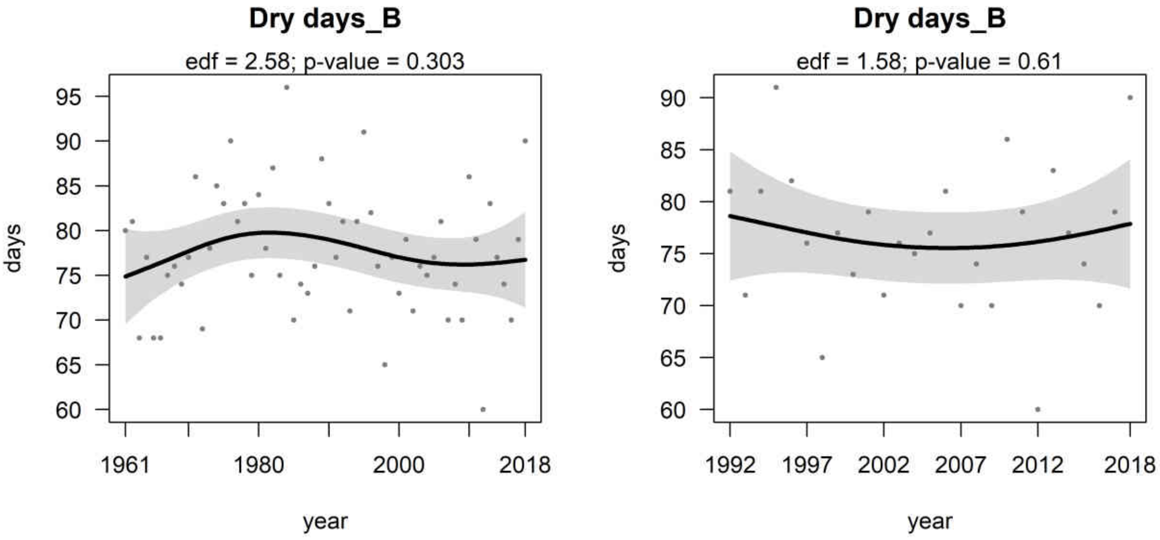
D) Breeding daily temperature range (DTR_B).



E) Breeding simple precipitation intensity index (SDII_B).



F) Breeding dry days (DD_B).



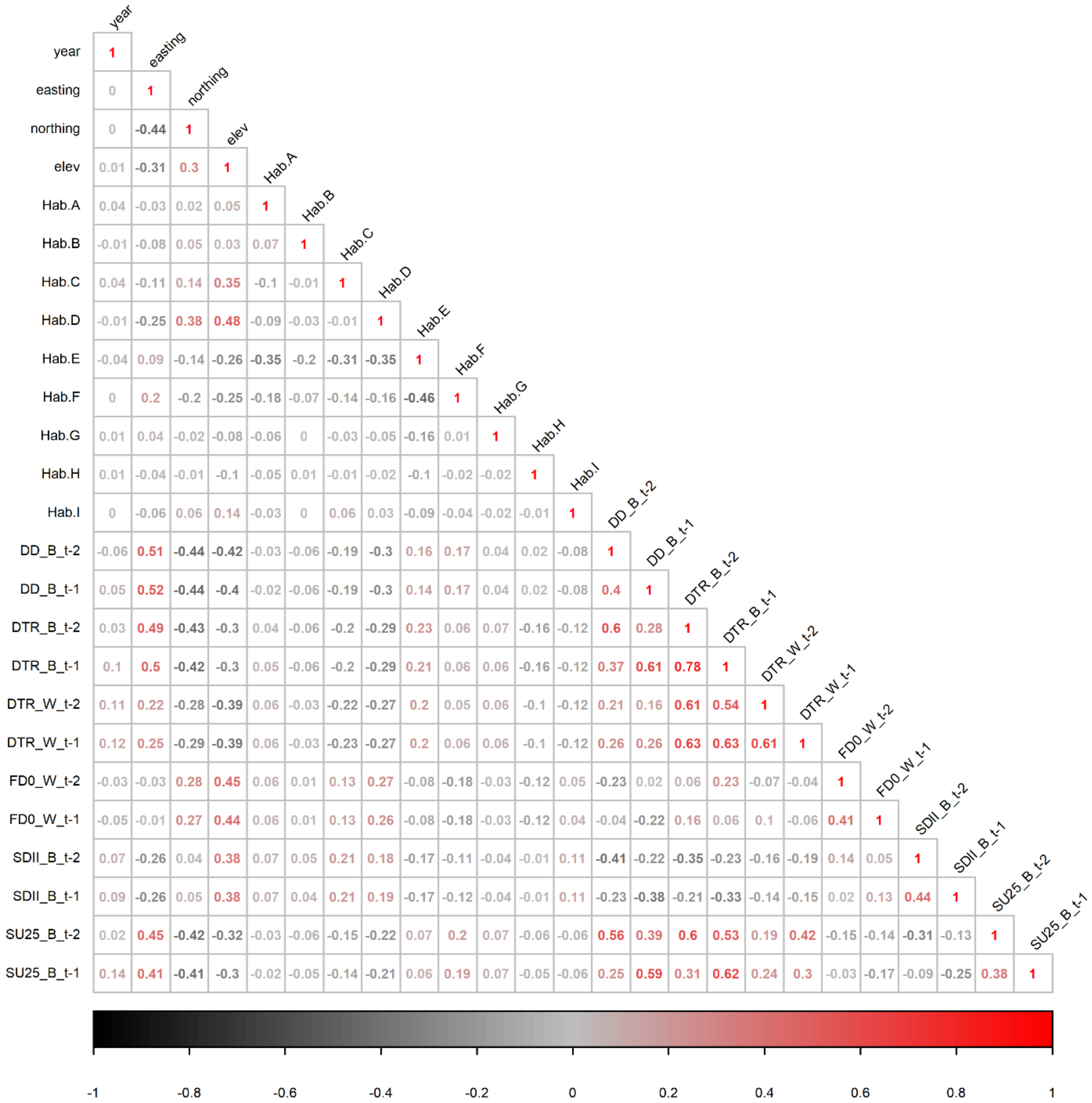
S5.2

Covariates used in the models in addition to the climatic variables. Habitat covers were calculated from information collected by surveyors describing the main types of habitats characterising each transect within each 1-km square.

Covariate	Definition	Unit
Elev	Mean elevation in the 1 × 1 km squares	m
Hab A	Woodland	%
Hab B	Scrubland	%
Hab C	Semi-natural grassland and marsh	%
Hab D	Heathland and bogs	%
Hab E	Farmland	%
Hab F	Human sites	%
Hab G	Waterbodies	%
Hab H	Coastal	%
Hab I	Inland rock	%
Northing	Northing of the bottom left corner of the sampling unit (1-km square) in the projected British National Grid system (Datum OSGB 1936)	km
Easting	Easting of the bottom left corner of the sampling unit (1-km square) in the projected British National Grid system (Datum OSGB 1936)	km
Year	Year of survey	-

S5.3

Pearson correlation coefficients between each pair of explanatory variables . Absolute values greater than 0.7 indicate high collinearity between two variables. Only one pairwise comparison revealed |Pearson’s r| > 0.7. See Section 5.2.2 in the main text and S5.1 for acronyms.

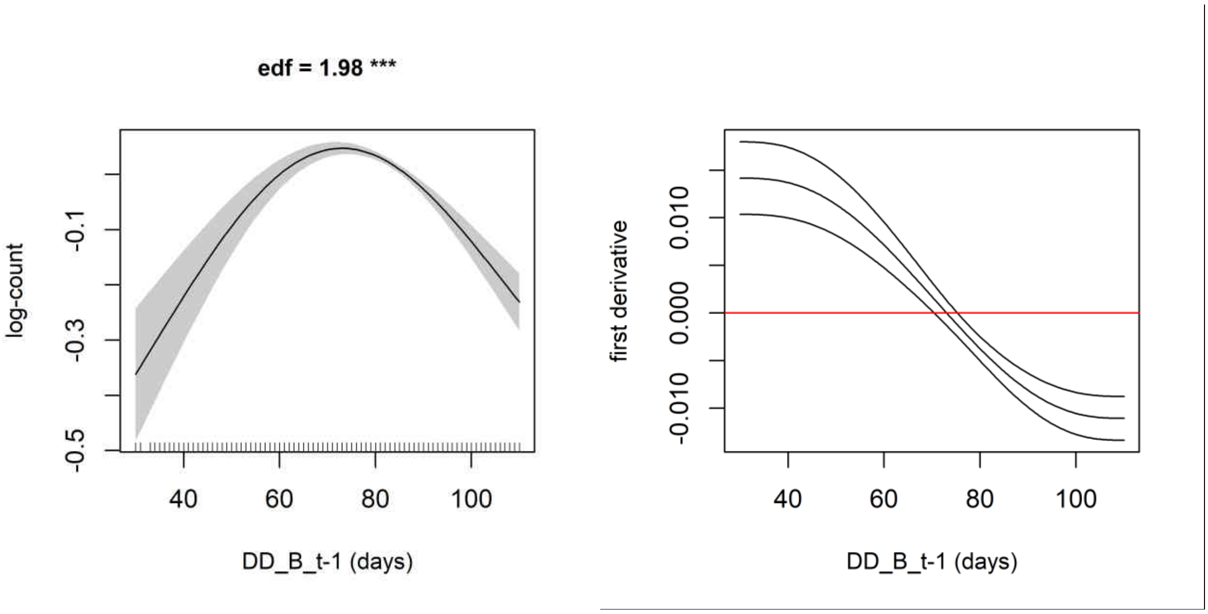


	year	easting	northing	elev	Hab.A	Hab.B	Hab.C	Hab.D	Hab.E	Hab.F	Hab.G	Hab.H	Hab.I	DD_B_t-2	DD_B_t-1	DTR_B_t-2	DTR_B_t-1	DTR_W_t-2	DTR_W_t-1	FD0_W_t-2	FD0_W_t-1	SDII_B_t-2	SDII_B_t-1	SU25_B_t-2	SU25_B_t-1
year	1																								
easting	0	1																							
northing	0	-0.44	1																						
elev	0.01	-0.31	0.3	1																					
Hab.A	0.04	-0.03	0.02	0.05	1																				
Hab.B	-0.01	-0.08	0.05	0.03	0.07	1																			
Hab.C	0.04	-0.11	0.14	0.35	-0.1	-0.01	1																		
Hab.D	-0.01	-0.25	0.38	0.48	-0.09	-0.03	-0.01	1																	
Hab.E	-0.04	0.09	-0.14	-0.26	-0.35	-0.2	-0.31	-0.35	1																
Hab.F	0	0.2	-0.2	-0.25	-0.18	-0.07	-0.14	-0.16	-0.46	1															
Hab.G	0.01	0.04	-0.02	-0.08	-0.06	0	-0.03	-0.05	-0.16	0.01	1														
Hab.H	0.01	-0.04	-0.01	-0.1	-0.05	0.01	-0.01	-0.02	-0.1	-0.02	-0.02	1													
Hab.I	0	-0.06	0.06	0.14	-0.03	0	0.06	0.03	-0.09	-0.04	-0.02	-0.01	1												
DD_B_t-2	-0.06	0.51	-0.44	-0.42	-0.03	-0.06	-0.19	-0.3	0.16	0.17	0.04	0.02	-0.08	1											
DD_B_t-1	0.05	0.52	-0.44	-0.4	-0.02	-0.06	-0.19	-0.3	0.14	0.17	0.04	0.02	-0.08	0.4	1										
DTR_B_t-2	0.03	0.49	-0.43	-0.3	0.04	-0.06	-0.2	-0.29	0.23	0.06	0.07	-0.16	-0.12	0.6	0.28	1									
DTR_B_t-1	0.1	0.5	-0.42	-0.3	0.05	-0.06	-0.2	-0.29	0.21	0.06	0.06	-0.16	-0.12	0.37	0.61	0.78	1								
DTR_W_t-2	0.11	0.22	-0.28	-0.39	0.06	-0.03	-0.22	-0.27	0.2	0.05	0.06	-0.1	-0.12	0.21	0.16	0.61	0.54	1							
DTR_W_t-1	0.12	0.25	-0.29	-0.39	0.06	-0.03	-0.23	-0.27	0.2	0.06	0.06	-0.1	-0.12	0.26	0.26	0.63	0.63	0.61	1						
FD0_W_t-2	-0.03	-0.03	0.28	0.45	0.06	0.01	0.13	0.27	-0.08	-0.18	-0.03	-0.12	0.05	-0.23	0.02	0.06	0.23	-0.07	-0.04	1					
FD0_W_t-1	-0.05	-0.01	0.27	0.44	0.06	0.01	0.13	0.26	-0.08	-0.18	-0.03	-0.12	0.04	-0.04	-0.22	0.16	0.06	0.1	-0.06	0.41	1				
SDII_B_t-2	0.07	-0.26	0.04	0.38	0.07	0.05	0.21	0.18	-0.17	-0.11	-0.04	-0.01	0.11	-0.41	-0.22	-0.35	-0.23	-0.16	-0.19	0.14	0.05	1			
SDII_B_t-1	0.09	-0.26	0.05	0.38	0.07	0.04	0.21	0.19	-0.17	-0.12	-0.04	-0.01	0.11	-0.23	-0.38	-0.21	-0.33	-0.14	-0.15	0.02	0.13	0.44	1		
SU25_B_t-2	0.02	0.45	-0.42	-0.32	-0.03	-0.06	-0.15	-0.22	0.07	0.2	0.07	-0.06	-0.06	0.56	0.39	0.6	0.53	0.19	0.42	-0.15	-0.14	-0.31	-0.13	1	
SU25_B_t-1	0.14	0.41	-0.41	-0.3	-0.02	-0.05	-0.14	-0.21	0.06	0.19	0.07	-0.05	-0.06	0.25	0.59	0.31	0.62	0.24	0.3	-0.03	-0.17	-0.09	-0.25	0.38	1

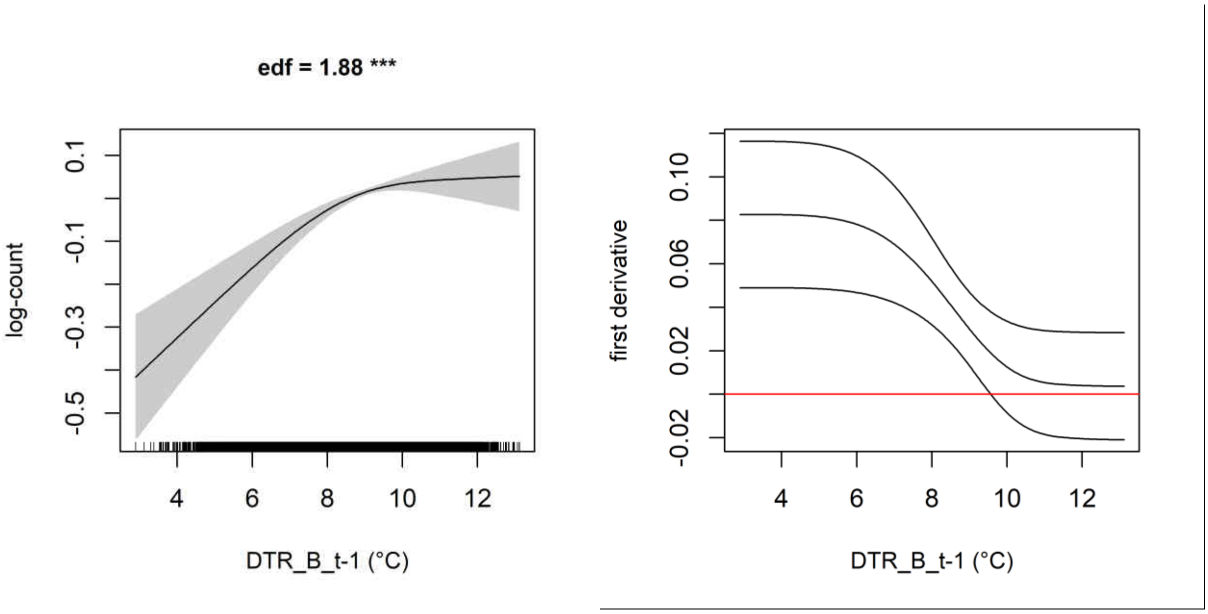
S5.4

Criterion used for the assignment of “high uncertainty” or “moderate uncertainty” in addition to the main categories describing the type of relationship between bird counts and the extreme climatic indices. On the left, smooth functions with the estimated degree of freedom (edf) and the corresponding level of significance (***: p-value ≤ 0.001; **: 0.001 < p-value ≤ 0.01; *: 0.1; p-value ≤ 0.05) are showed (see Figure 5.2 in the main text for details on the features of the graphs). On the right, the first derivative with confidence interval of the function is showed, and the red line indicates the zero value where the slope is null. In the case A), the assessment of the effects was straightforward, since the confidence intervals around both the estimated smooth and the first derivative of the smooth function were consistent. In the case B), the relationship was specified as “moderate uncertainty” because the confidence interval of the smooth showed opposite directions for a restricted interval of values of the explanatory variable and the confidence interval for the first derivative included the zero value for that interval. In the case C), along the entire domain of the function, the confidence interval of the smooth showed opposite directions and that of the first derivative always included the zero value.

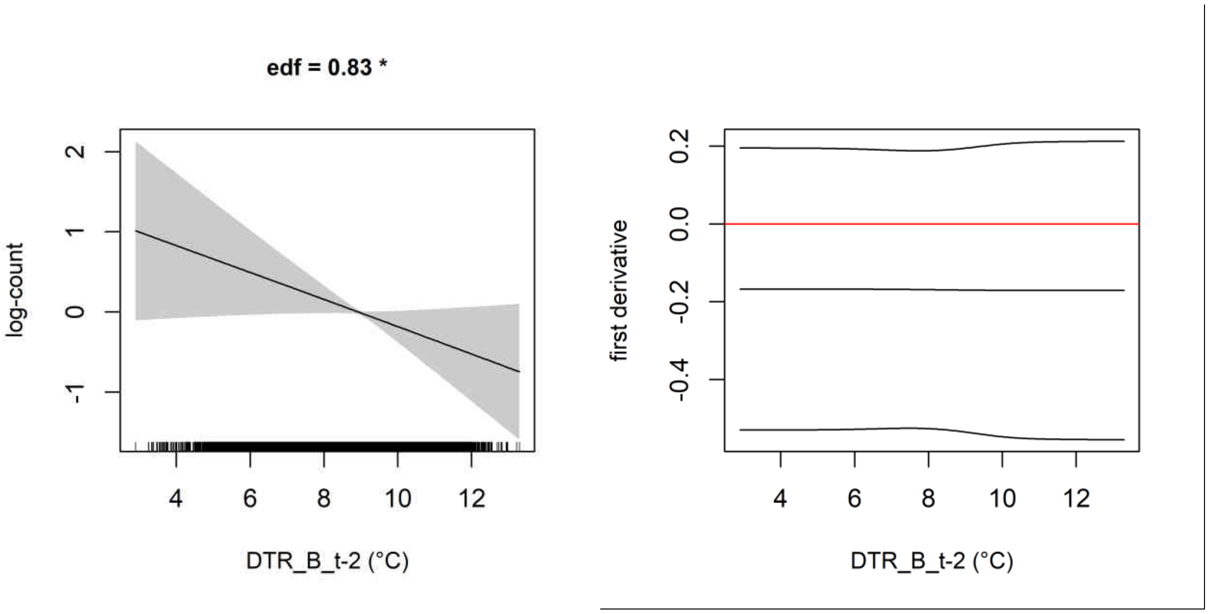
A) The effect was not specified neither as “moderate uncertainty” nor as “high uncertainty” (Song Thrush *Turdus philomelos*, DD_B_t-1 = Dry days in the breading season at the time *t-1*).



B) The effect was specified as “moderate uncertainty” (Eurasian Wren *Troglodytes troglodytes*, DTR_B_t-1 = diurnal temperature range in the breading season at the time *t-1*)



C) The effect was specified as “high uncertainty” (Twite *Linaria flavirostris*, DTR_B_t-2 = diurnal temperature range in the breading season at the time *t-2*).



S5.5

AIC comparison between the Poisson and the negative binomial GAMs. NB = negative binomial; POIS = Poisson. In the negative binomial GAMs, the variance is a quadratic function of the mean ($\sigma^2 = \mu + \mu^2/\theta$) (Zuur et al., 2009). The smaller the dispersion parameter θ, the larger the overdispersion. Bird species are listed according to the International Ornithological Committee (IOC) World Bird List (Gill et al., 2022) following the taxonomic order.

Species	Model	AIC	θ
Little Grebe	NB-GAM	19,318	0.042
(*Tachybaptus ruficollis*)	POIS-GAM	25,214	-
Great Crested Grebe	NB-GAM	20,973	0.031
(*Podiceps cristatus*)	POIS-GAM	38,686	-
Great Cormorant	NB-GAM	54,329	0.135
(*Phalacrocorax carbo*)	POIS-GAM	80,106	-
Little Egret	NB-GAM	13,243	0.099
(*Egretta garzetta*)	POIS-GAM	18,244	-
Grey Heron	NB-GAM	102,683	0.548
(*Ardea cinerea*)	POIS-GAM	114,531	-
Mute Swan	NB-GAM	65,444	0.075
(*Cygnus olor*)	POIS-GAM	169,388	-
Greylag Goose	NB-GAM	75,307	0.044
(*Anser anser*)	POIS-GAM	297,005	-
Canada Goose	NB-GAM	132,710	0.084
(*Branta canadensis*)	POIS-GAM	468,442	-
Egyptian Goose	NB-GAM	8305	0.032
(*Alopochen aegyptiaca*)	POIS-GAM	16,344	-
Common Shelduck	NB-GAM	41,204	0.065
(*Tadorna tadorna*)	POIS-GAM	122,801	-
Mandarin Duck	NB-GAM	10,330	0.017
(*Aix galericulata*)	POIS-GAM	16,340	-
Gadwall	NB-GAM	14,423	0.025
(*Mareca strepera*)	POIS-GAM	27,997	-
Eurasian Teal	NB-GAM	11,341	0.010
(*Anas crecca*)	POIS-GAM	26,371	-
Mallard	NB-GAM	258,548	0.360
(*Anas platyrhynchos*)	POIS-GAM	493,862	-
Tufted Duck	NB-GAM	48,722	0.028
(*Aythya fuligula*)	POIS-GAM	148,007	-
Common Merganser	NB-GAM	11,972	0.030
(*Mergus merganser*)	POIS-GAM	17,813	-
Red Kite	NB-GAM	40,861	0.150
(*Milvus milvus*)	POIS-GAM	53,751	-
Western Marsh Harrier	NB-GAM	5,495	0.436
(*Circus aeruginosus*)	POIS-GAM	5,743	-

S5.5 (cont.)

Hen Harrier	NB-GAM	3,741	0.102
(*Circus cyaneus*)	POIS-GAM	4,002	-
Northern Goshawk	NB-GAM	2,910	0.283
(*Accipiter gentilis*)	POIS-GAM	2,940	-
Eurasian Sparrowhawk	NB-GAM	54,421	1.939
(*Accipiter nisus*)	POIS-GAM	54,584	-
Common Buzzard	NB-GAM	141,264	2.226
(*Buteo buteo*)	POIS-GAM	145,295	-
Common Kestrel	NB-GAM	87,368	2.926
(*Falco tinnunculus*)	POIS-GAM	87,745	-
Merlin	NB-GAM	4,112	0.199
(*Falco columbarius*)	POIS-GAM	4,213	-
Peregrine Falcon	NB-GAM	11,954	0.111
(*Falco peregrinus*)	POIS-GAM	12,572	-
Willow Ptarmigan	NB-GAM	27,002	0.435
(*Lagopus lagopus*)	POIS-GAM	41,289	-
Black Grouse	NB-GAM	3,734	0.033
(*Lyrurus tetrix*)	POIS-GAM	6,018	-
Red-legged Partridge	NB-GAM	112,058	0.321
(*Alectoris rufa*)	POIS-GAM	149,418	-
Grey Partridge	NB-GAM	48,490	0.122
(*Perdix perdix*)	POIS-GAM	64,188	-
Common Pheasant	NB-GAM	293,605	1.032
(*Phasianus colchicus*)	POIS-GAM	411,557	
Indian Peafowl	NB-GAM	8,934	0.012
(*Pavo cristatus*)	POIS-GAM	15,487	-
Common Moorhen	NB-GAM	107,452	0.434
(*Gallinula chloropus*)	POIS-GAM	125,333	-
Eurasian Coot	NB-GAM	68,608	0.069
(*Fulica atra*)	POIS-GAM	153,660	-
Eurasian Oystercatcher	NB-GAM	77,239	0.158
(*Haematopus ostralegus*)	POIS-GAM	155,803	-
Common Ringed Plover	NB-GAM	8,386	0.018
(*Charadrius hiaticula*)	POIS-GAM	23,071	-
European Golden Plover	NB-GAM	32,407	0.020
(*Pluvialis apricaria*)	POIS-GAM	197,996	-
Northern Lapwing	NB-GAM	150,104	0.149
(*Vanellus vanellus*)	POIS-GAM	385,827	-
Common Snipe	NB-GAM	33,099	0.210
(*Gallinago gallinago*)	POIS-GAM	42,192	-
Eurasian Woodcock	NB-GAM	3,360	0.044
(*Scolopax rusticola*)	POIS-GAM	3,562	-

S5.4 (cont.)

Eurasian Curlew	NB-GAM	104,154	0.226
(*Numenius arquata*)	POIS-GAM	179,712	-
Common Redshank	NB-GAM	24,076	0.030
(*Tringa totanus*)	POIS-GAM	54,069	-
Feral Pigeon	NB-GAM	183,088	0.110
(*Columba livia*)	POIS-GAM	689,152	-
Stock Dove	NB-GAM	158,887	0.310
(*Columba oenas*)	POIS-GAM	236,477	-
Common Wood Pigeon	NB-GAM	524,360	1.749
(*Columba palumbus*)	POIS-GAM	124,9704	-
Eurasian Collared Dove	NB-GAM	227,306	0.753
(*Streptopelia decaocto*)	POIS-GAM	307,907	-
Rose-ringed Parakeet	NB-GAM	17,981	0.359
(*Psittacula krameri*)	POIS-GAM	31,866	-
Western Barn Owl	NB-GAM	11,131	0.466
(*Tyto alba*)	POIS-GAM	11,276	-
Little Owl	NB-GAM	18,054	0.361
(*Athene noctua*)	POIS-GAM	18,362	-
Tawny Owl	NB-GAM	19,720	0.393
(*Strix aluco*)	POIS-GAM	19,996	-
Short-eared Owl	NB-GAM	4,265	0.090
(*Asio flammeus*)	POIS-GAM	4,664	-
Common Kingfisher	NB-GAM	12,554	0.221
(*Alcedo atthis*)	POIS-GAM	12,998	-
European Green Woodpecker	NB-GAM	109,915	1.786
(*Picus viridis*)	POIS-GAM	113,137	-
Great Spotted Woodpecker	NB-GAM	145,758	2.083
(*Dendrocopos major*)	POIS-GAM	150,021	-
Lesser Spotted Woodpecker	NB-GAM	5,646	0.048
(*Dryobates minor*)	POIS-GAM	6,113	-
Eurasian Skylark	NB-GAM	322,014	0.691
(*Alauda arvensis*)	POIS-GAM	520,001	-
Meadow Pipit	NB-GAM	185,448	0.348
(*Anthus pratensis*)	POIS-GAM	338,906	-
Grey Wagtail	NB-GAM	45,711	0.166
(*Motacilla cinerea*)	POIS-GAM	51,817	-
White Wagtail	NB-GAM	176,680	1.010
(*Motacilla alba*)	POIS-GAM	192,952	-
White-throated Dipper	NB-GAM	13,359	0.167
(*Cinclus cinclus*)	POIS-GAM	14,279	-
Eurasian Wren	NB-GAM	408,065	2.140
(*Troglodytes troglodytes*)	POIS-GAM	525,328	-

S5.5 (cont.)

Dunnock	NB-GAM	289,119	2.010
(*Prunella modularis*)	POIS-GAM	326,508	-
European Robin	NB-GAM	366,071	2.692
(*Erithacus rubecula*)	POIS-GAM	436,402	-
European Stonechat	NB-GAM	34,746	0.167
(*Saxicola rubicola*)	POIS-GAM	44,675	-
Common Blackbird	NB-GAM	419,651	3.323
(*Turdus merula*)	POIS-GAM	537,834	-
Fieldfare	NB-GAM	16,189	0.004
(*Turdus pilaris*)	POIS-GAM	207,284	-
Song Thrush	NB-GAM	269,617	2.183
(*Turdus philomelos*)	POIS-GAM	294,758	-
Redwing	NB-GAM	4,981	0.002
(*Turdus iliacus*)	POIS-GAM	27,780	-
Mistle Thrush	NB-GAM	170,635	0.685
(*Turdus viscivorus*)	POIS-GAM	195,102	-
Cetti's Warbler	NB-GAM	7,694	0.119
(*Cettia cetti*)	POIS-GAM	9,523	-
Goldcrest	NB-GAM	141,265	0.498
(*Regulus regulus*)	POIS-GAM	177,541	-
Long-tailed Tit	NB-GAM	178,589	0.406
(*Aegithalos caudatus*)	POIS-GAM	241,179	-
Marsh Tit	NB-GAM	30,988	0.161
(*Poecile palustris*)	POIS-GAM	36,197	-
Willow Tit	NB-GAM	11,864	0.040
(*Poecile montanus*)	POIS-GAM	14,646	-
Coal Tit	NB-GAM	146,565	0.557
(*Periparus ater*)	POIS-GAM	183,423	-
Eurasian Blue Tit	NB-GAM	383,630	1.978
(*Cyanistes caeruleus*)	POIS-GAM	512,345	-
Great Tit	NB-GAM	325,694	2.137
(*Parus major*)	POIS-GAM	384,297	-
Eurasian Nuthatch	NB-GAM	92,844	0.523
(*Sitta europaea*)	POIS-GAM	106,637	-
Eurasian Treecreeper	NB-GAM	64,959	0.418
(*Certhia familiaris*)	POIS-GAM	70,455	-
Eurasian Jay	NB-GAM	117,423	0.957
(*Garrulus glandarius*)	POIS-GAM	124,645	-
Eurasian Magpie	NB-GAM	291,250	1.444
(*Pica pica*)	POIS-GAM	357,679	
Western Jackdaw	NB-GAM	401,354	0.409
(*Coloeus monedula*)	POIS-GAM	1,180,042	-

S5.5 (cont.)

Rook	NB-GAM	356,882	0.185
(*Corvus frugilegus*)	POIS-GAM	2,153,213	-
Carrion Crow	NB-GAM	436,559	1.207
(*Corvus corone*)	POIS-GAM	854,899	-
Hooded Crow	NB-GAM	24,395	0.733
(*Corvus cornix*)	POIS-GAM	31,770	-
Northern Raven	NB-GAM	64,714	0.282
(*Corvus corax*)	POIS-GAM	84,583	-
Common Starling	NB-GAM	401,004	0.363
(*Sturnus vulgaris*)	POIS-GAM	1,466,556	-
House Sparrow	NB-GAM	360,725	0.475
(*Passer domesticus*)	POIS-GAM	869,844	-
Eurasian Tree Sparrow	NB-GAM	51,610	0.071
(*Passer montanus*)	POIS-GAM	101,802	-
Common Chaffinch	NB-GAM	422,530	2.479
(*Fringilla coelebs*)	POIS-GAM	551,913	-
European Greenfinch	NB-GAM	270,762	0.902
(*Chloris chloris*)	POIS-GAM	366,628	-
European Goldfinch	NB-GAM	298,947	0.882
(*Carduelis carduelis*)	POIS-GAM	414,138	-
Eurasian Siskin	NB-GAM	49,396	0.087
(*Spinus spinus*)	POIS-GAM	88,843	-
Common Linnet	NB-GAM	245,630	0.329
(*Linaria cannabina*)	POIS-GAM	464,910	-
Twite	NB-GAM	5,910	0.021
(*Linaria flavirostris*)	POIS-GAM	10,533	-
Lesser Redpoll	NB-GAM	42,279	0.066
(*Acanthis cabaret*)	POIS-GAM	80,791	-
Red Crossbill	NB-GAM	17,134	0.033
(*Loxia curvirostra*)	POIS-GAM	42,327	-
Eurasian Bullfinch	NB-GAM	113,174	0.411
(*Pyrrhula pyrrhula*)	POIS-GAM	128,298	-
Yellowhammer	NB-GAM	208,303	0.669
(*Emberiza citrinella*)	POIS-GAM	273,161	-
Common Reed Bunting	NB-GAM	99,024	0.272
(*Emberiza schoeniclus*)	POIS-GAM	128,530	-
Corn Bunting	NB-GAM	38,818	0.055
(*Emberiza calandra*)	POIS-GAM	74,884	-

S5.6

Explained deviance (%) for the negative binomial GAMs. Bird species are listed according to the International Ornithological Committee (IOC) World Bird List (Gill et al., 2022) following the taxonomic order.

Species	Explained deviance (%)
Little Grebe (*Tachybaptus ruficollis)*	19.65
Great Crested Grebe (*Podiceps cristatus)*	36.34
Great Cormorant (*Phalacrocorax carbo)*	31.02
Little Egret (*Egretta garzetta*)	58.49
Grey Heron (*Ardea cinerea*)	14.98
Mute Swan (*Cygnus olor*)	38.47
Greylag Goose (*Anser anser*)	22.70
Canada Goose (*Branta canadensis*)	15.47
Egyptian Goose (*Alopochen aegyptiaca*)	65.45
Common Shelduck (*Tadorna tadorna*)	55.91
Mandarin Duck (*Aix galericulata*)	32.77
Gadwall (*Mareca strepera*)	45.25
Eurasian Teal (*Anas crecca*)	30.06
Mallard (*Anas platyrhynchos*)	17.46
Tufted Duck (*Aythya fuligula*)	21.27
Common Merganser (*Mergus merganser*)	36.74
Red Kite (*Milvus milvus*)	38.01
Western Marsh Harrier (*Circus aeruginosus*)	59.61
Hen Harrier (*Circus cyaneus*)	42.07
Northern Goshawk (*Accipiter gentilis*)	32.73

S5.6 (cont.)

Eurasian Sparrowhawk (*Accipiter nisus*)	4.33
Common Buzzard (*Buteo buteo*)	30.18
Common Kestrel (*Falco tinnunculus*)	9.99
Merlin (*Falco columbarius*)	36.50
Peregrine Falcon (*Falco peregrinus*)	17.63
Willow Ptarmigan (*Lagopus lagopus*)	85.88
Black Grouse (*Lyrurus tetrix*)	72.80
Red-legged Partridge (*Alectoris rufa*)	38.40
Grey Partridge (*Perdix perdix*)	32.49
Common Pheasant (*Phasianus colchicus*)	31.48
Indian Peafowl (*Pavo cristatus*)	24.95
Common Moorhen (*Gallinula chloropus*)	25.41
Eurasian Coot (*Fulica atra*)	28.53
Eurasian Oystercatcher (*Haematopus ostralegus*)	50.00
Common Ringed Plover (*Charadrius hiaticula*)	64.67
European Golden Plover (*Pluvialis apricaria*)	38.14
Northern Lapwing (*Vanellus vanellus*)	27.60
Common Snipe (*Gallinago gallinago*)	52.19
Eurasian Woodcock (*Scolopax rusticola*)	26.59
Eurasian Curlew (*Numenius arquata*)	45.57
Common Redshank (*Tringa totanus*)	36.87
Feral Pigeon (*Columba livia*)	25.83
Stock Dove (*Columba oenas*)	20.93
Common Wood Pigeon (*Columba palumbus*)	45.55

S5.6 (cont.)

Eurasian Collared Dove (*Streptopelia decaocto*)	40.51
Rose-ringed Parakeet (*Psittacula krameri*)	88.42
Western Barn Owl (*Tyto alba*)	26.95
Little Owl (*Athene noctua*)	18.96
Tawny Owl (*Strix aluco*)	12.05
Short-eared Owl (*Asio flammeus*)	46.21
Common Kingfisher (*Alcedo atthis*)	25.46
European Green Woodpecker (*Picus viridis*)	36.77
Great Spotted Woodpecker (*Dendrocopos major*)	29.85
Lesser Spotted Woodpecker (*Dryobates minor*)	22.75
Eurasian Skylark (*Alauda arvensis*)	26.43
Meadow Pipit (*Anthus pratensis*)	56.90
Grey Wagtail (*Motacilla cinerea*)	13.91
White Wagtail (*Motacilla alba*)	9.72
White-throated Dipper (*Cinclus cinclus*)	35.45
Eurasian Wren (*Troglodytes troglodytes*)	26.34
Dunnock (*Prunella modularis*)	26.77
European Robin (*Erithacus rubecula*)	37.86
European Stonechat (*Saxicola rubicola*)	48.30
Common Blackbird (*Turdus merula*)	50.04
Fieldfare (*Turdus pilaris*)	19.30
Song Thrush (*Turdus philomelos*)	24.83
Redwing (*Turdus iliacus*)	24.04
Mistle Thrush (*Turdus viscivorus*)	9.52

S5.6 (cont.)

Cetti's Warbler (*Cettia cetti*)	64.02
Goldcrest (*Regulus regulus*)	32.43
Long-tailed Tit (*Aegithalos caudatus*)	17.96
Marsh Tit (*Poecile palustris*)	33.53
Willow Tit (*Poecile montanus*)	27.39
Coal Tit (*Periparus ater*)	36.81
Eurasian Blue Tit (*Cyanistes caeruleus*)	38.39
Great Tit (*Parus major*)	33.17
Eurasian Nuthatch (*Sitta europaea*)	39.00
Eurasian Treecreeper (*Certhia familiaris*)	21.14
Eurasian Jay (*Garrulus glandarius*)	24.21
Eurasian Magpie (*Pica pica*)	37.42
Western Jackdaw (*Coloeus monedula*)	13.55
Rook (*Corvus frugilegus*)	13.03
Carrion Crow (*Corvus corone*)	24.07
Hooded Crow (*Corvus cornix*)	86.88
Northern Raven (*Corvus corax*)	42.21
Common Starling (*Sturnus vulgaris*)	25.37
House Sparrow (*Passer domesticus*)	35.37
Eurasian Tree Sparrow (*Passer montanus*)	38.43
Common Chaffinch (*Fringilla coelebs*)	30.44
European Greenfinch (*Chloris chloris*)	34.74
European Goldfinch (*Carduelis carduelis*)	26.36
Eurasian Siskin (*Spinus spinus*)	43.01

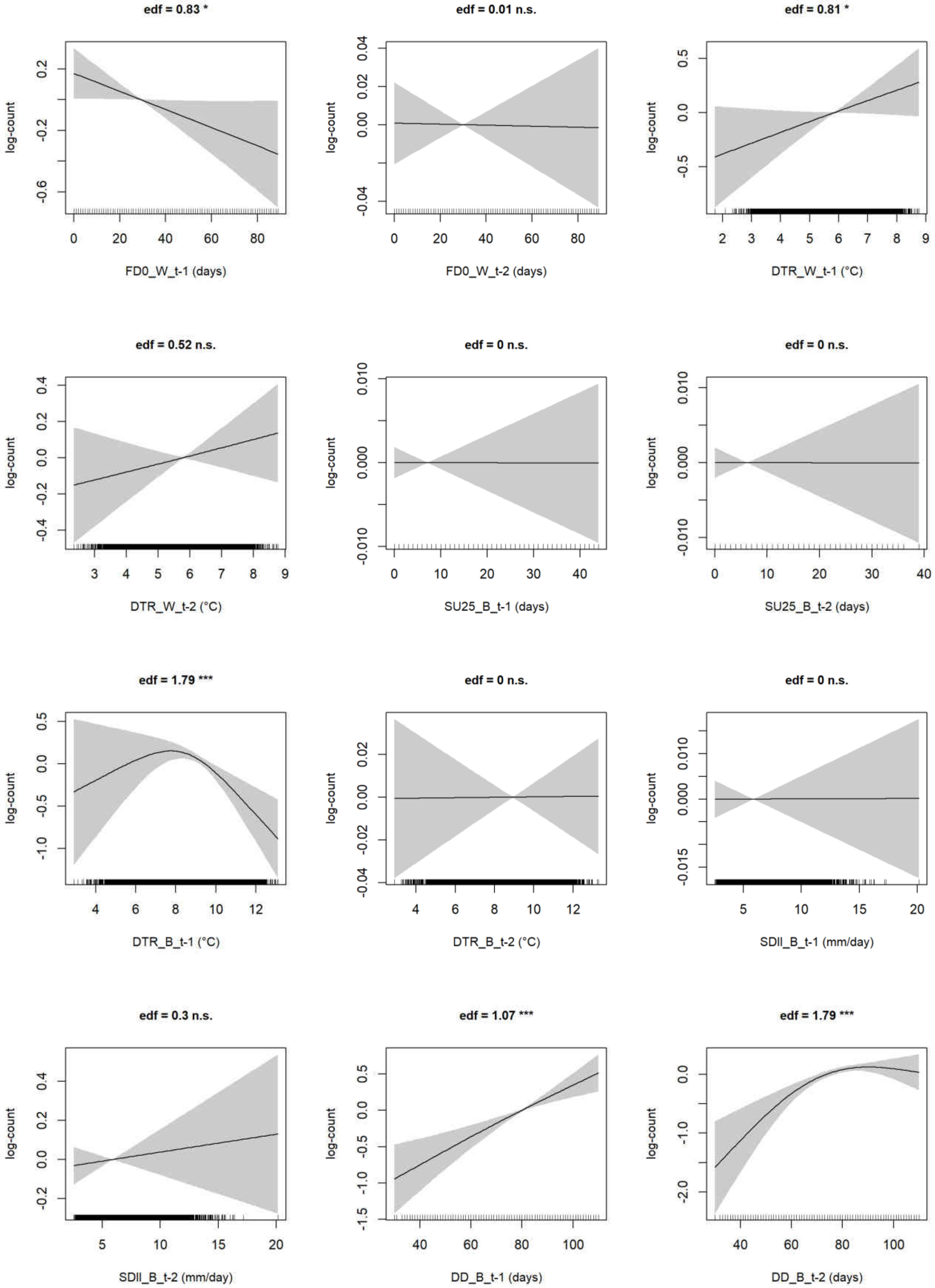
S5.6 (cont.)

Common Linnet (*Linaria cannabina*)	17.98
Twite (*Linaria flavirostris*)	63.33
Lesser Redpoll (*Acanthis cabaret*)	36.82
Red Crossbill (*Loxia curvirostra*)	57.48
Eurasian Bullfinch (*Pyrrhula pyrrhula*)	13.50
Yellowhammer (*Emberiza citrinella*)	38.84
Common Reed Bunting (*Emberiza schoeniclus*)	27.13
Corn Bunting (*Emberiza calandra*)	36.83

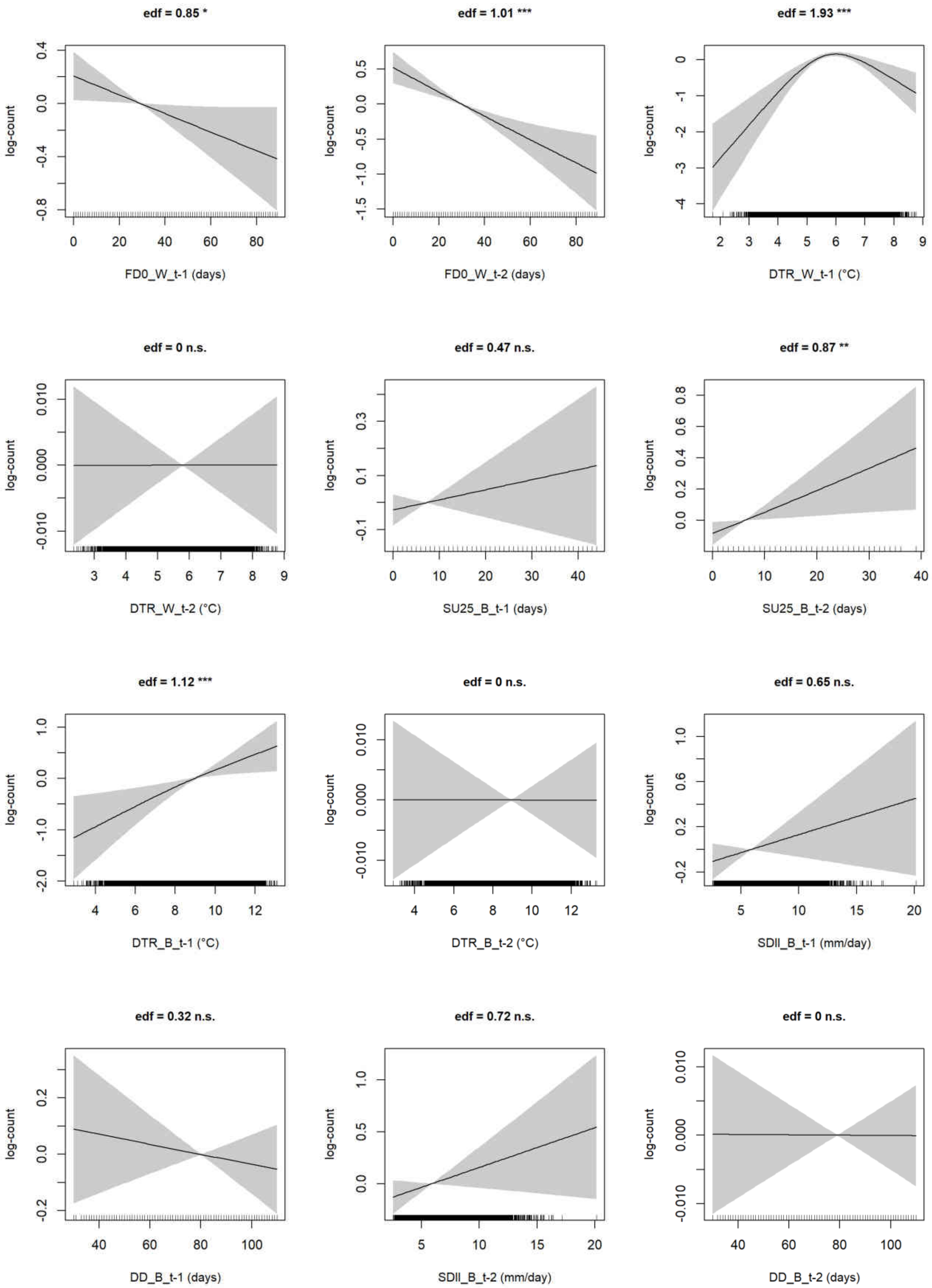
S5.7

Effects of extreme climatic events (ECEs) on bird relative abundance (counts). For each of the 100 species, partial effect plots describe the relationship between log-count (y-axis) and each climatic index (x-axis) net of the effects of the other explanatory variables included in the model. Extreme climatic indices: FD0 = frost days; DTR = daily temperature range; SU25 = summer days; SDII = simple precipitation intensity index; DD = dry days. After the variable name, "W" indicates the winter season, and "B" the breading season. Then, "*t-1*" indicates the association between counts in the year *t* and the weather variable of the preceding year, while "*t-2*" the association with the two-previous year (i.e. lagged effects, see Section 5.2.2 in the main text). Rugs on the x-axis represent the distribution of values of the variable. The estimated degree of freedom (edf) and the statistical significance (***: p-value ≤ 0.001; **: 0.001 < p-value ≤ 0.01; *: 0.1; p-value ≤ 0.05; n.s.: p-value > 0.05) for the smooths are shown on the top of the graph. The grey area represents the 95% confidence interval of the regression line.

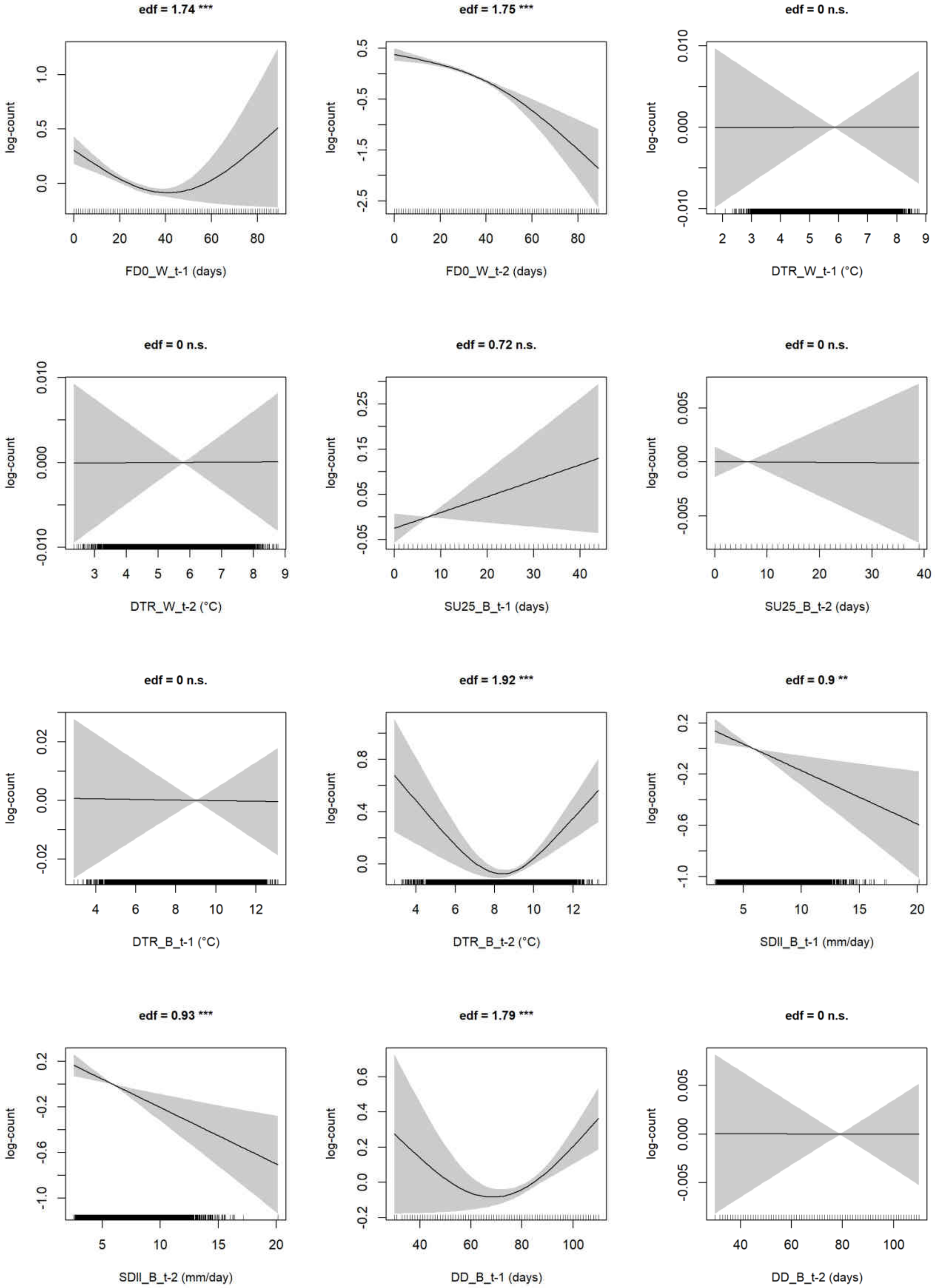
Little Grebe *Tachybaptus ruficollis*



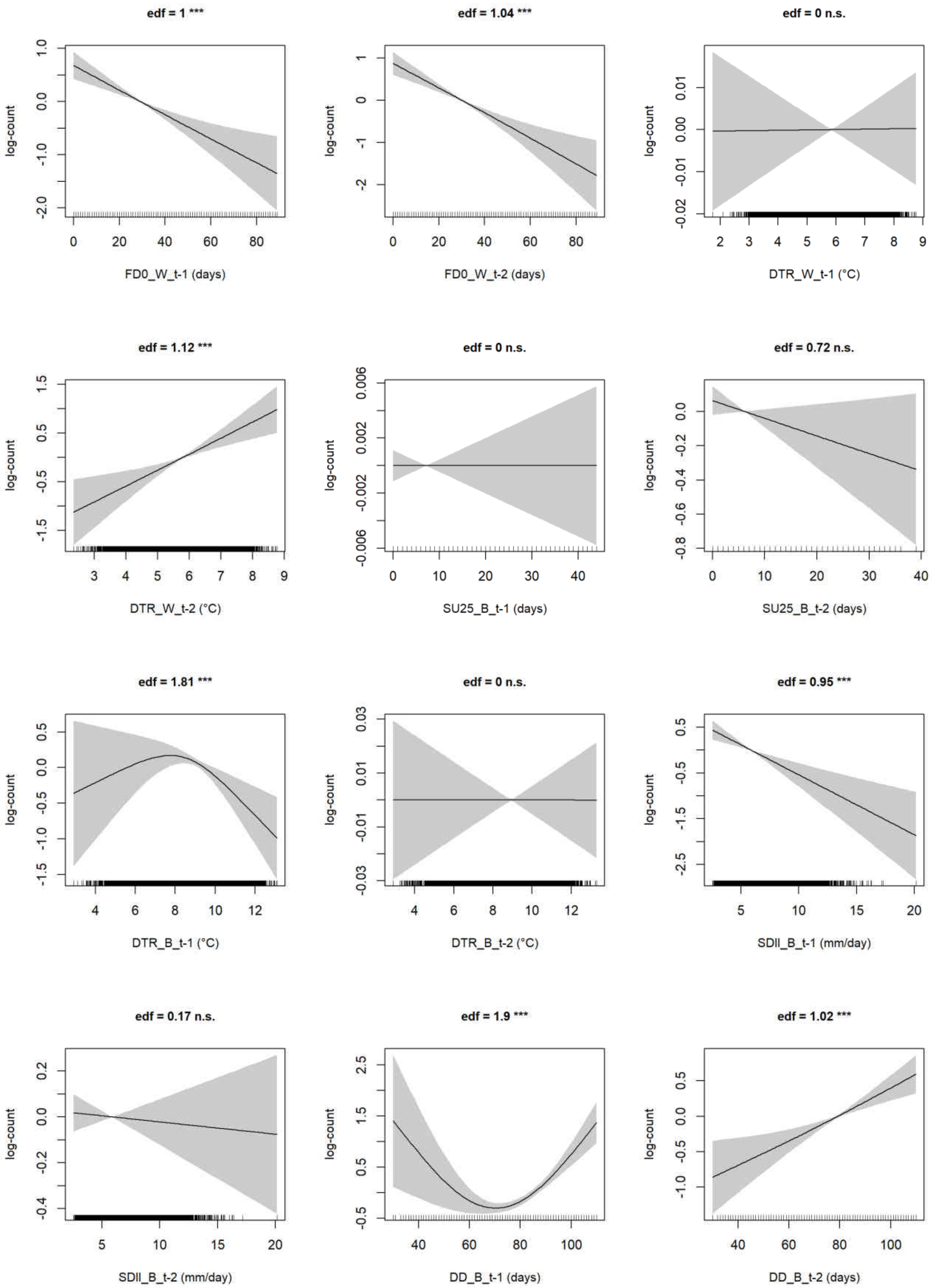
Great Crested Grebe *Podiceps cristatus*



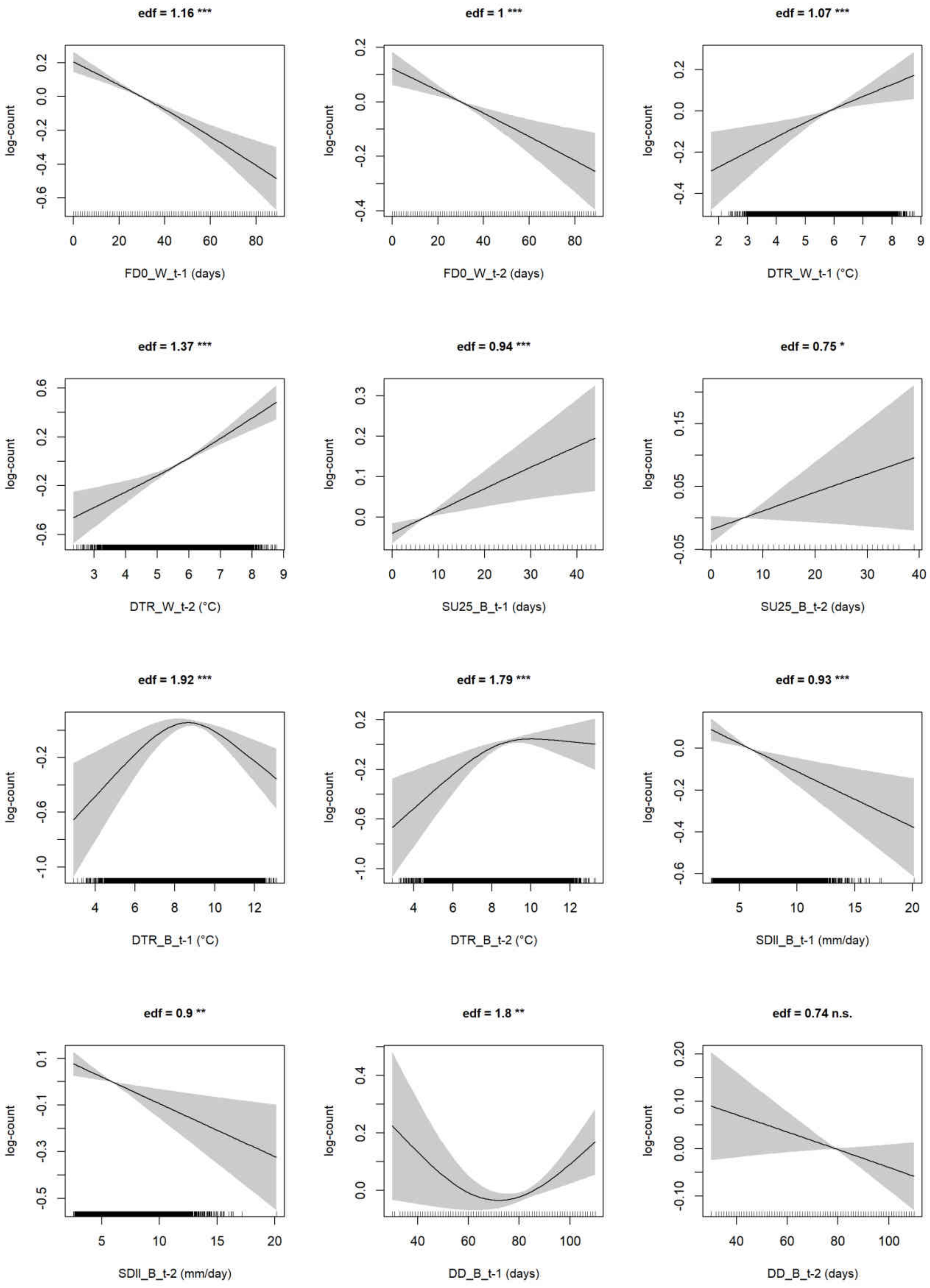
Great Cormorant *Phalacrocorax carbo*



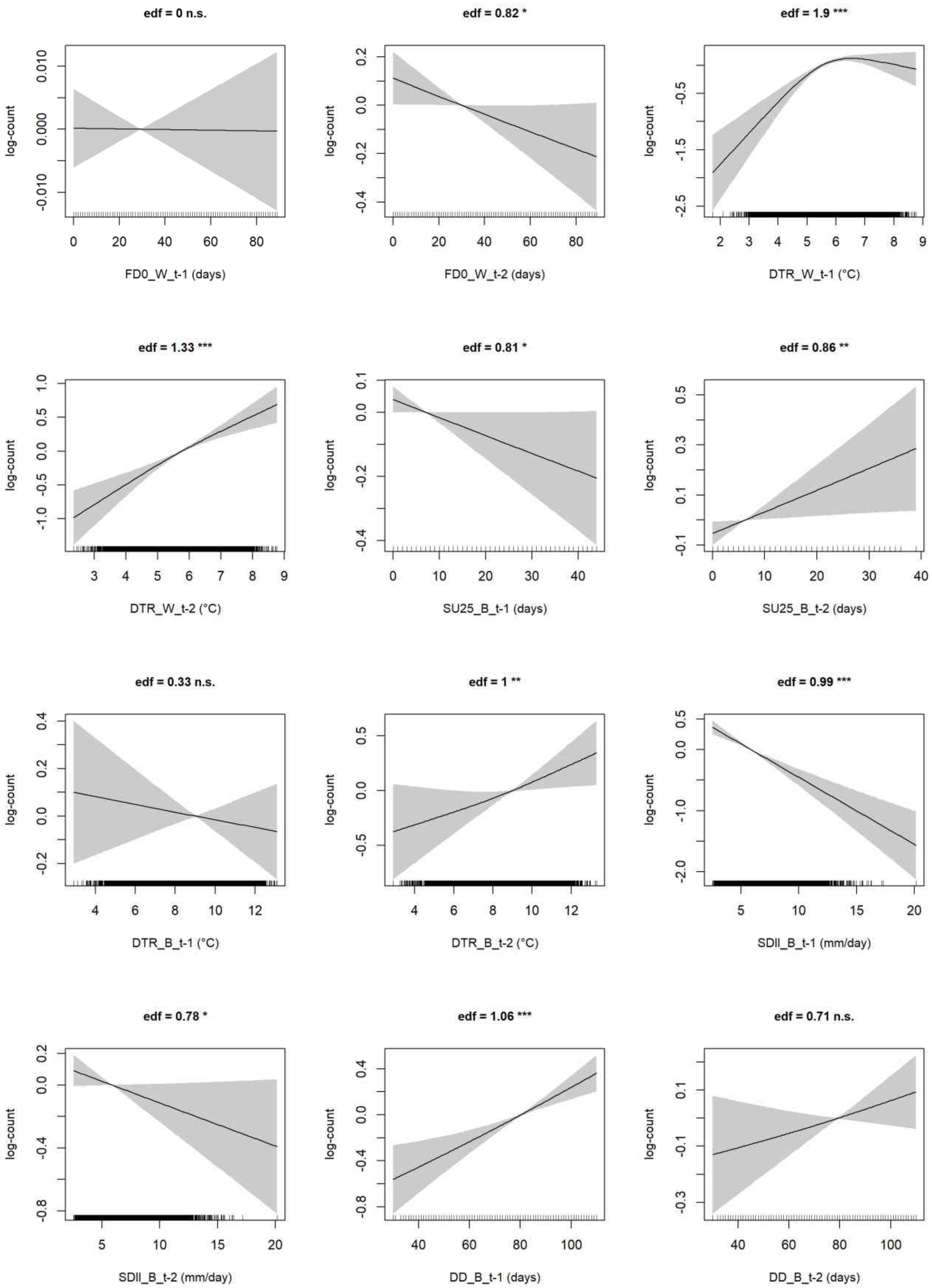
Little Egret *Egretta garzetta*



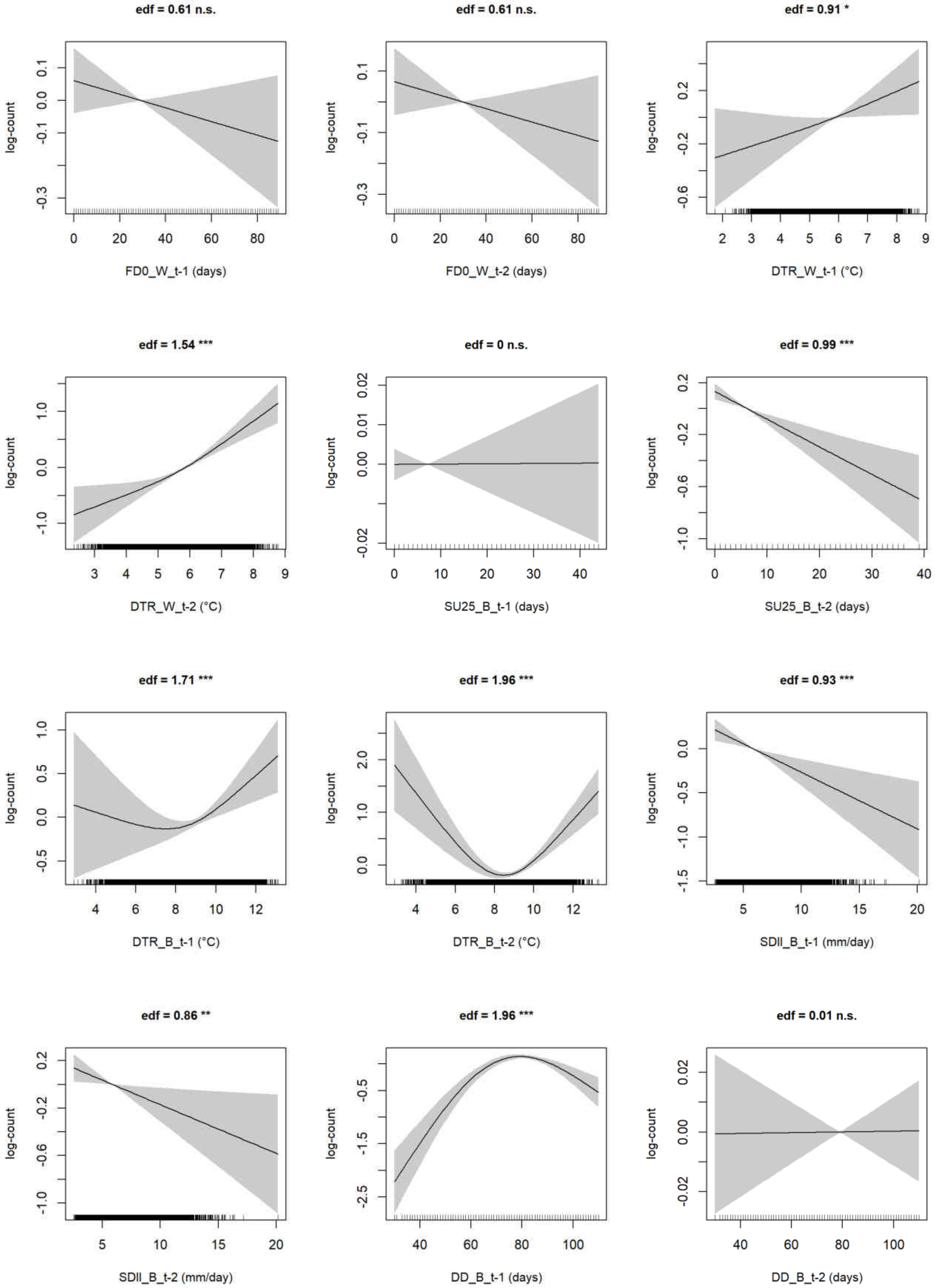
Grey Heron *Ardea cinerea*



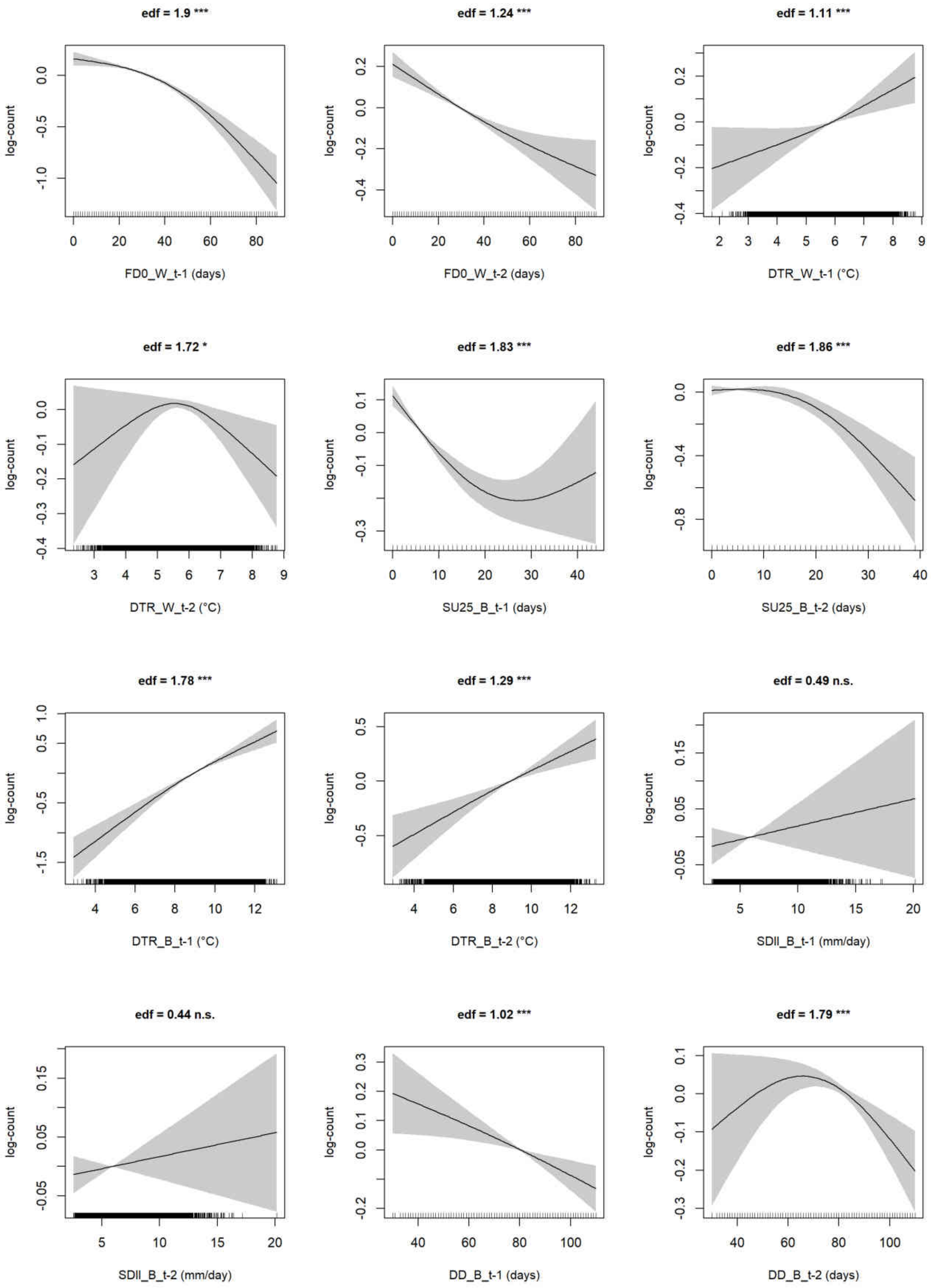
Mute Swan *Cygnus olor*



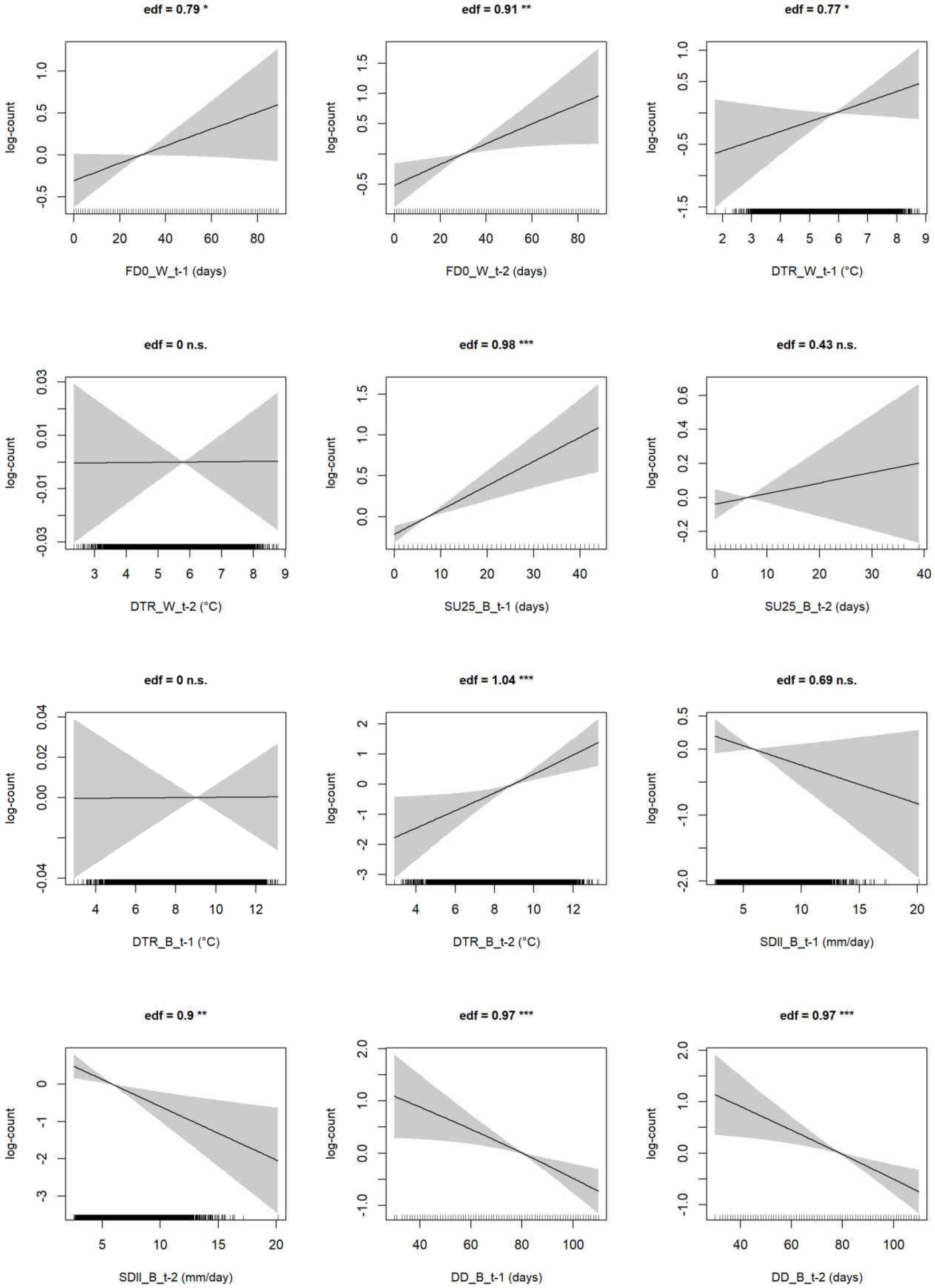
Greylag Goose *Anser anser*



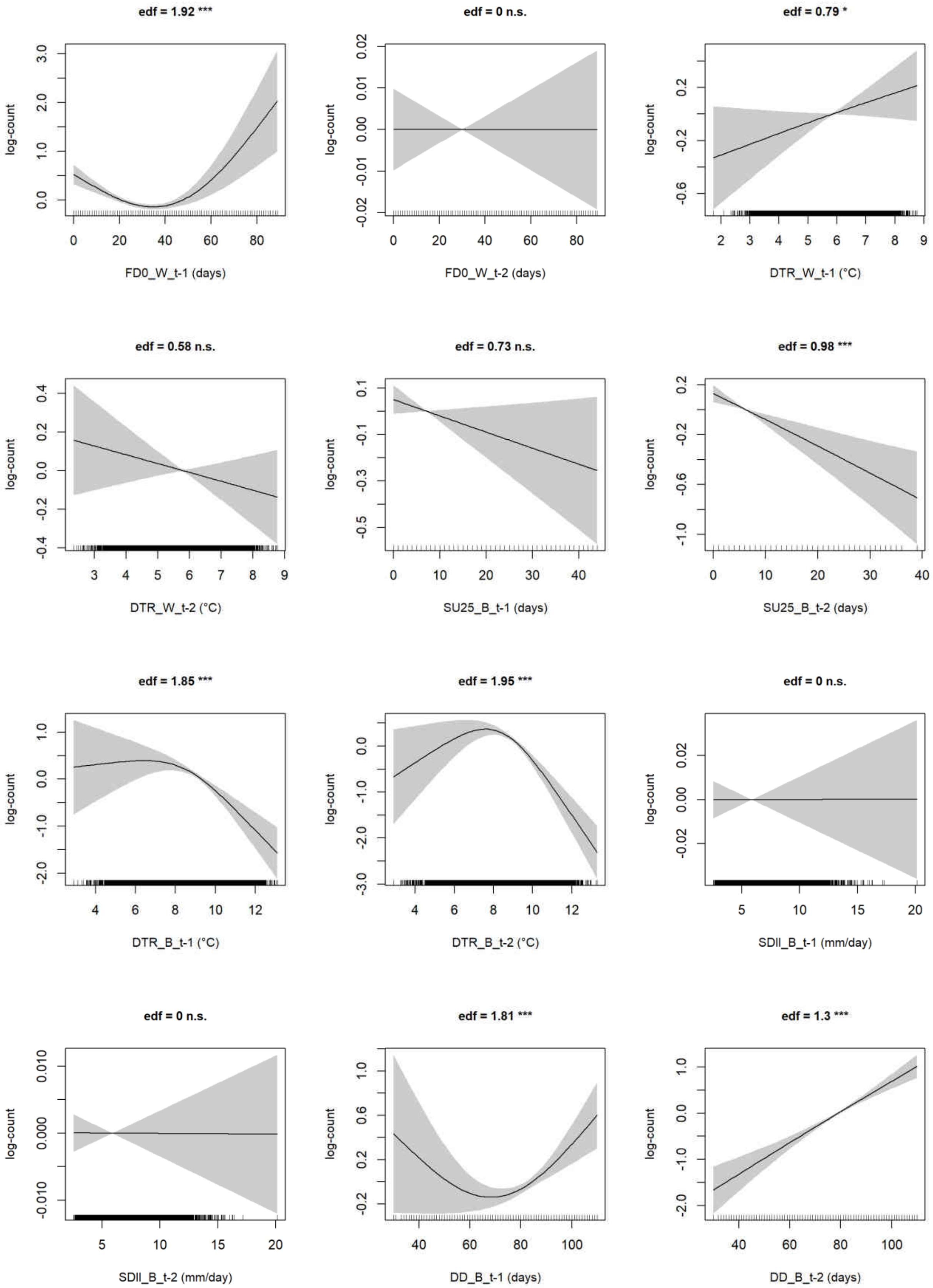
Canada Goose *Branta canadensis*



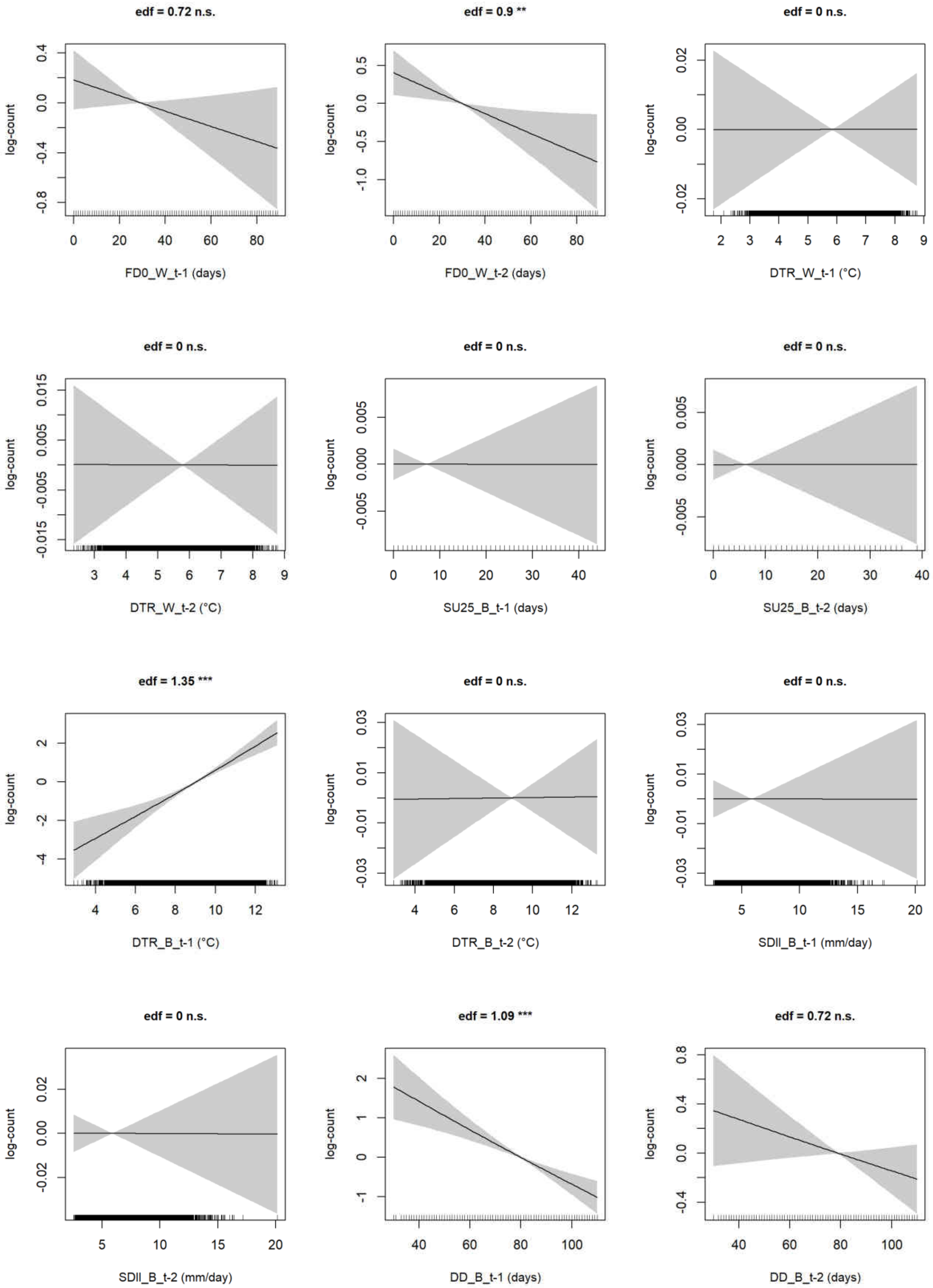
Egyptian Goose *Alopochen aegyptiaca*



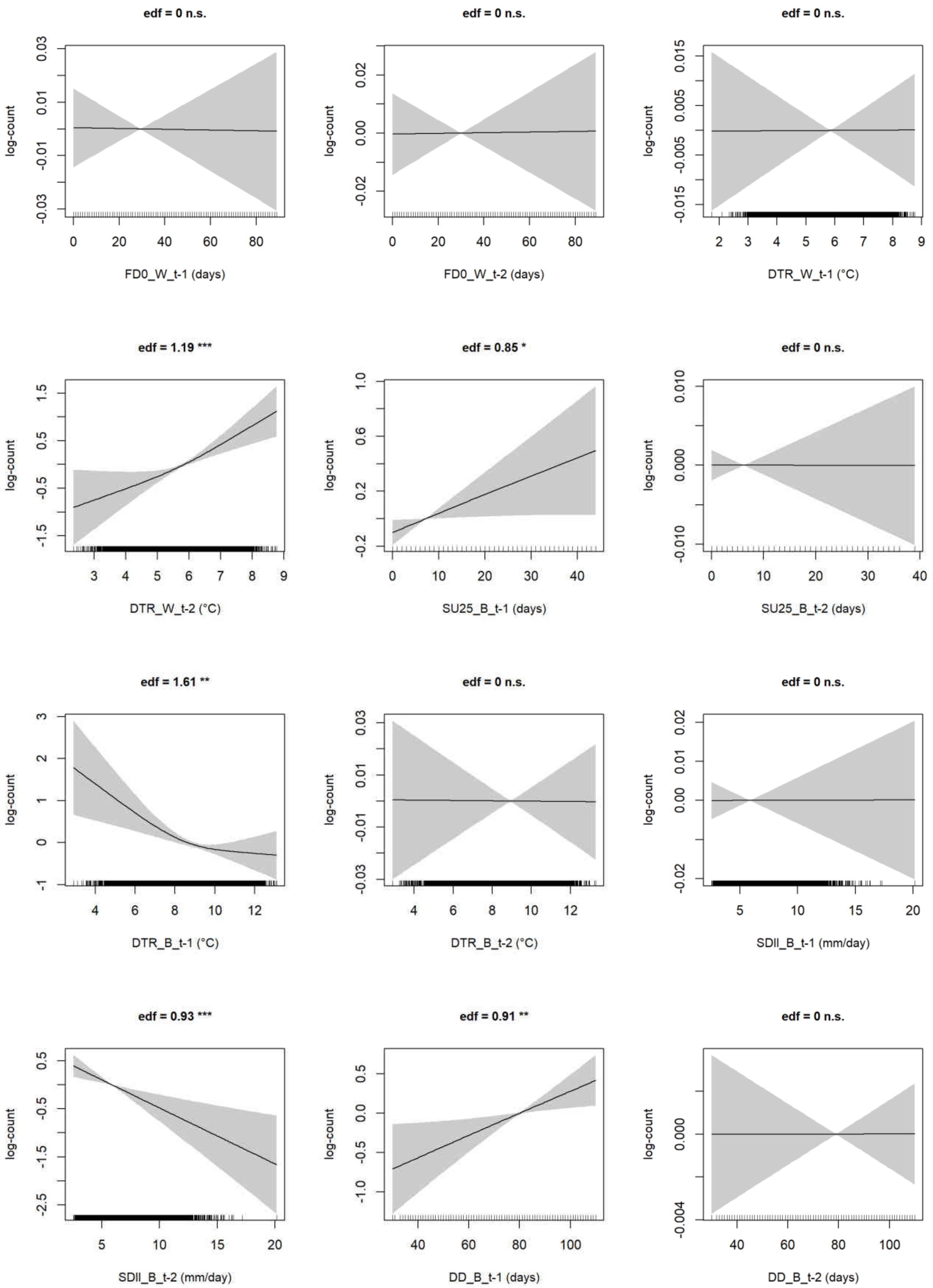
Common Shelduck *Tadorna tadorna*



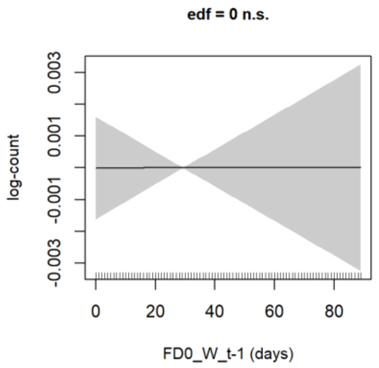
Mandarin Duck *Aix galericulata*

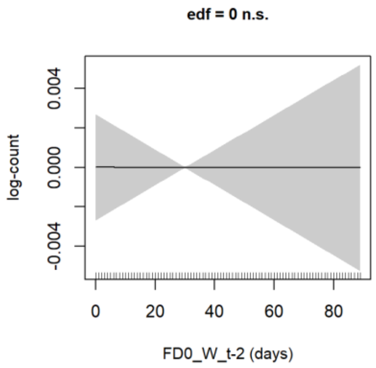


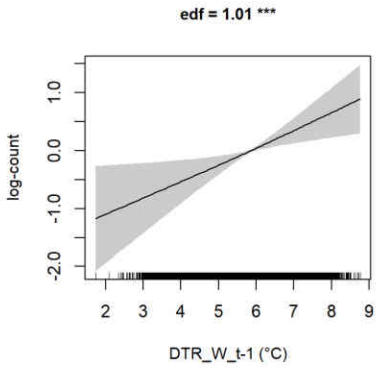
Gadwall *Mareca strepera*

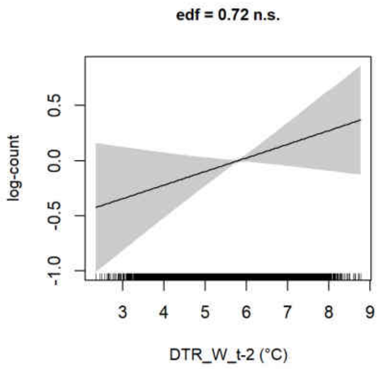


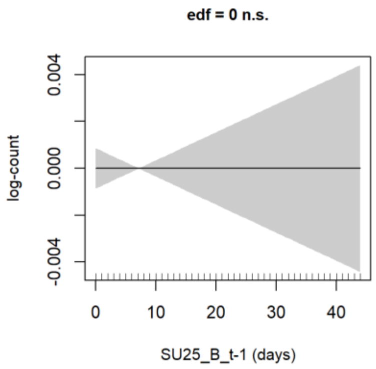
Eurasian Teal *Anas crecca*

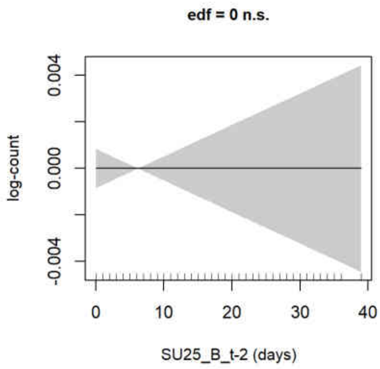


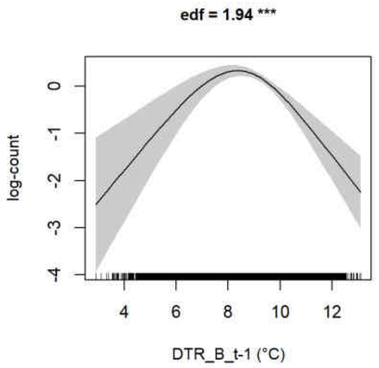


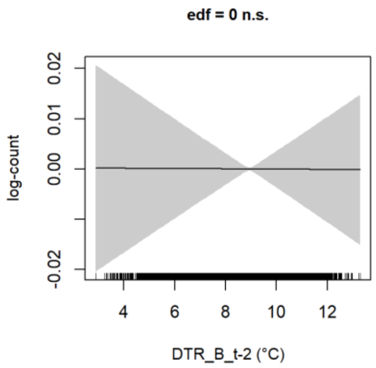


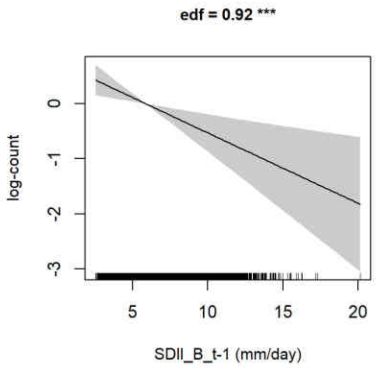


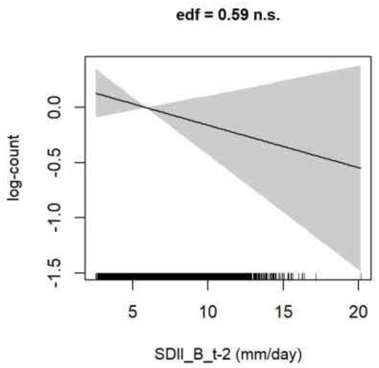


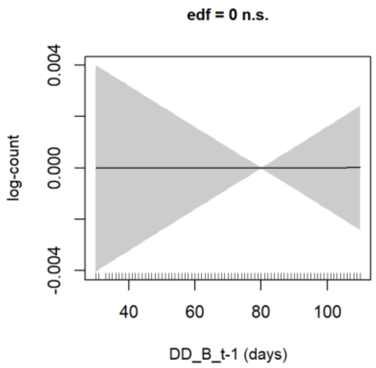


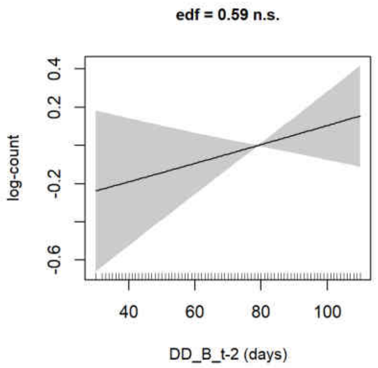




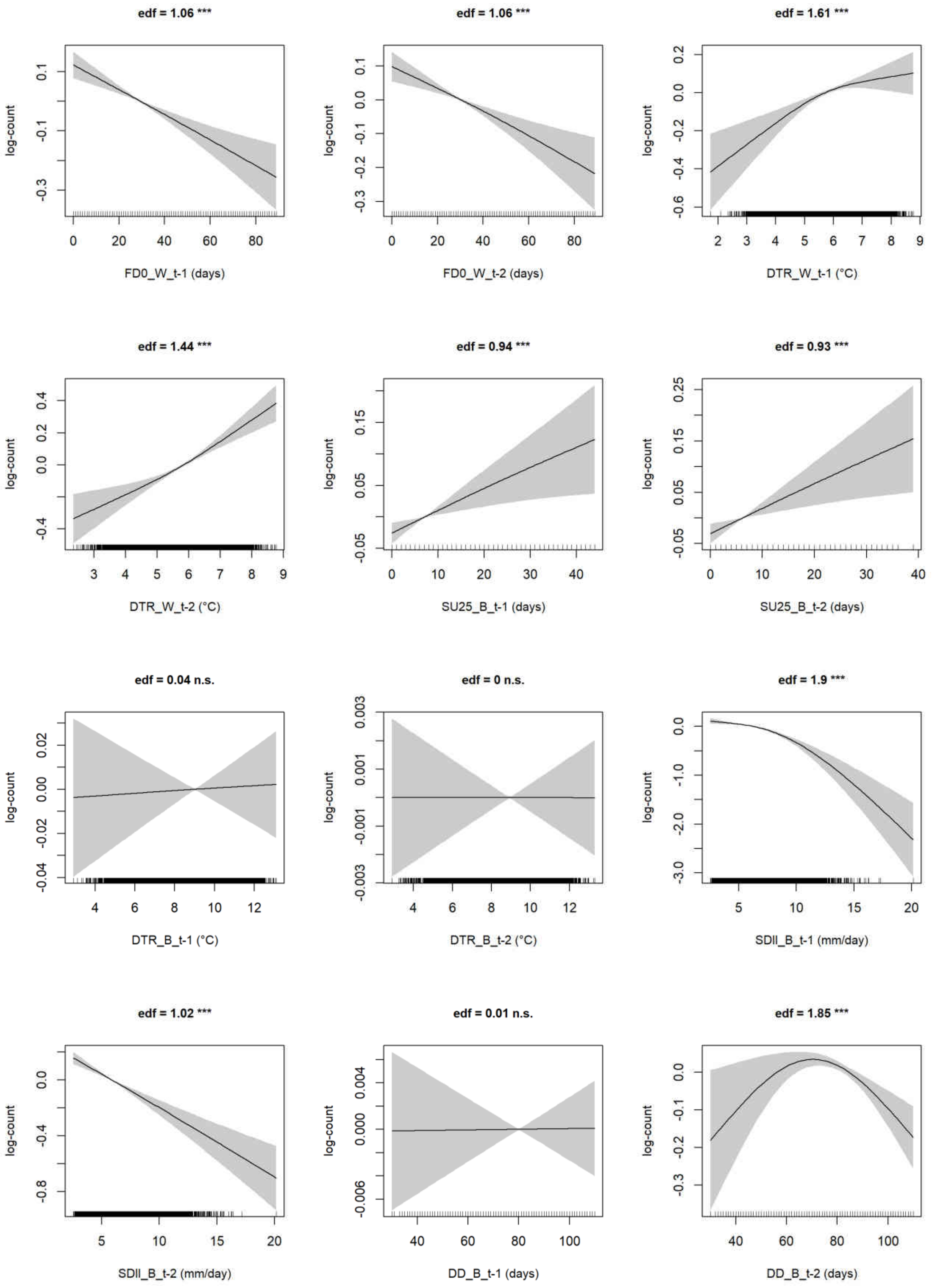




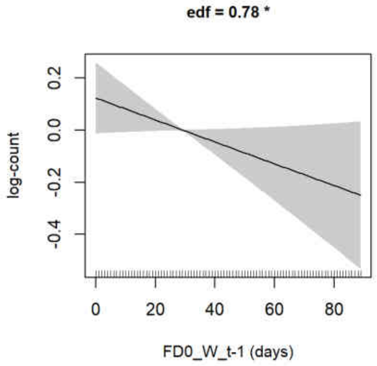


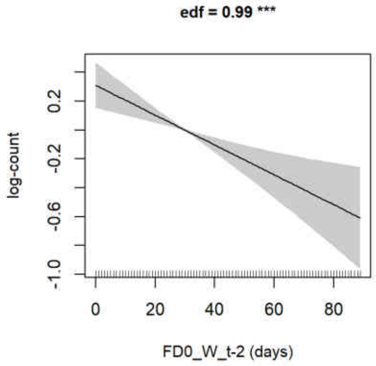


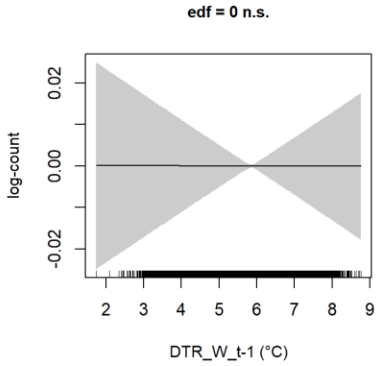
Mallard *Anas platyrhynchos*

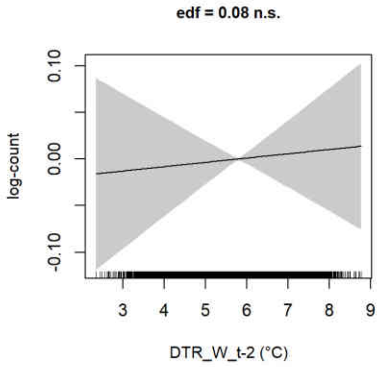


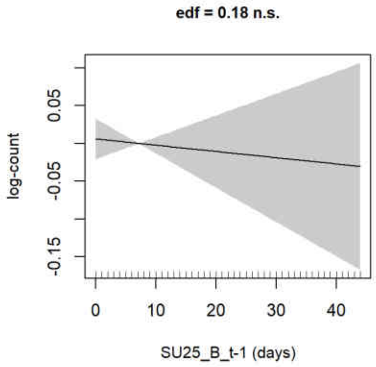
Tufted Duck *Aythya fuligula*

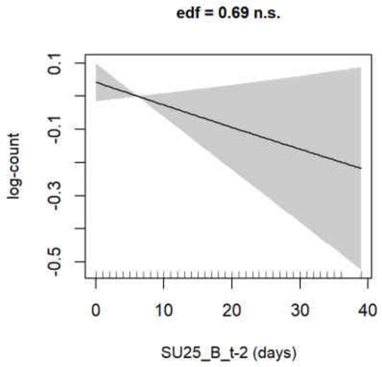


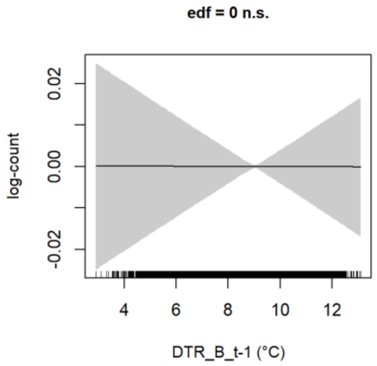


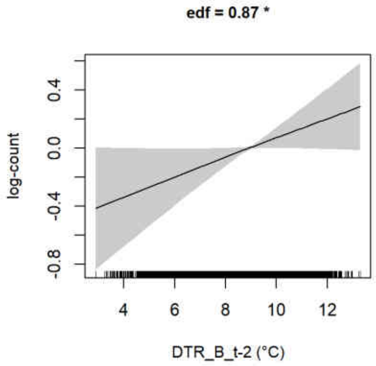


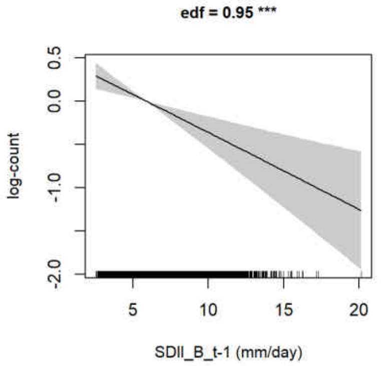


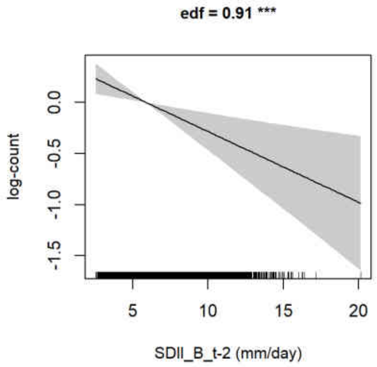


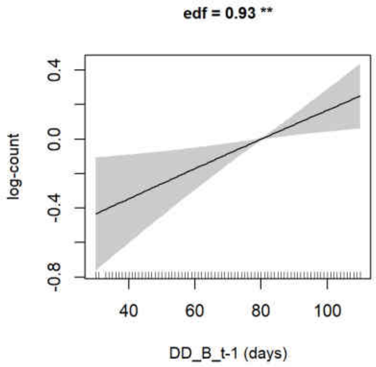


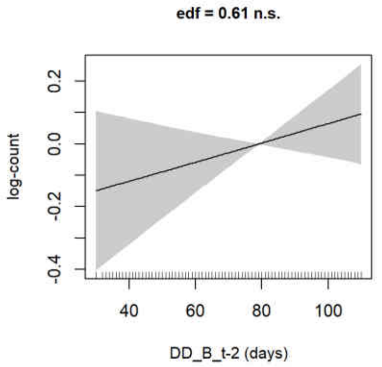




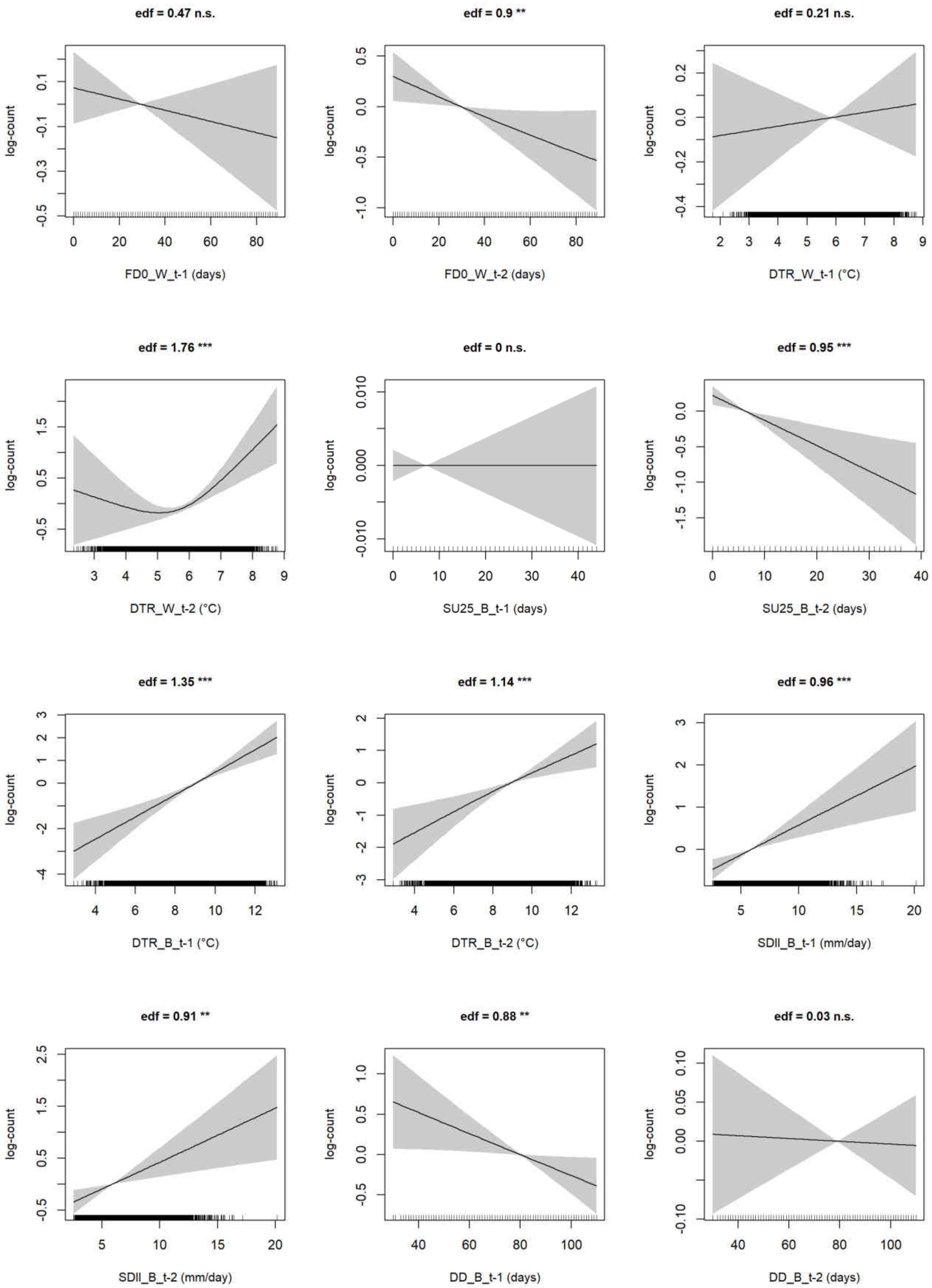




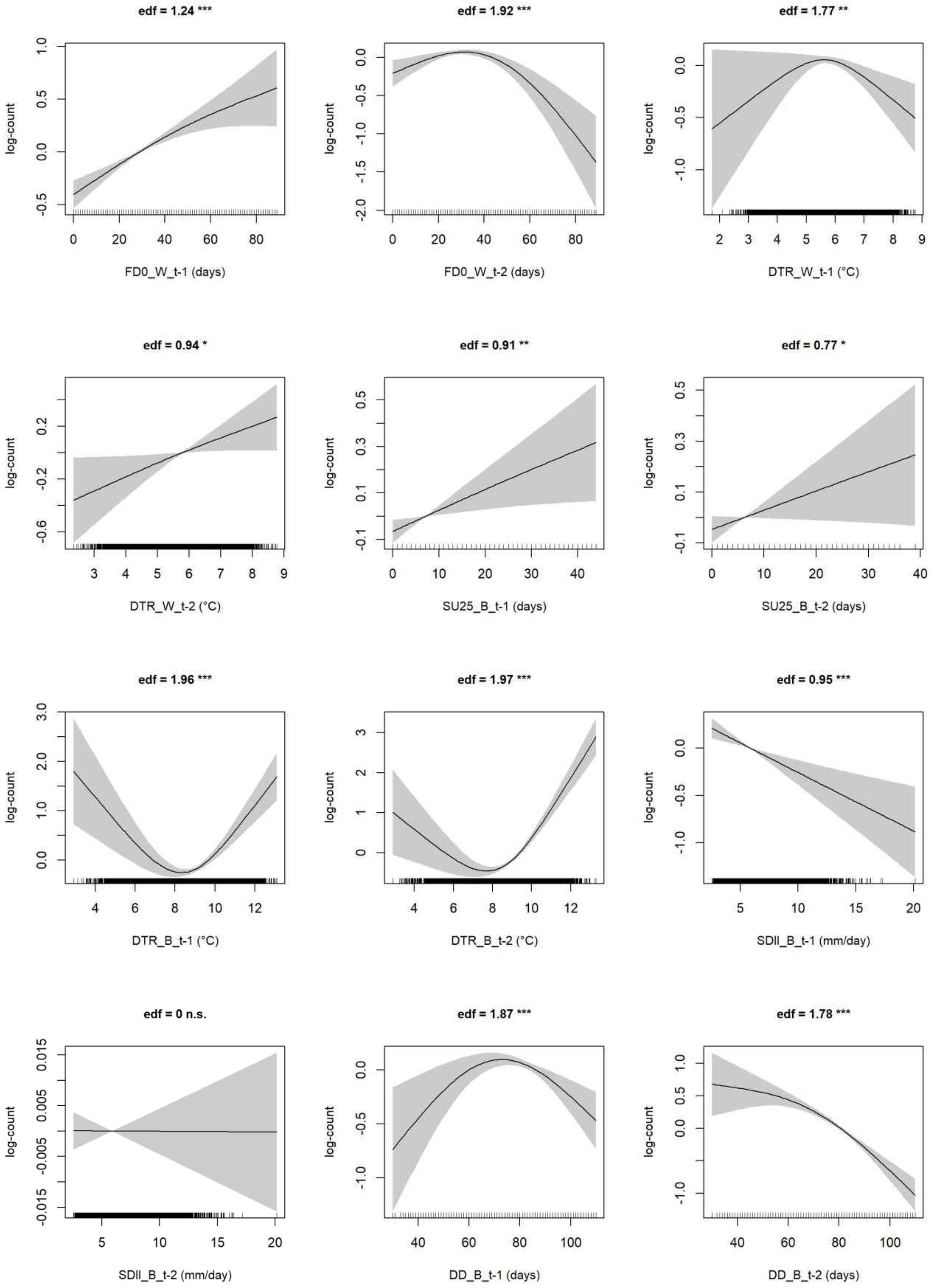




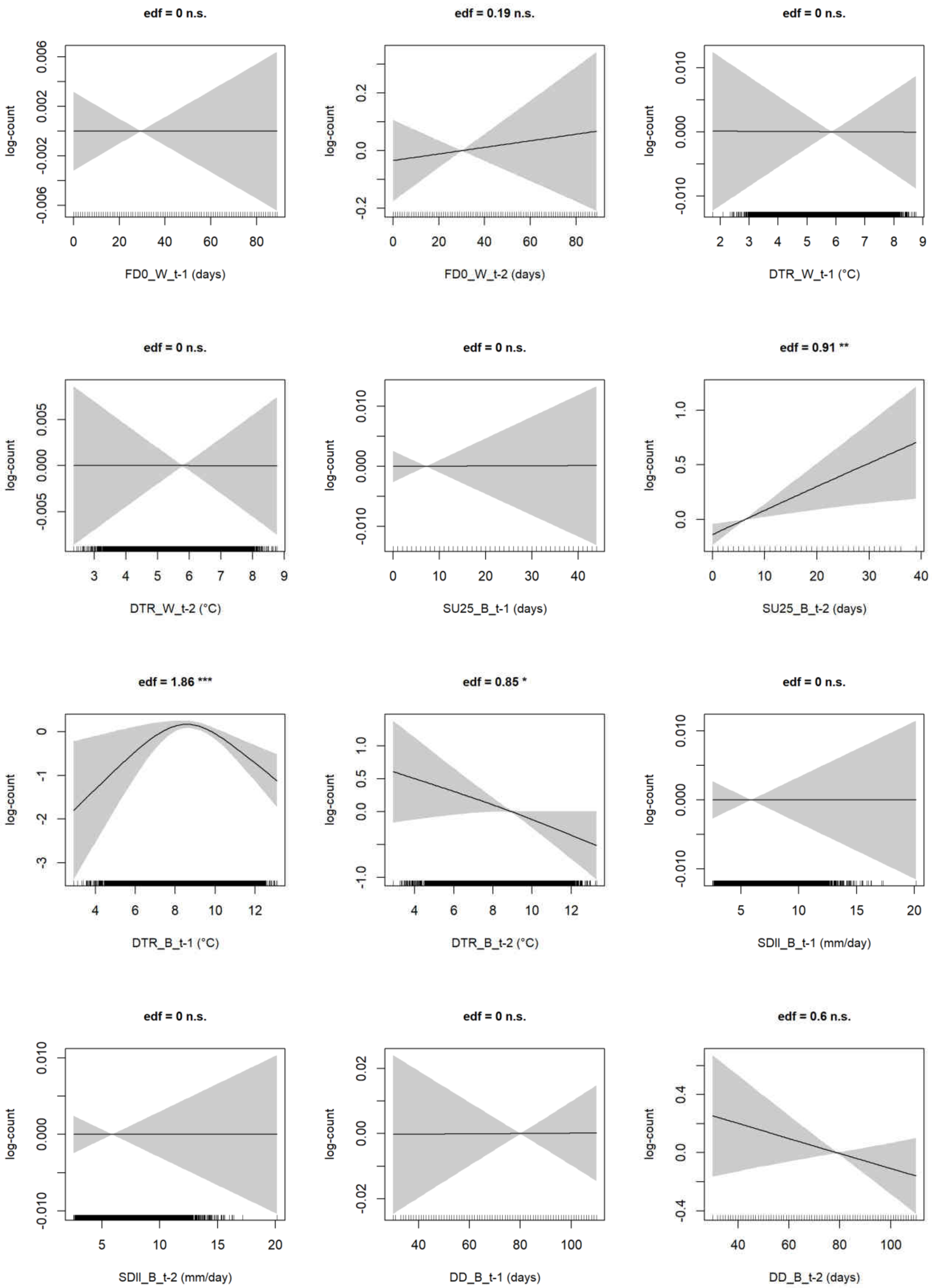
Common Merganser *Mergus merganser*



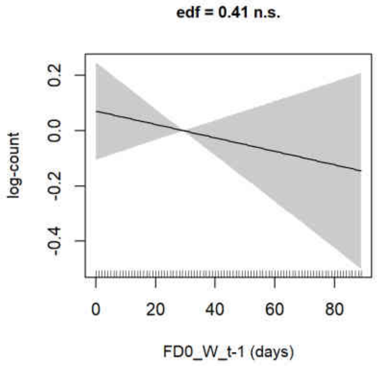
Red Kite *Milvus milvus*



Western Marsh Harrier *Circus aeruginosus*



Hen Harrier *Circus cyaneus*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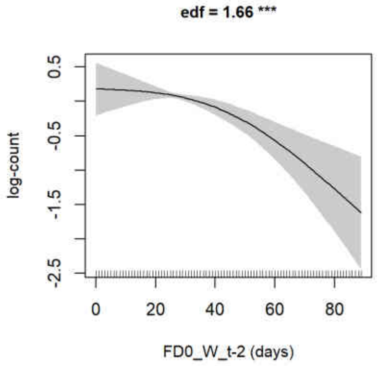
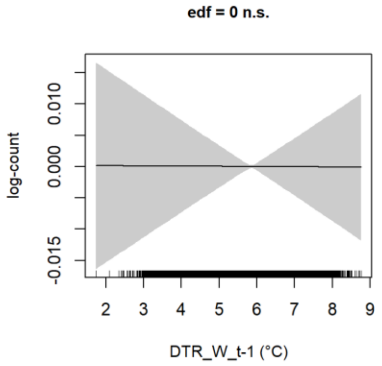
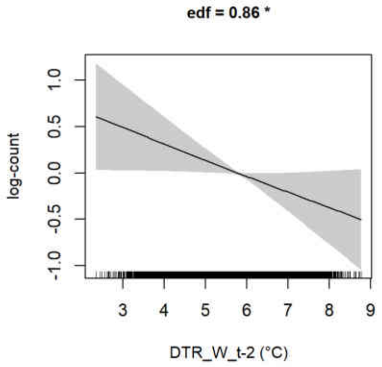
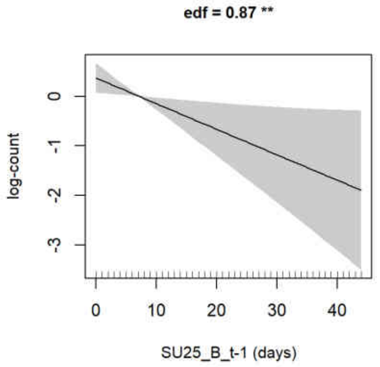
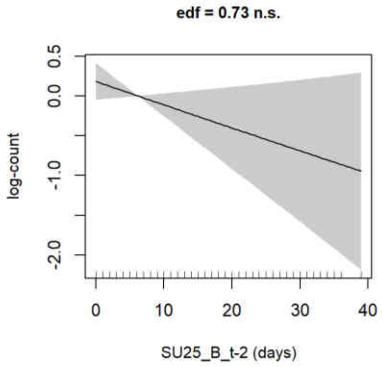
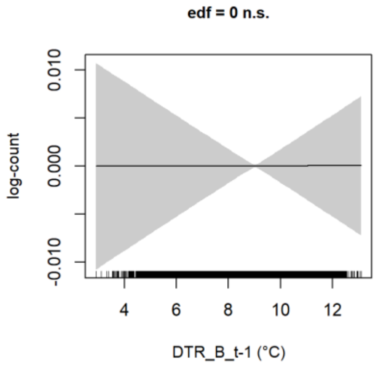

edf = 1.66 ***

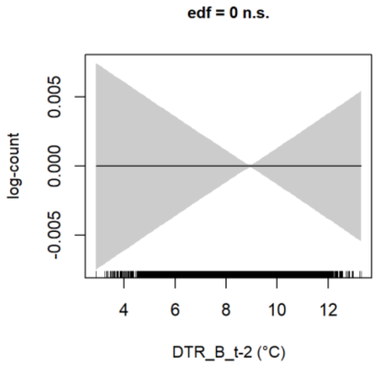

edf = 0 n.s.

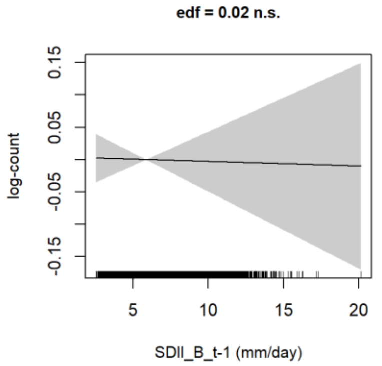

edf = 0.86 *


edf = 0.87 **


edf = 0.73 n.s.


edf = 0 n.s.


edf = 0 n.s.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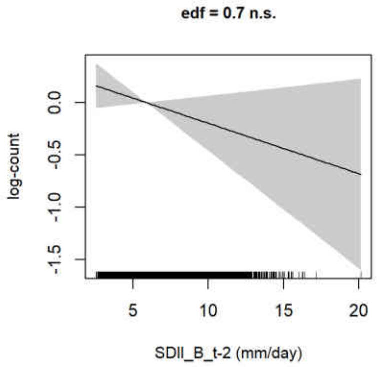
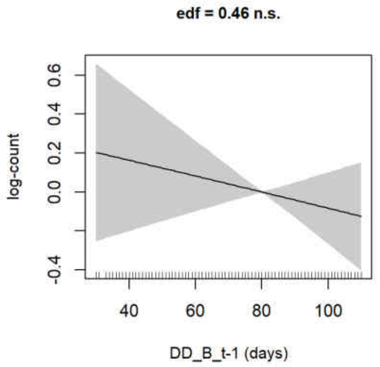
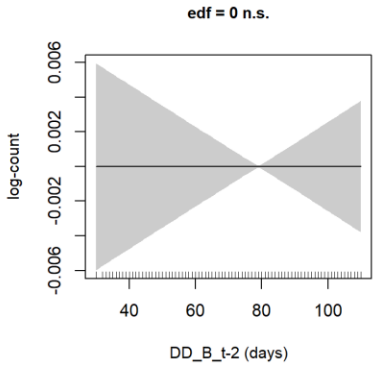
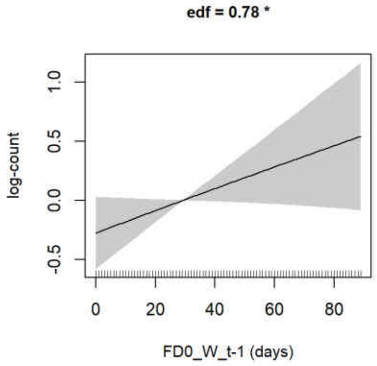
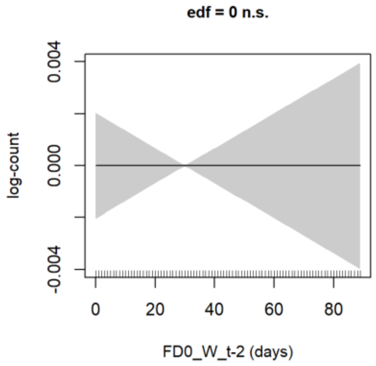

edf = 0.7 n.s.

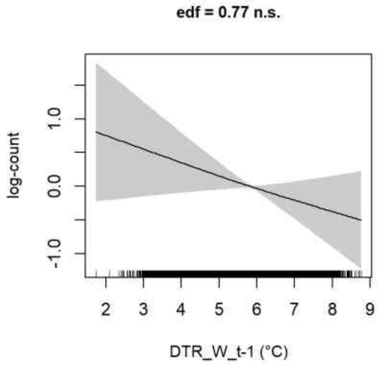

edf = 0.46 n.s.

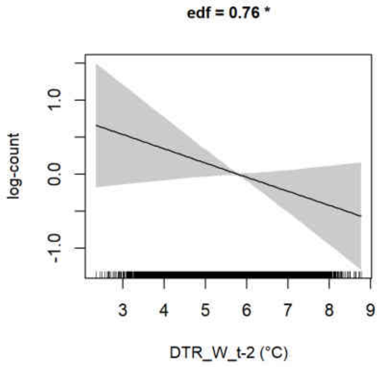

edf = 0 n.s.

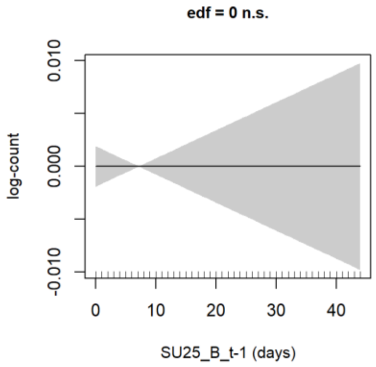
Northern Goshawk *Accipiter gentilis*

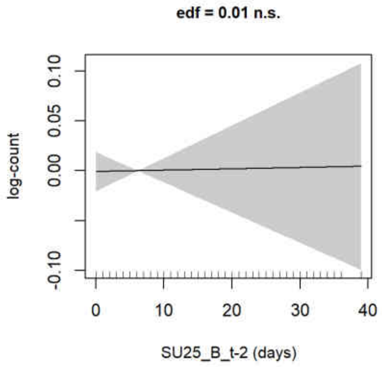


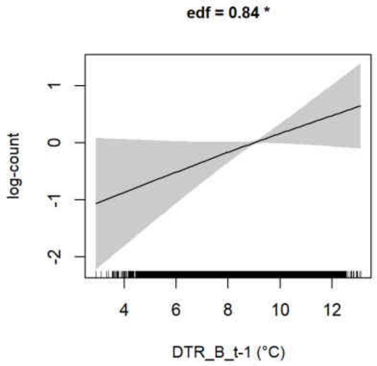


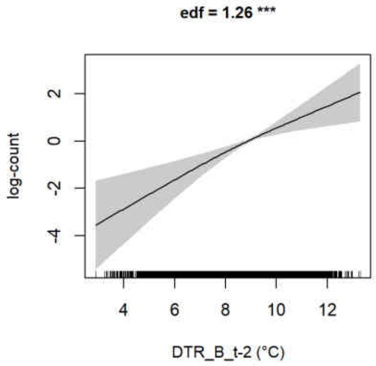


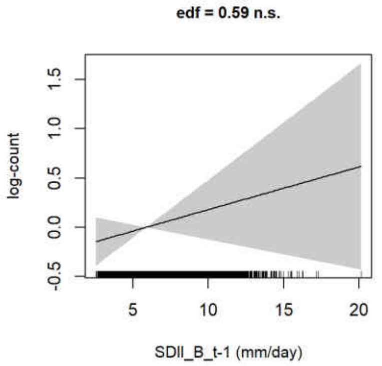


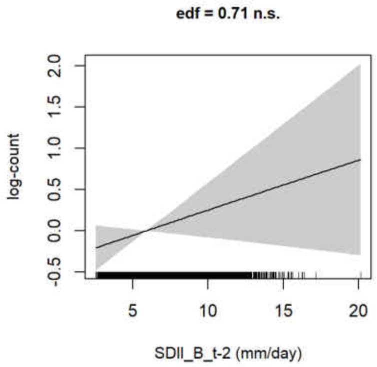


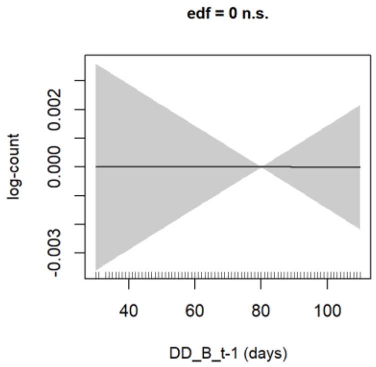


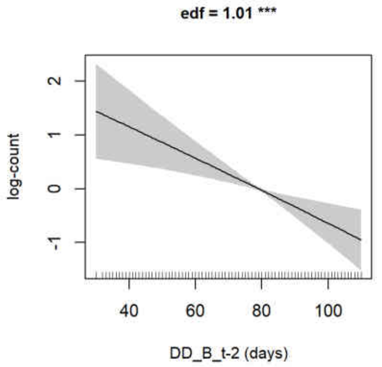




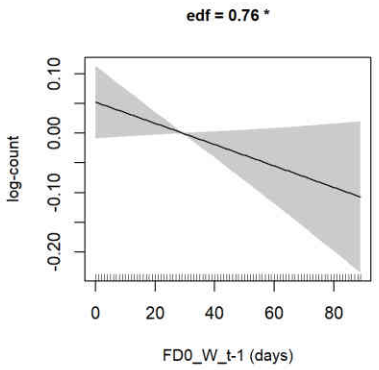


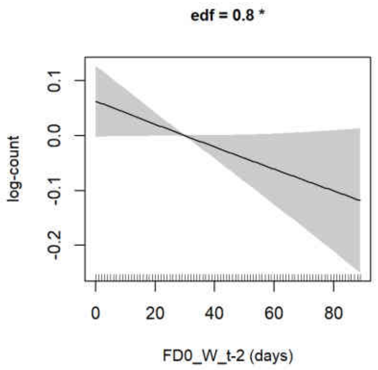


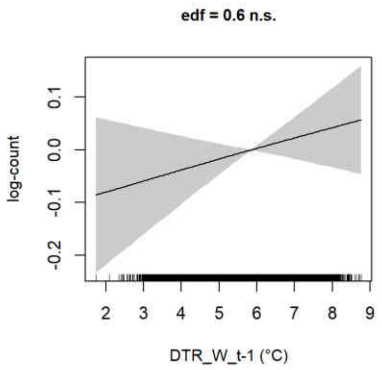


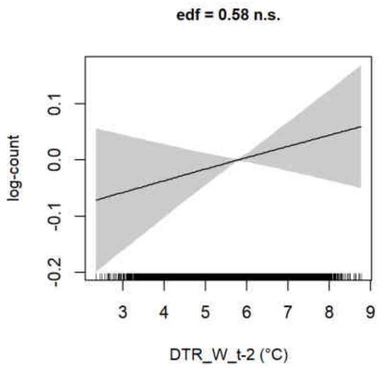


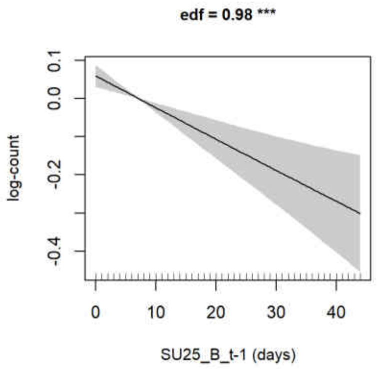
Eurasian Sparrowhawk *Accipiter nisus*

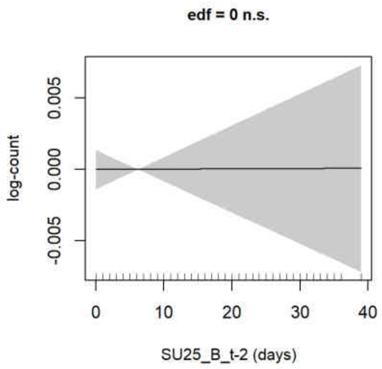


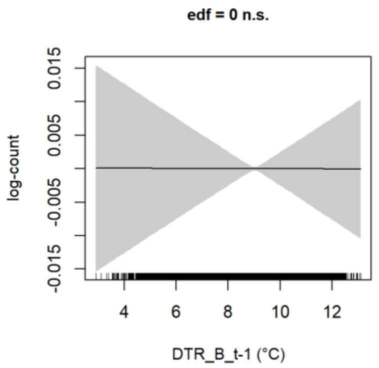


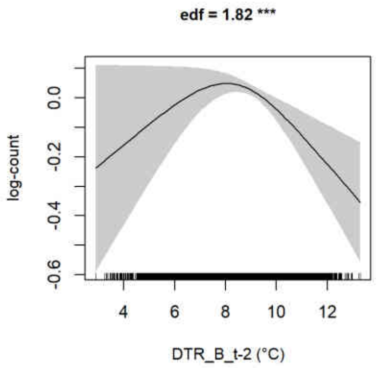


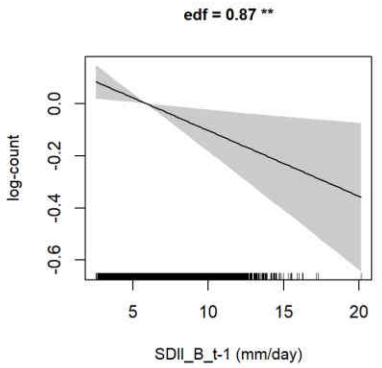


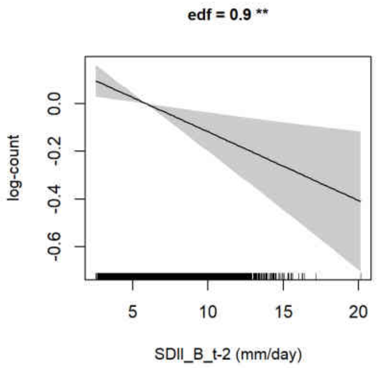


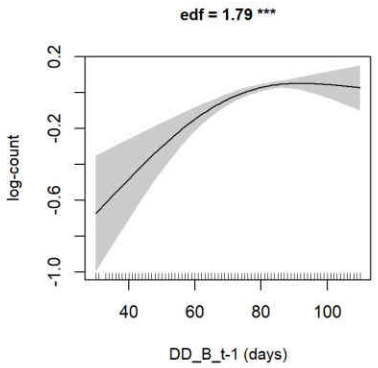


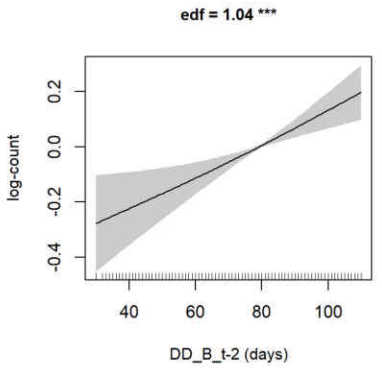




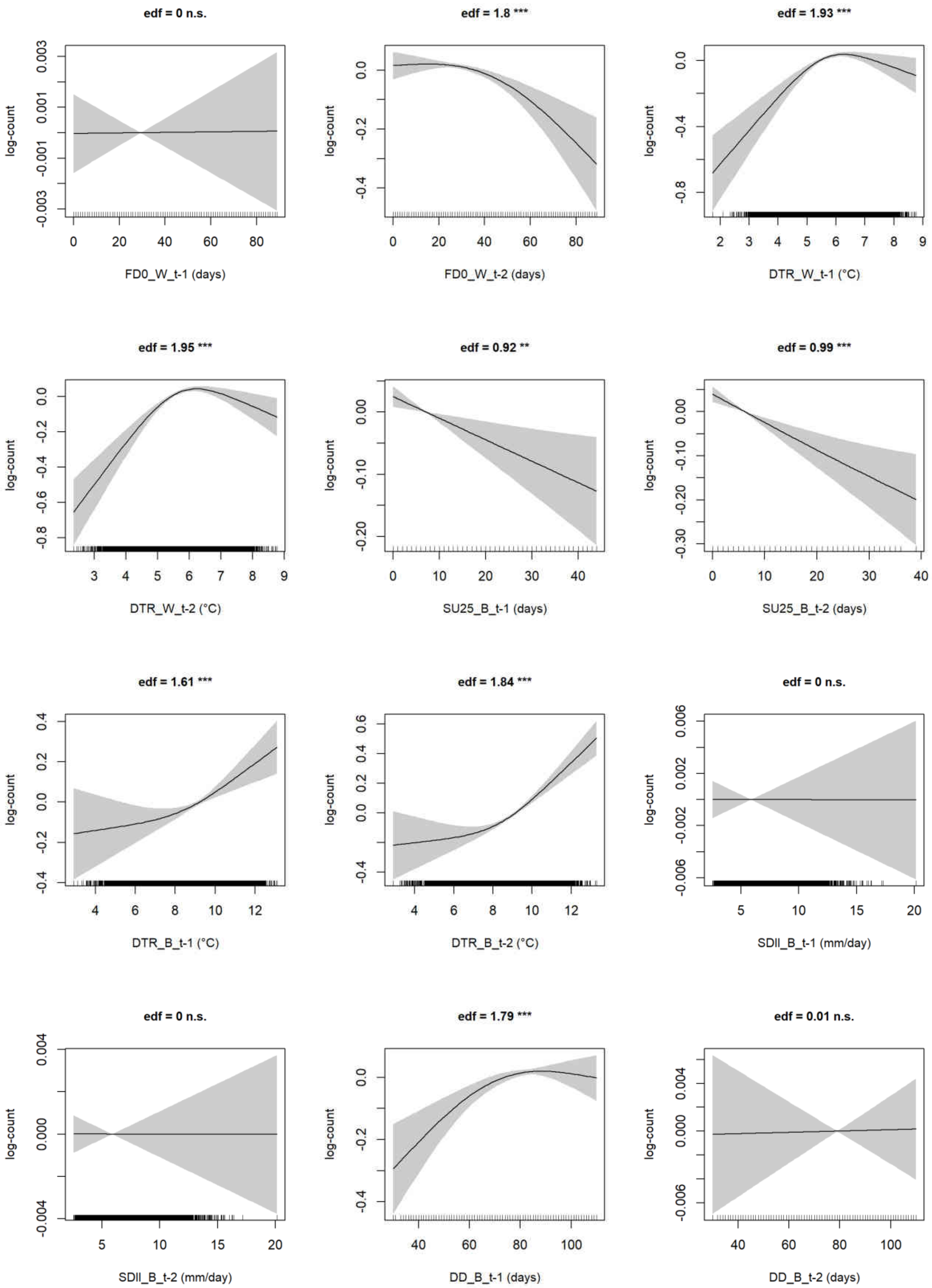




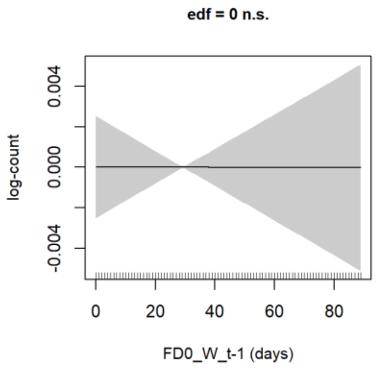


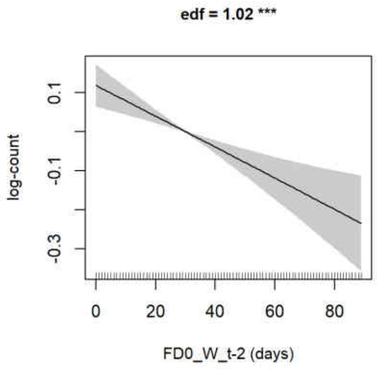


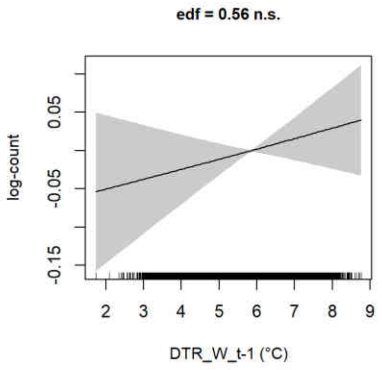
Common Buzzard *Buteo buteo*

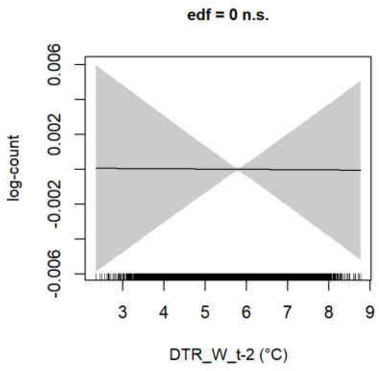


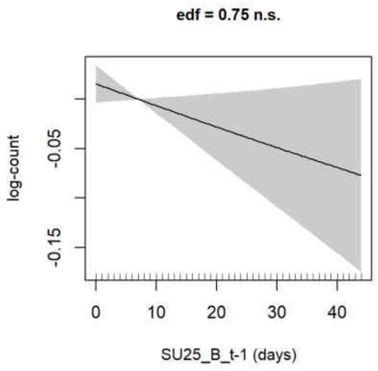
Common Kestrel *Falco tinnunculus*

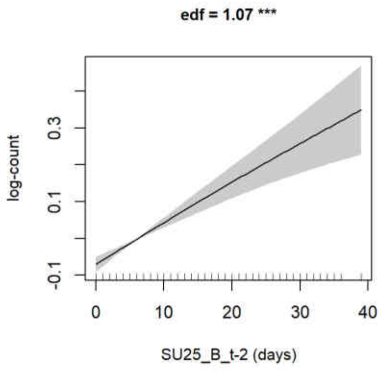


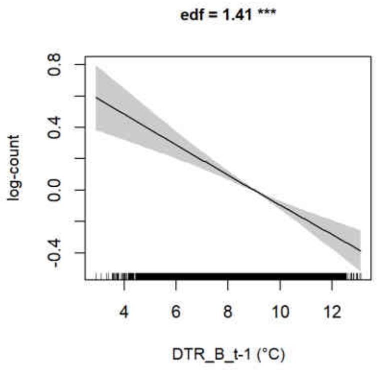


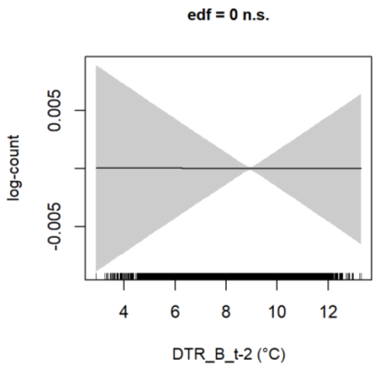


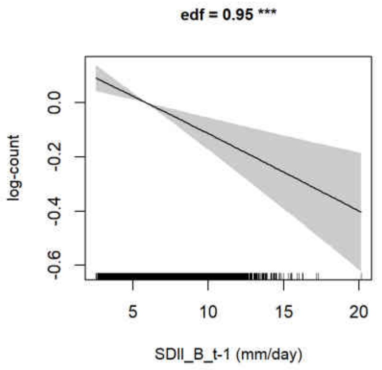


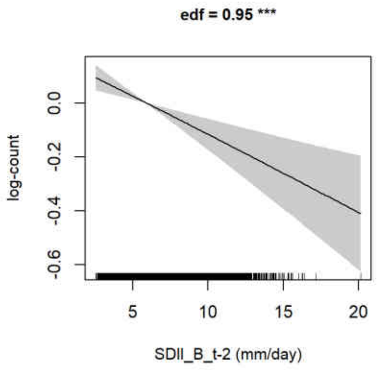


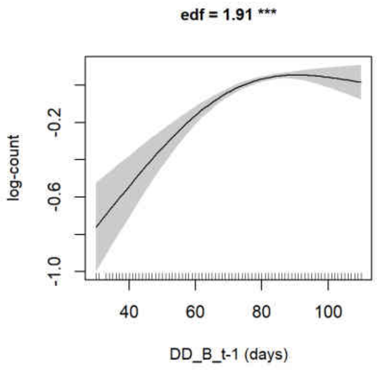


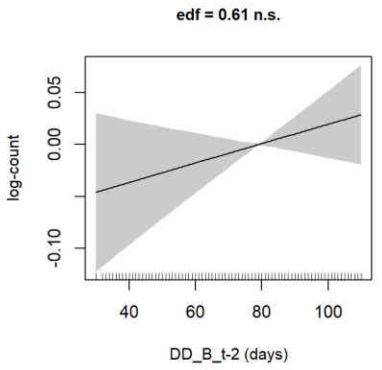




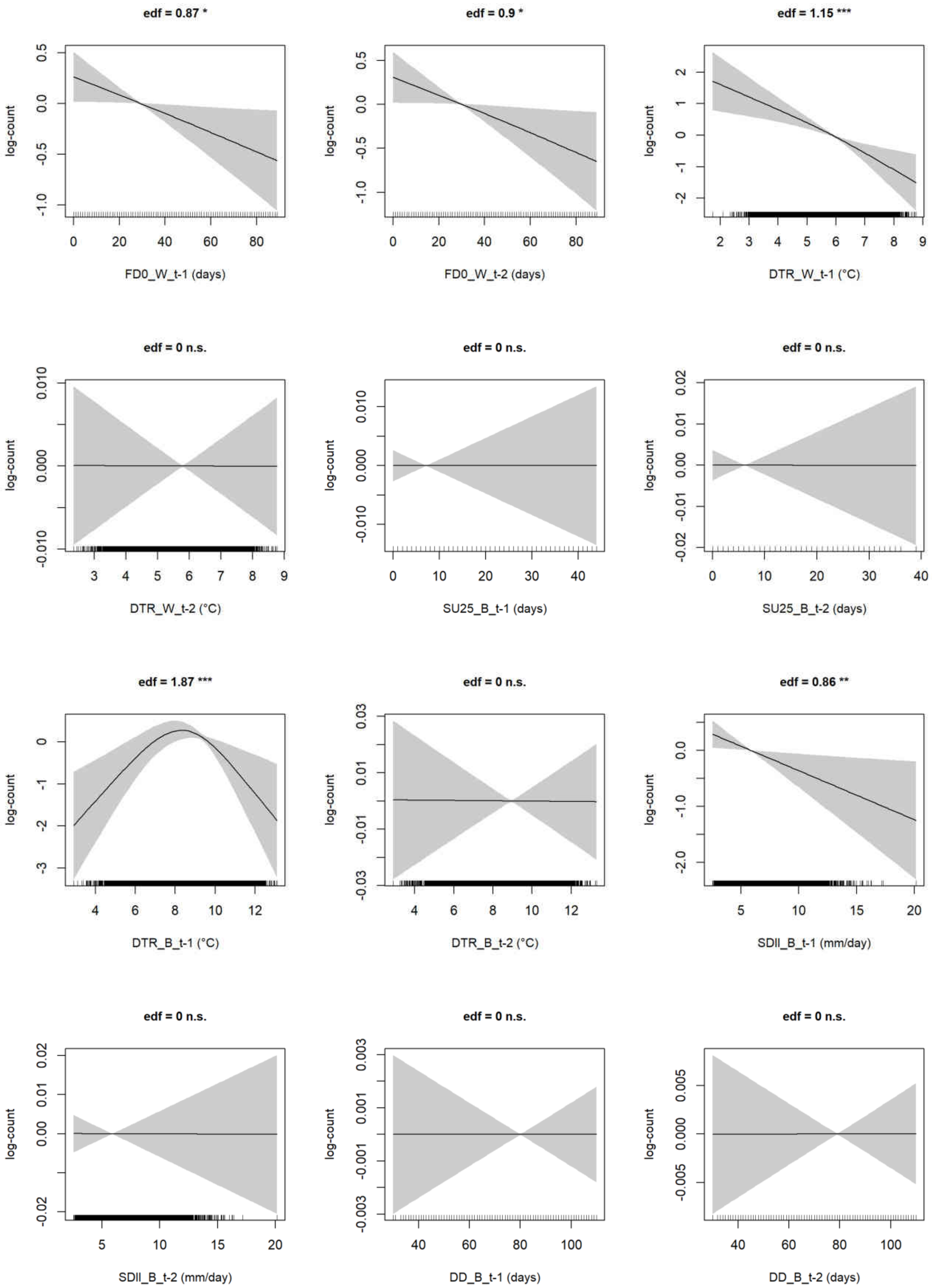




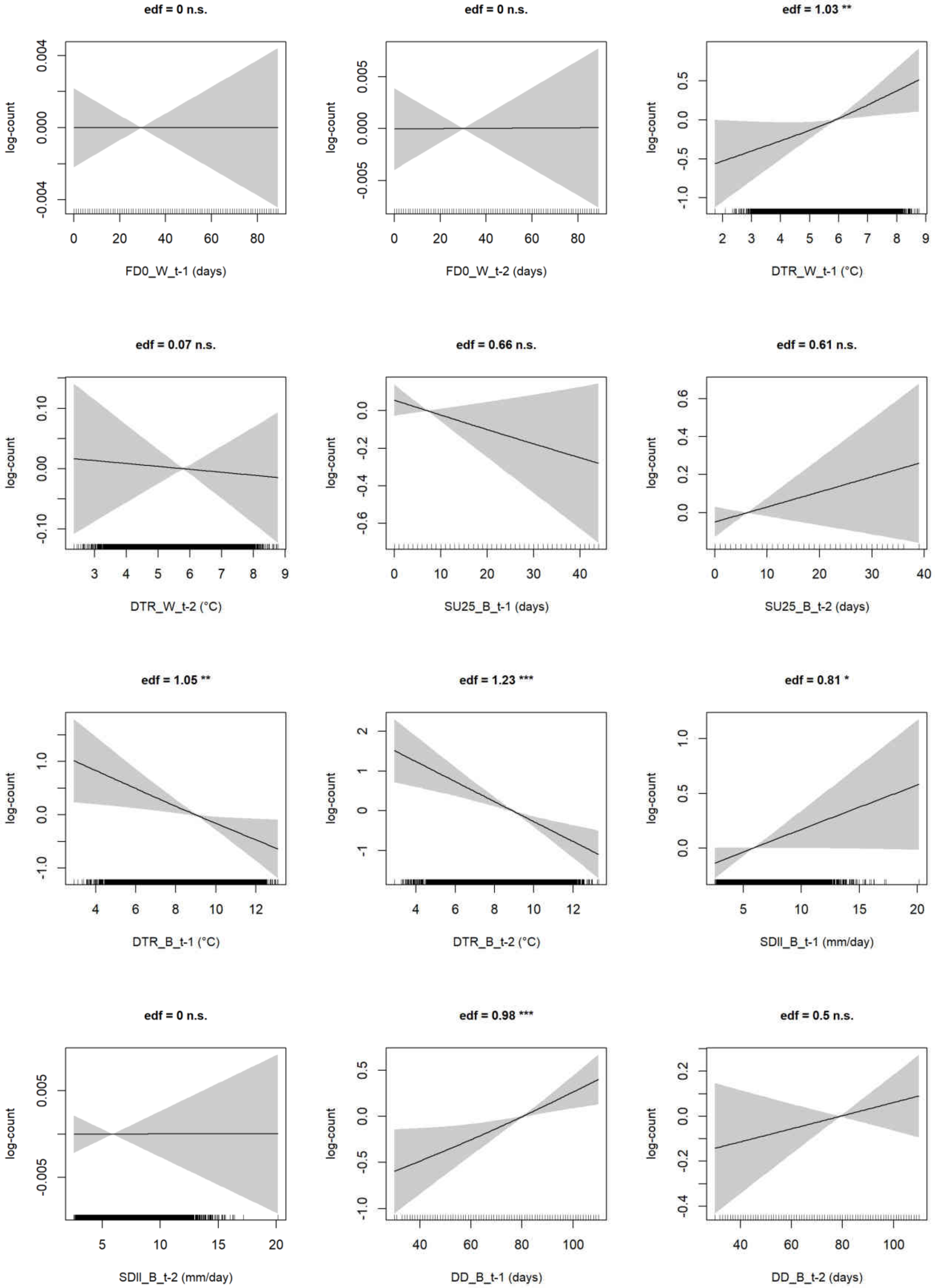




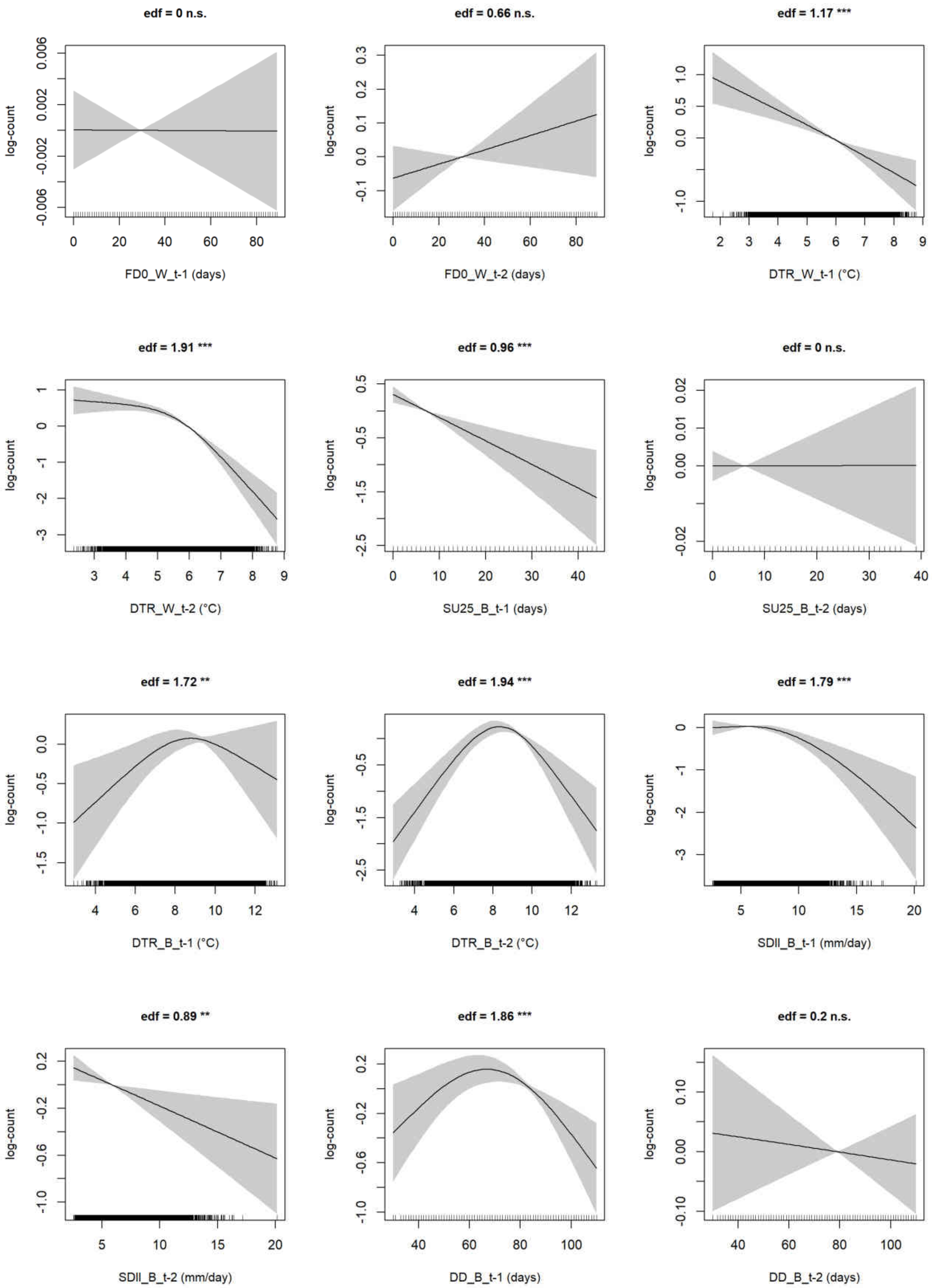
Merlin *Falco columbarius*



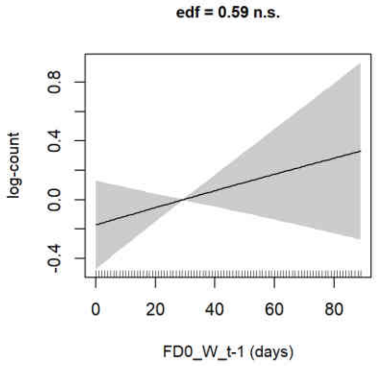
Peregrine Falcon *Falco peregrinus*

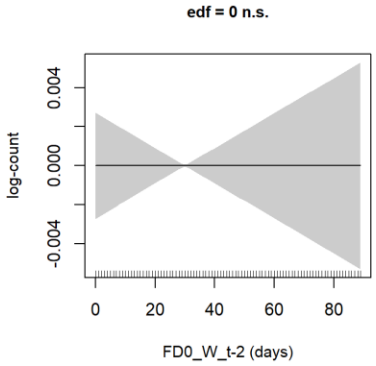


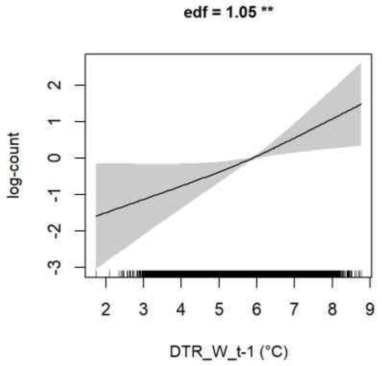
Willow Ptarmigan *Lagopus lagopus*

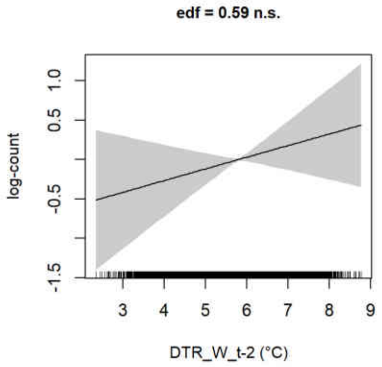


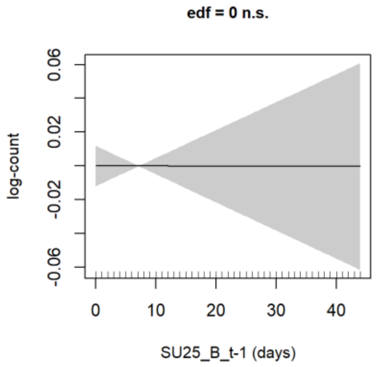
Black Grouse *Lyrurus tetrix*

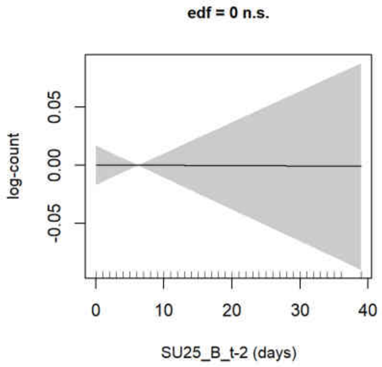


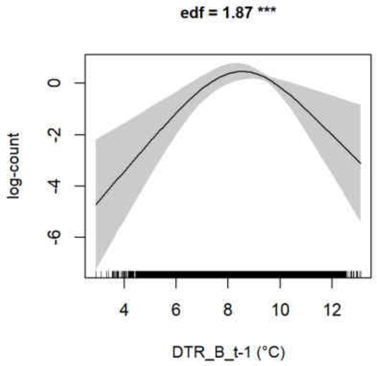


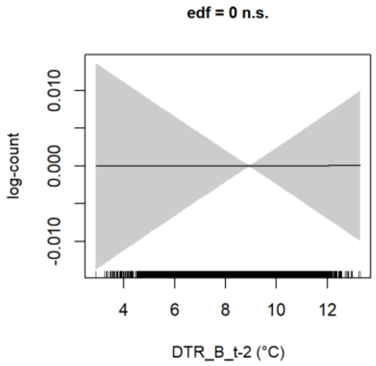


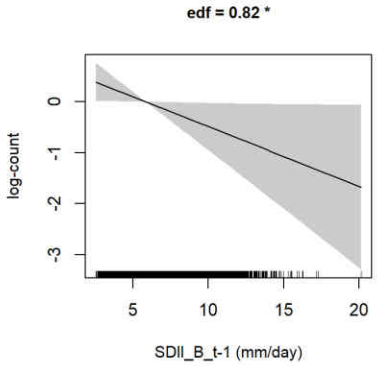


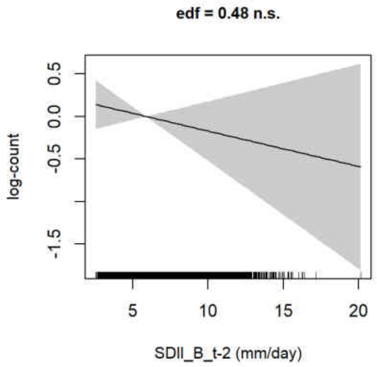


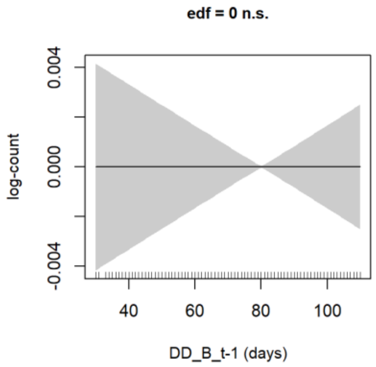


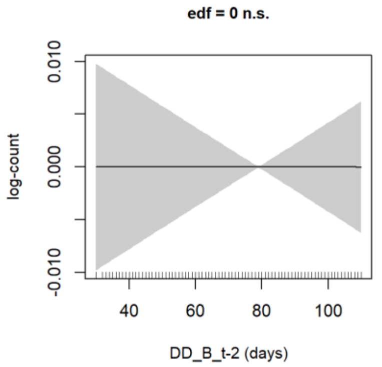




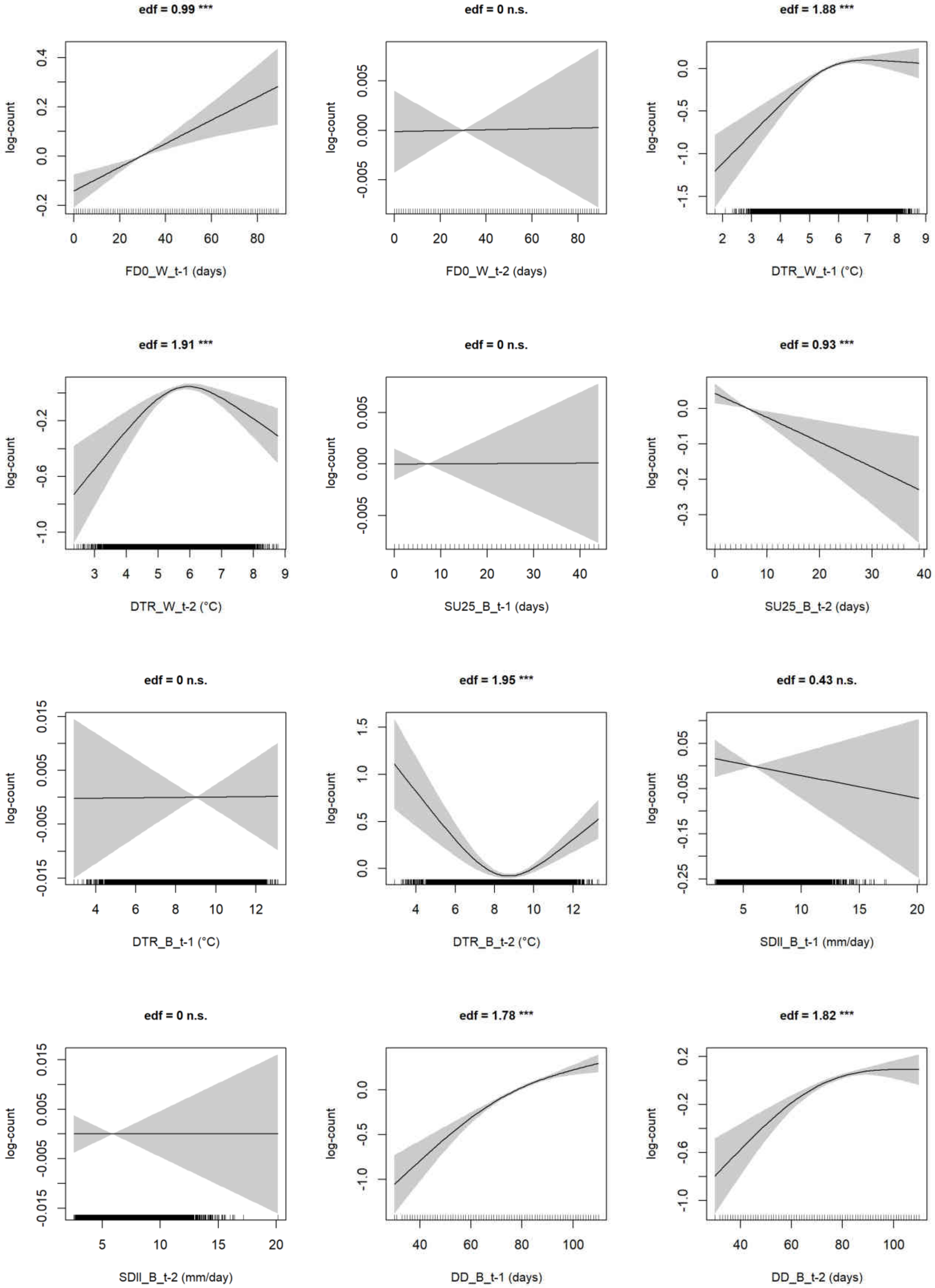




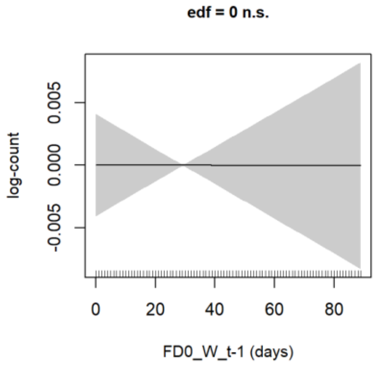


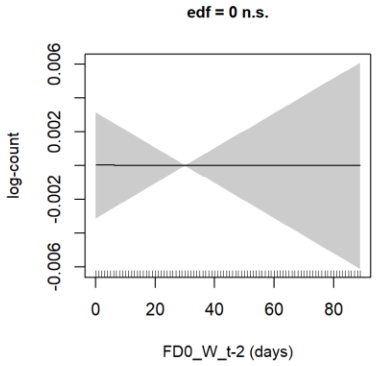


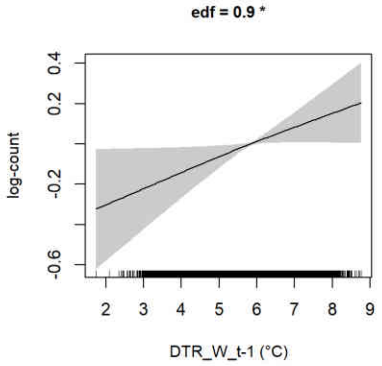
Red-legged Partridge *Alectoris rufa*

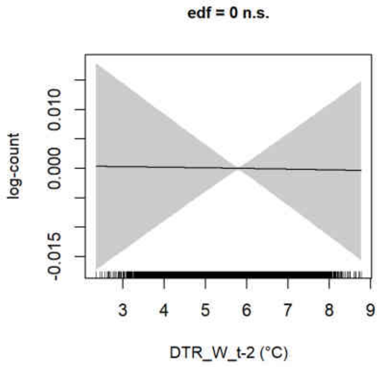


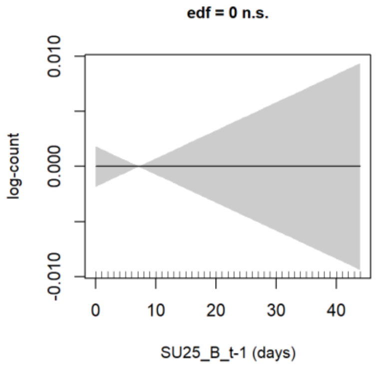
Grey Partridge *Perdix perdix*

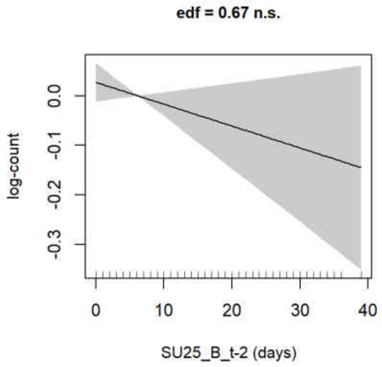


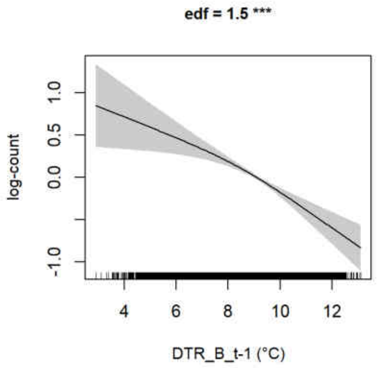


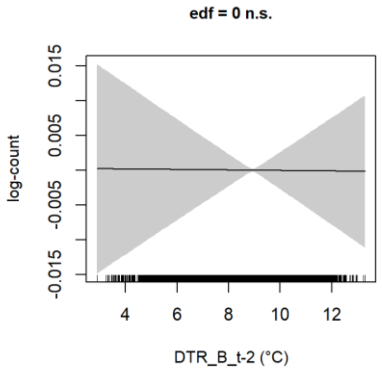


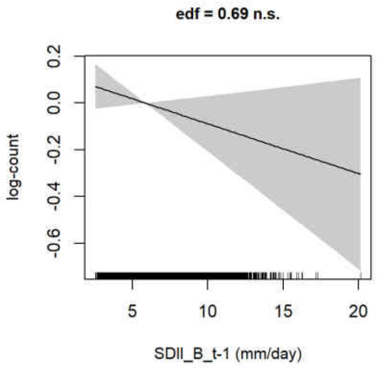


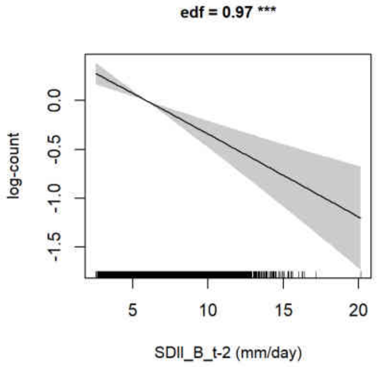


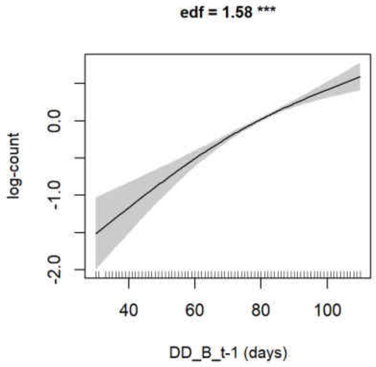


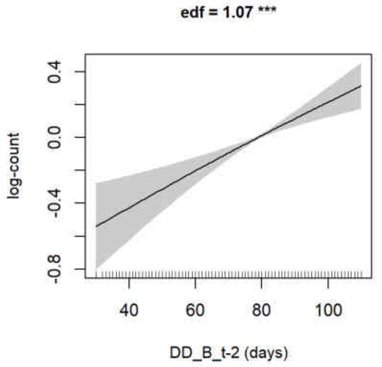




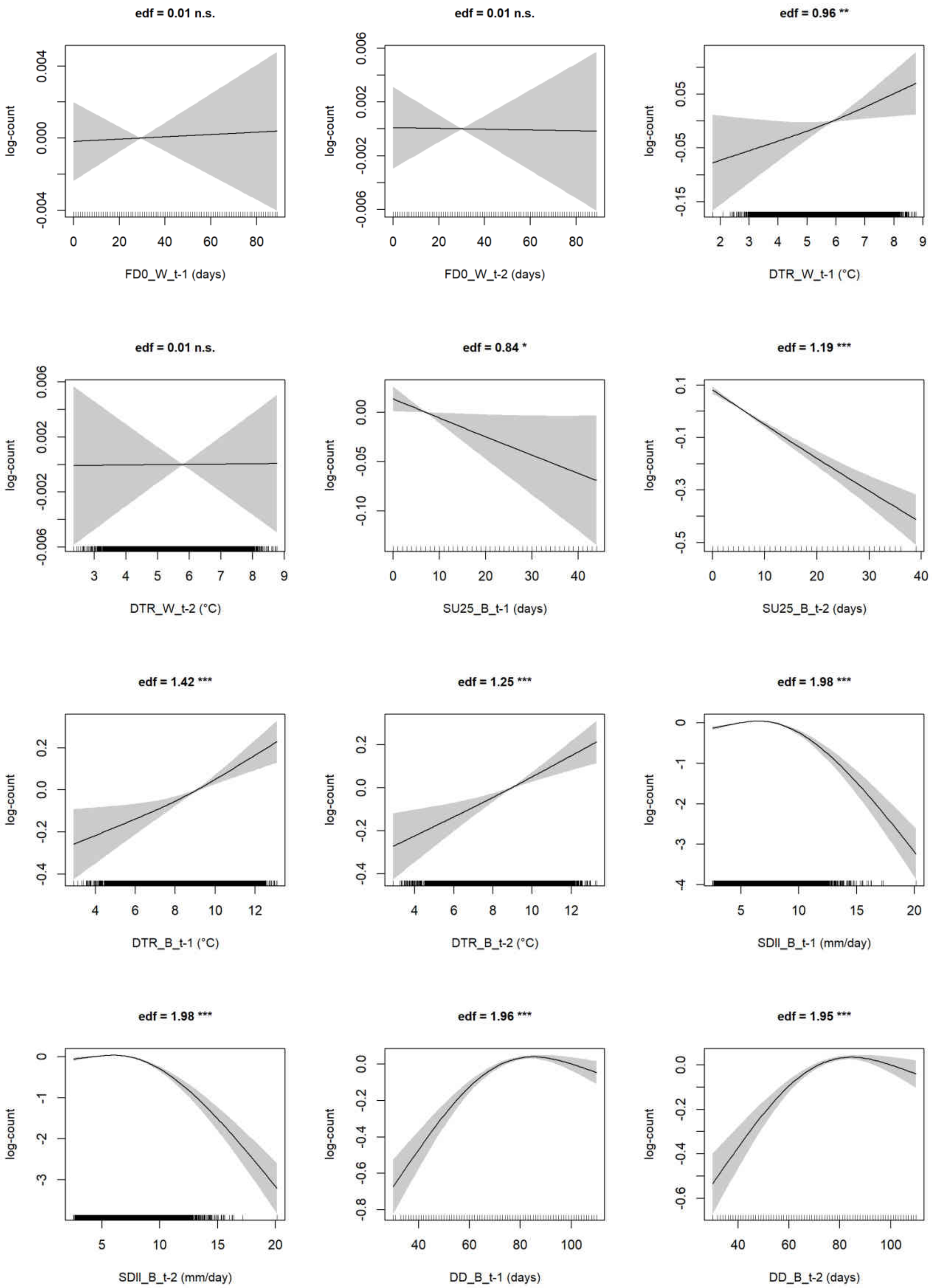




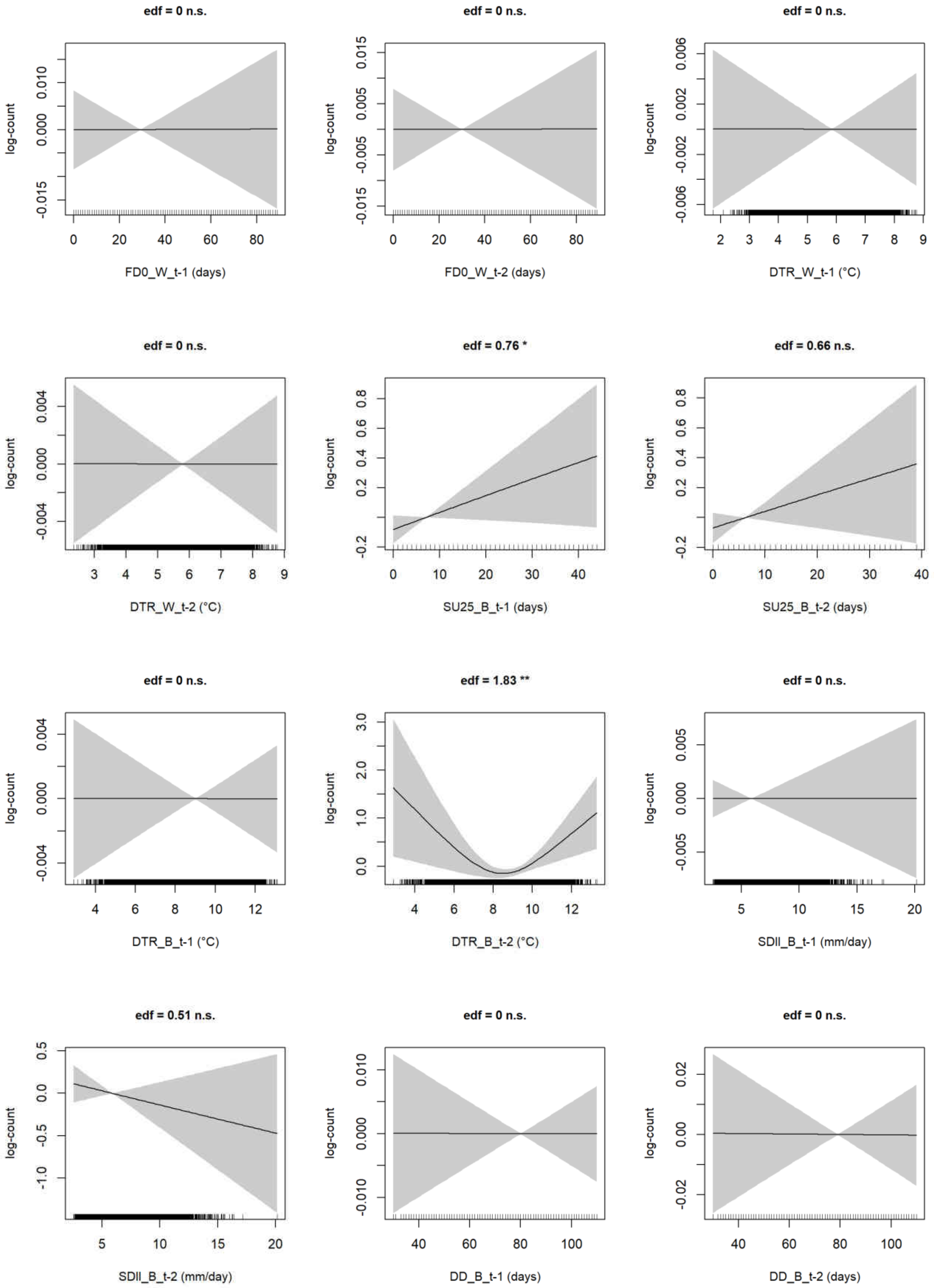




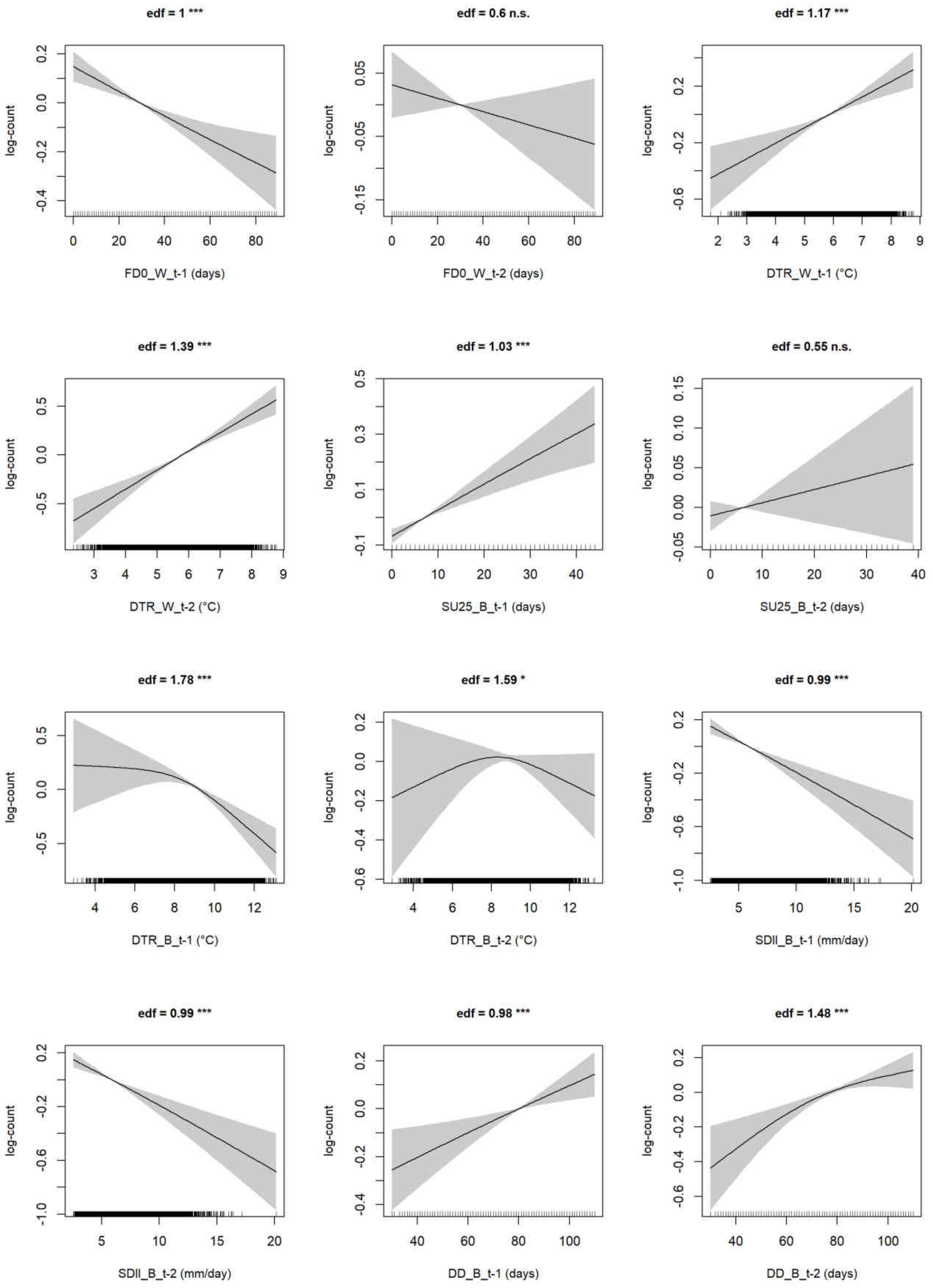
Common Pheasant *Phasianus colchicus*



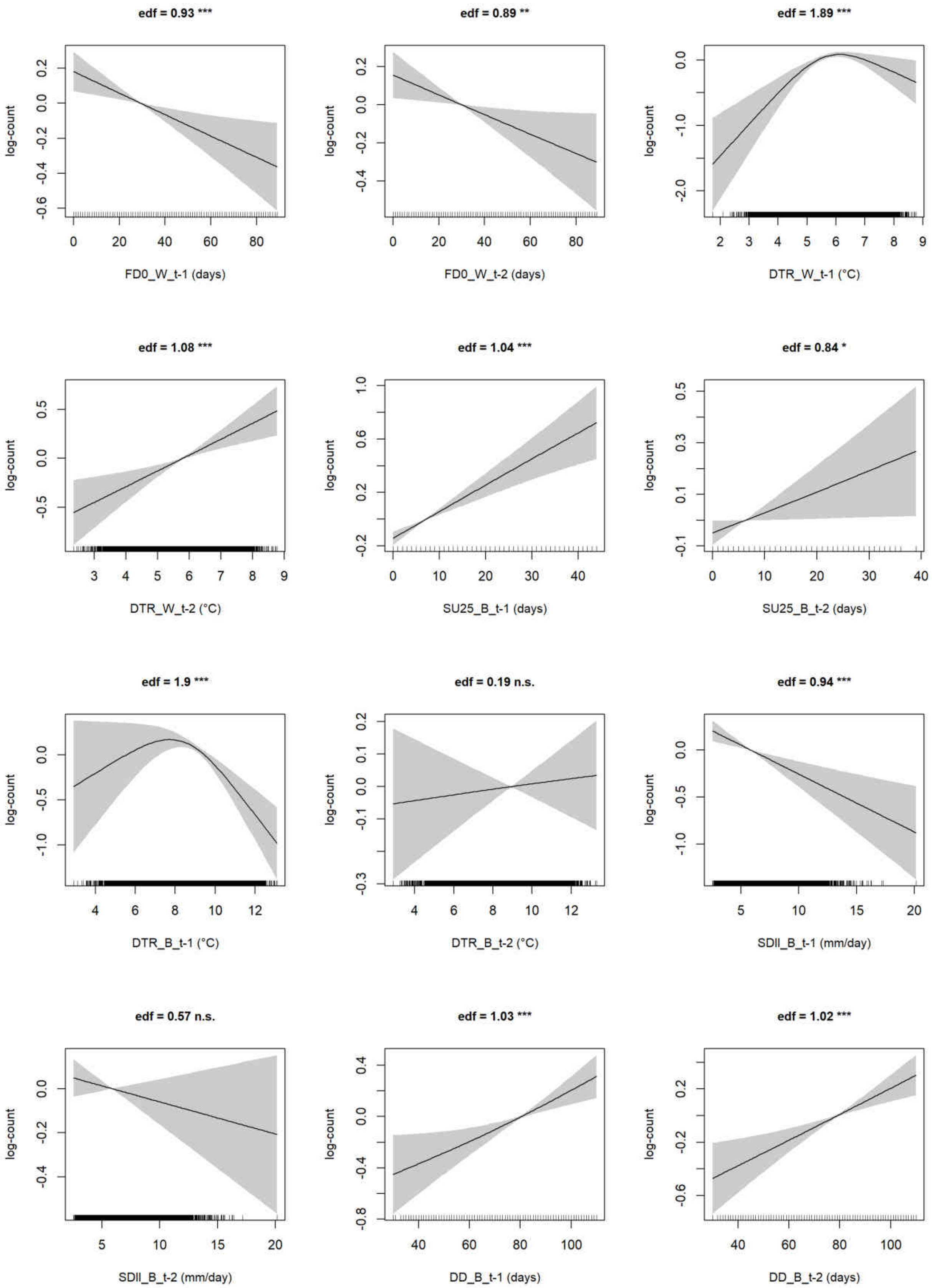
Indian Peafowl *Pavo cristatus*



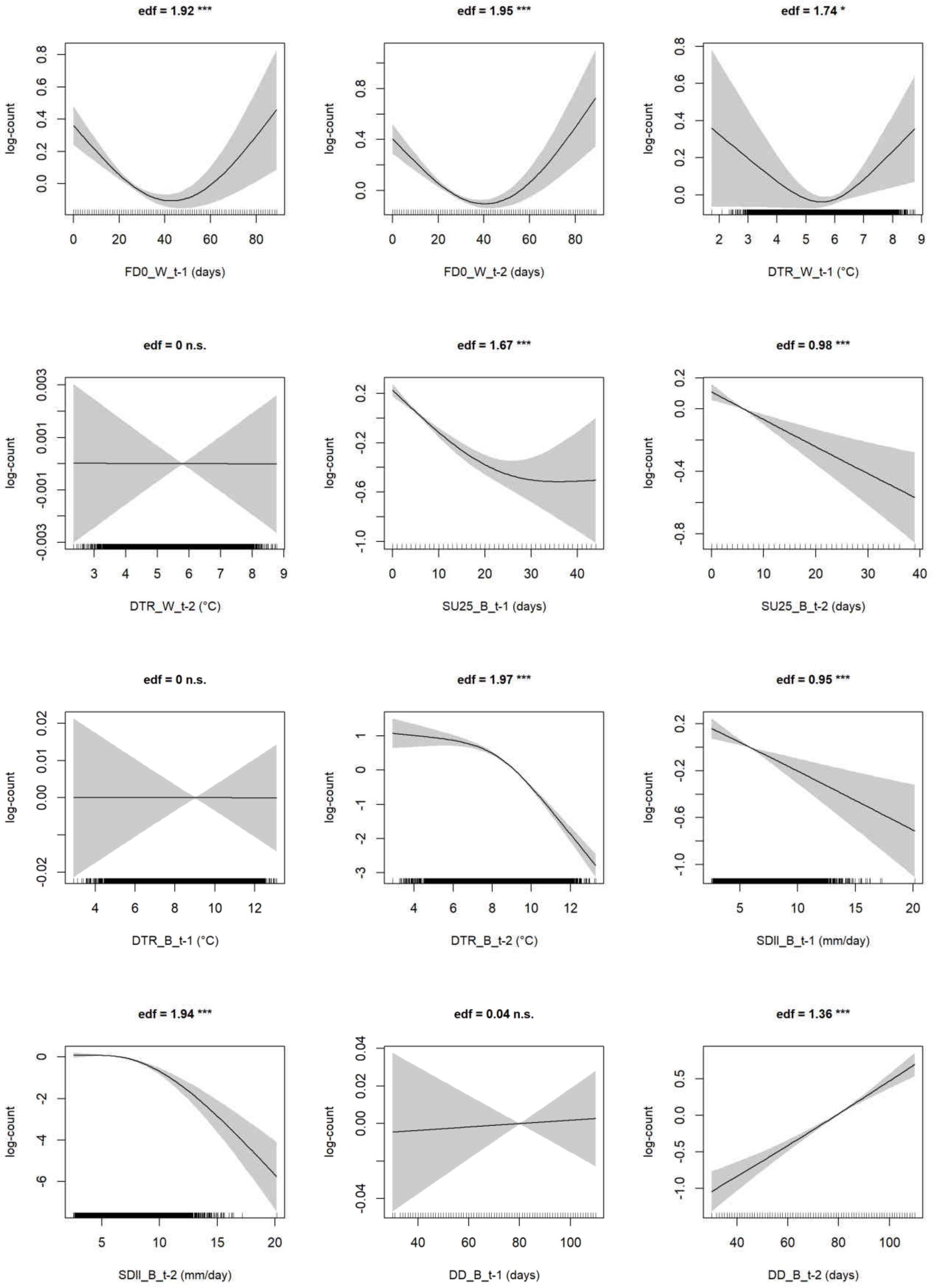
Common Moorhen *Gallinula chloropus*



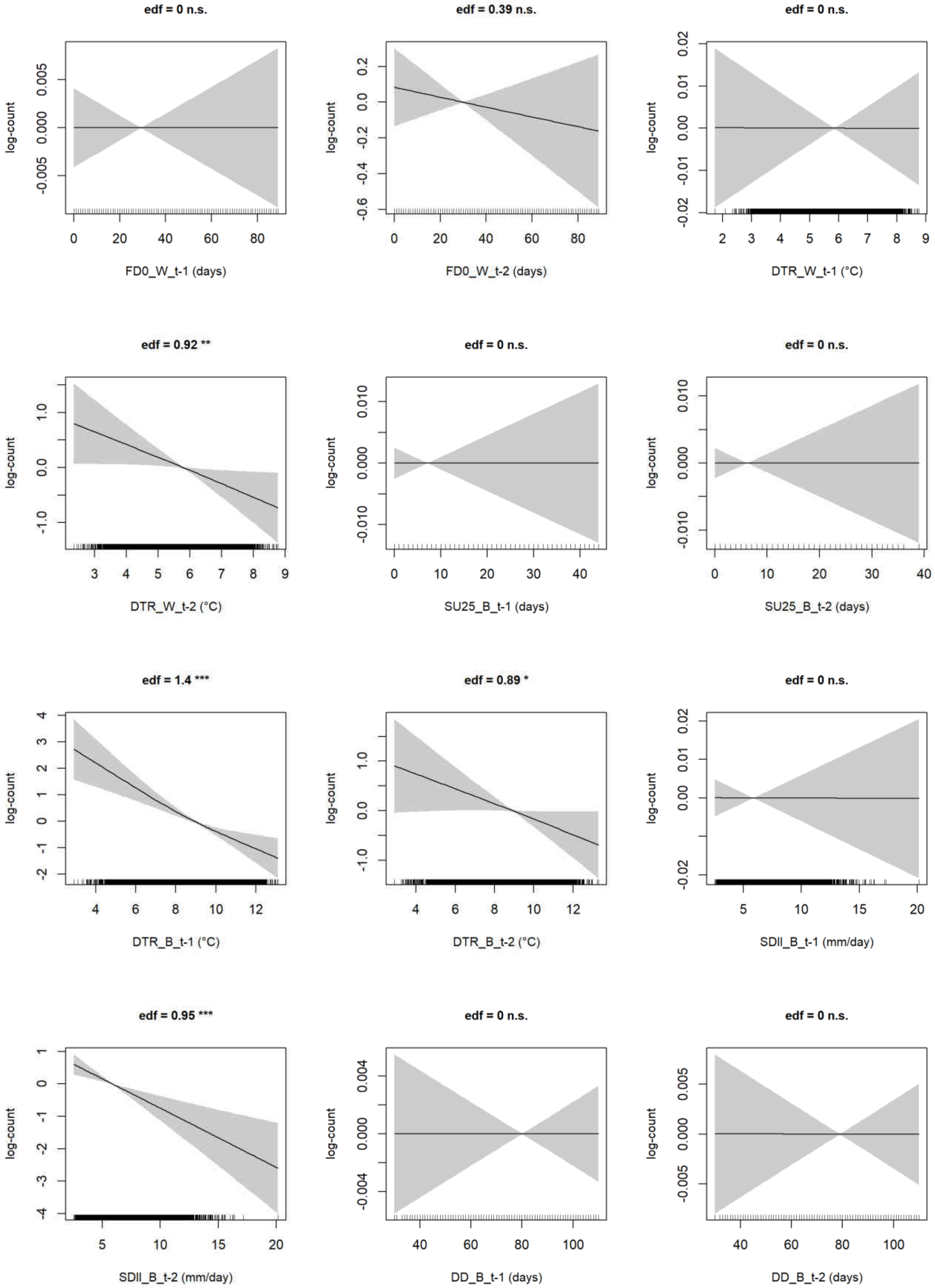
Eurasian Coot *Fulica atra*



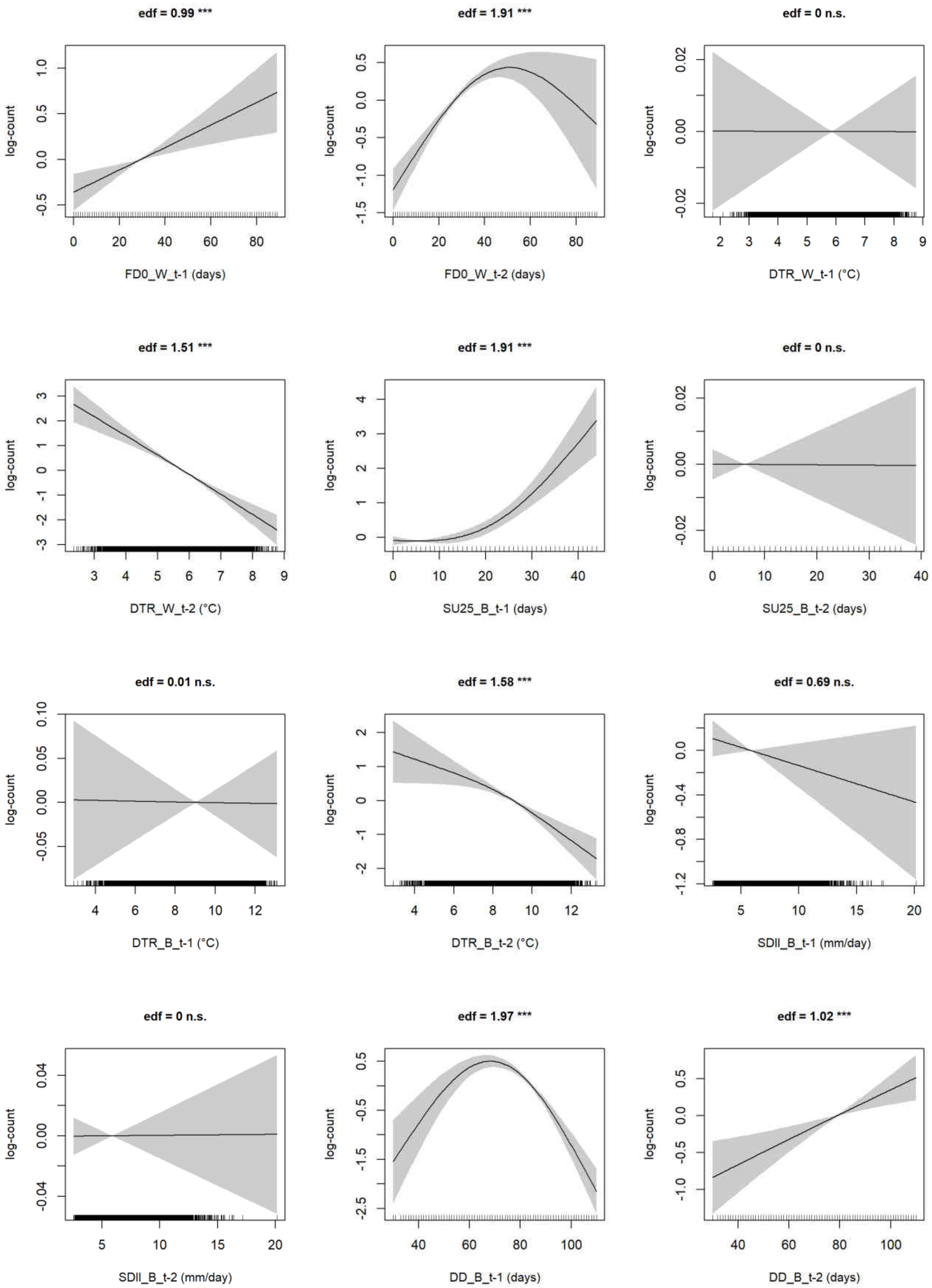
Eurasian Oystercatcher *Haematopus ostralegus*



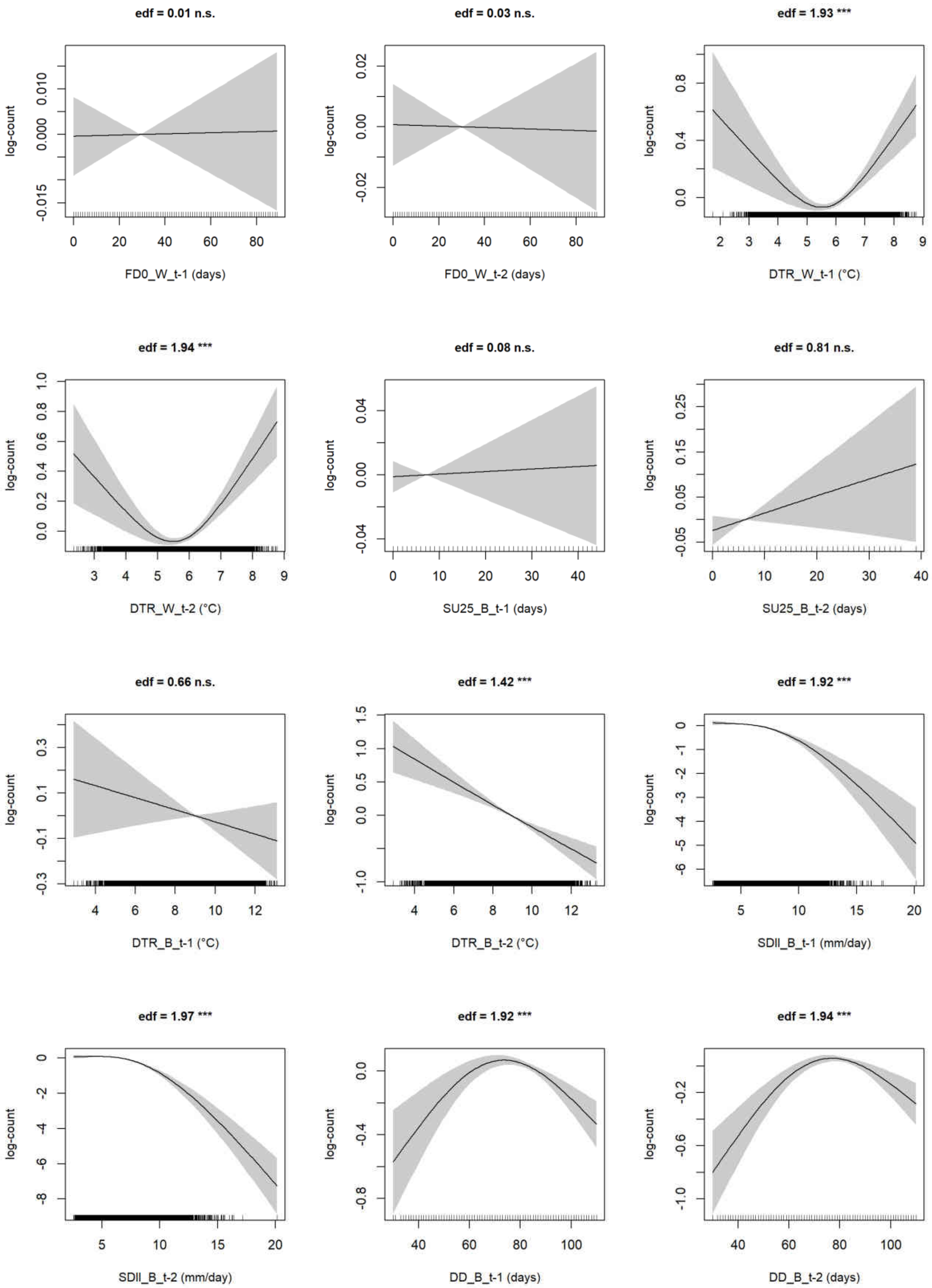
Common Ringed Plover *Charadrius hiaticula*



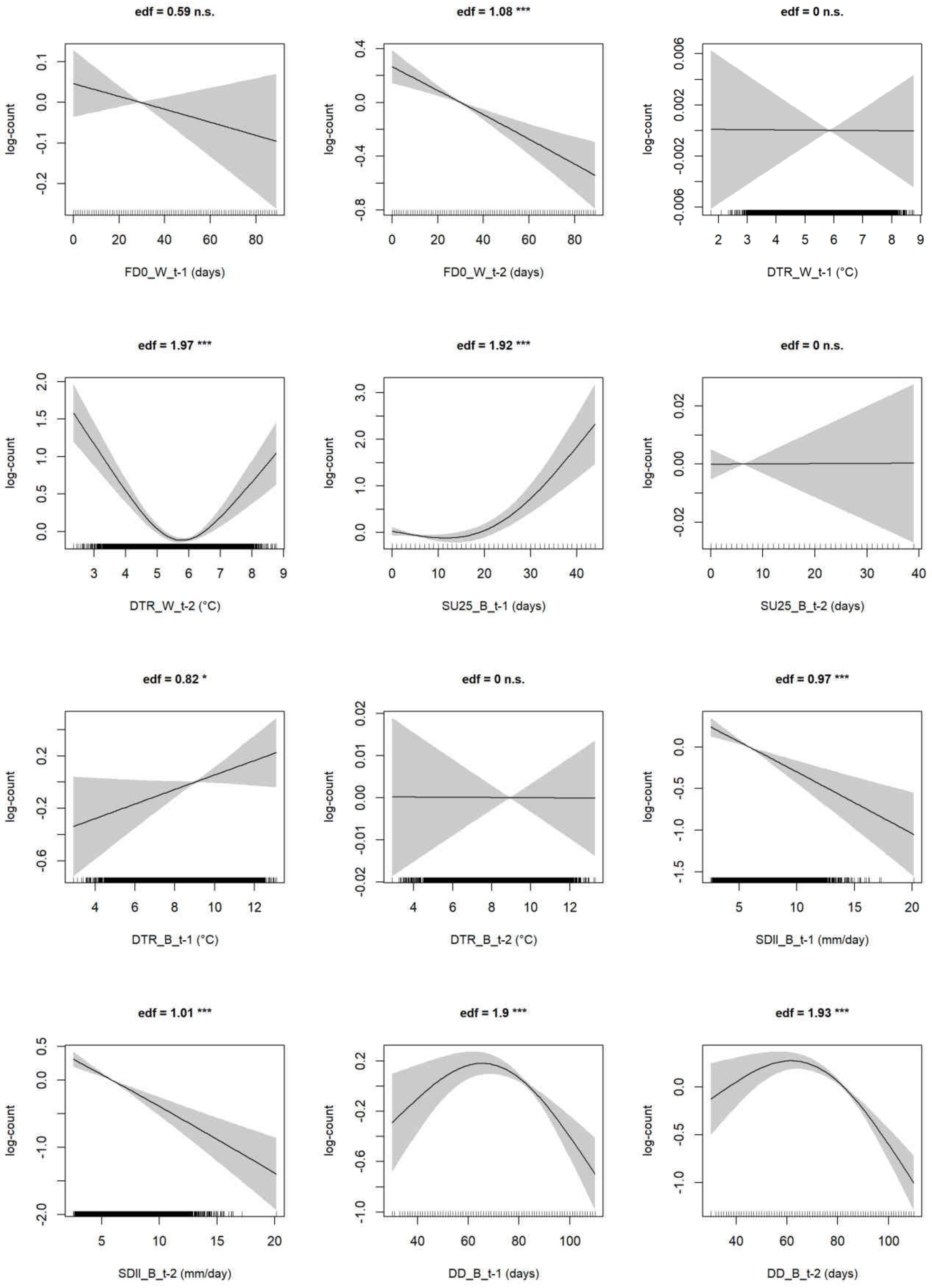
European Golden Plover *Pluvialis apricaria*



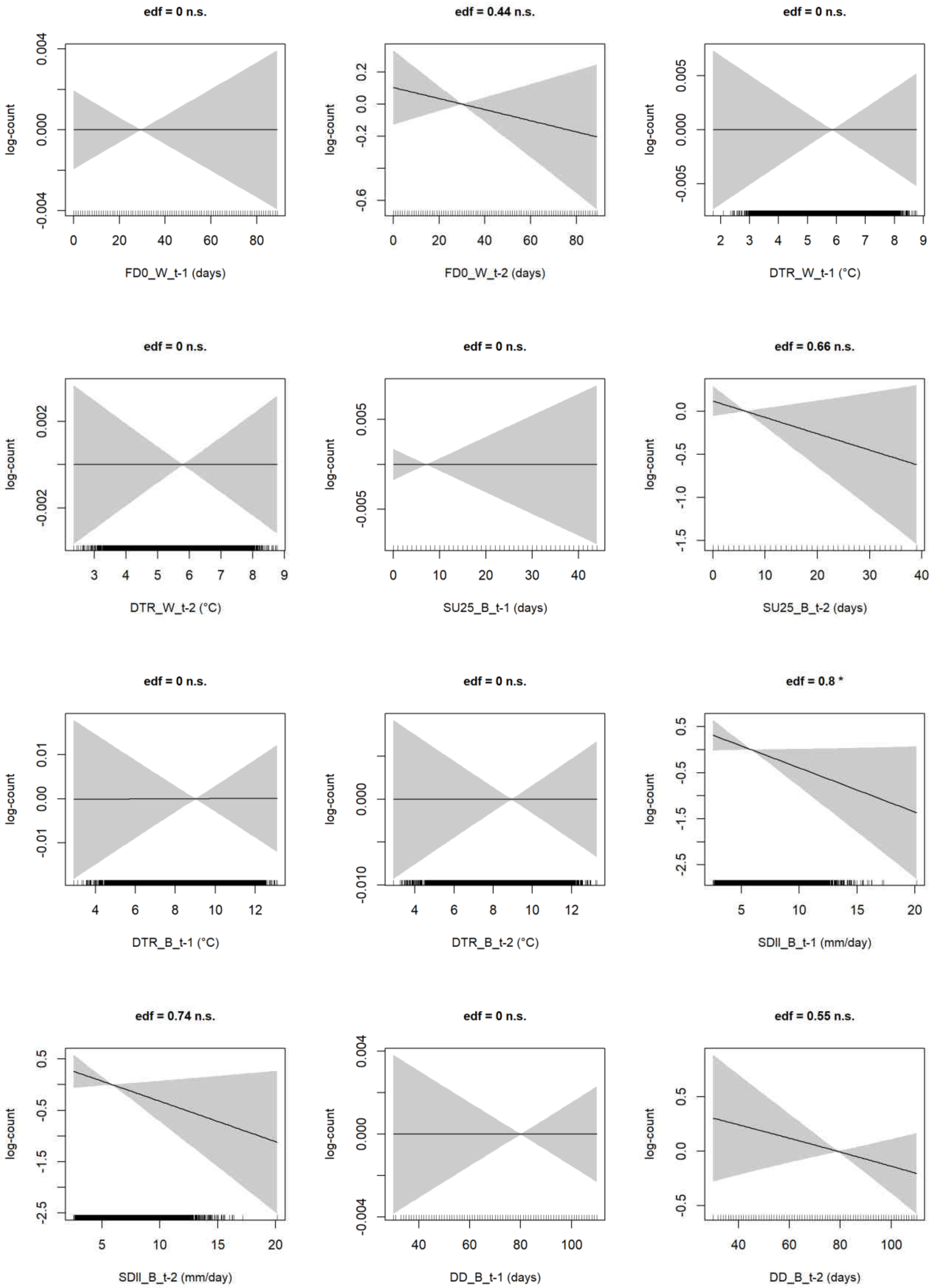
Northern Lapwing *Vanellus vanellus*



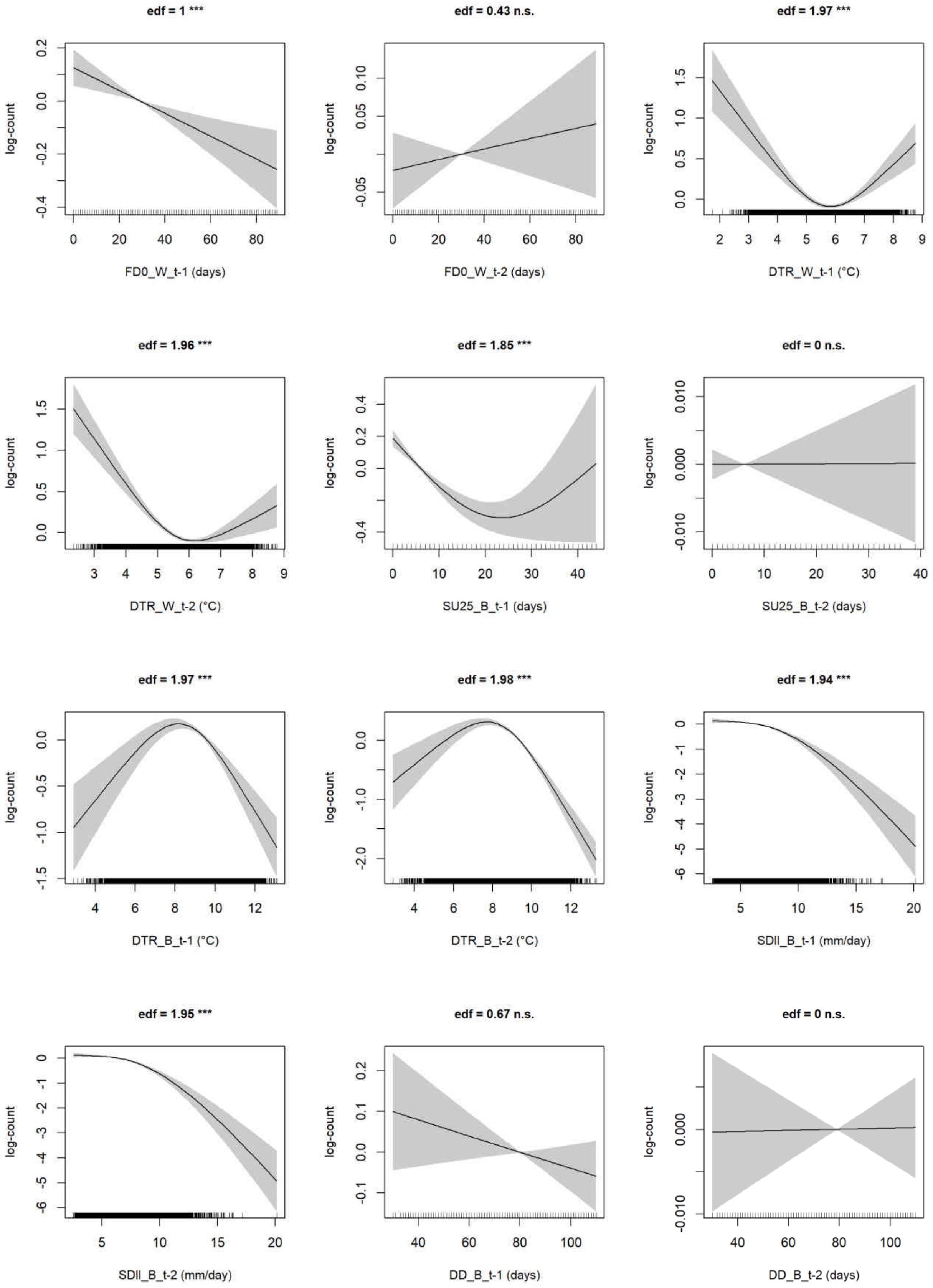
Common Snipe *Gallinago gallinago*



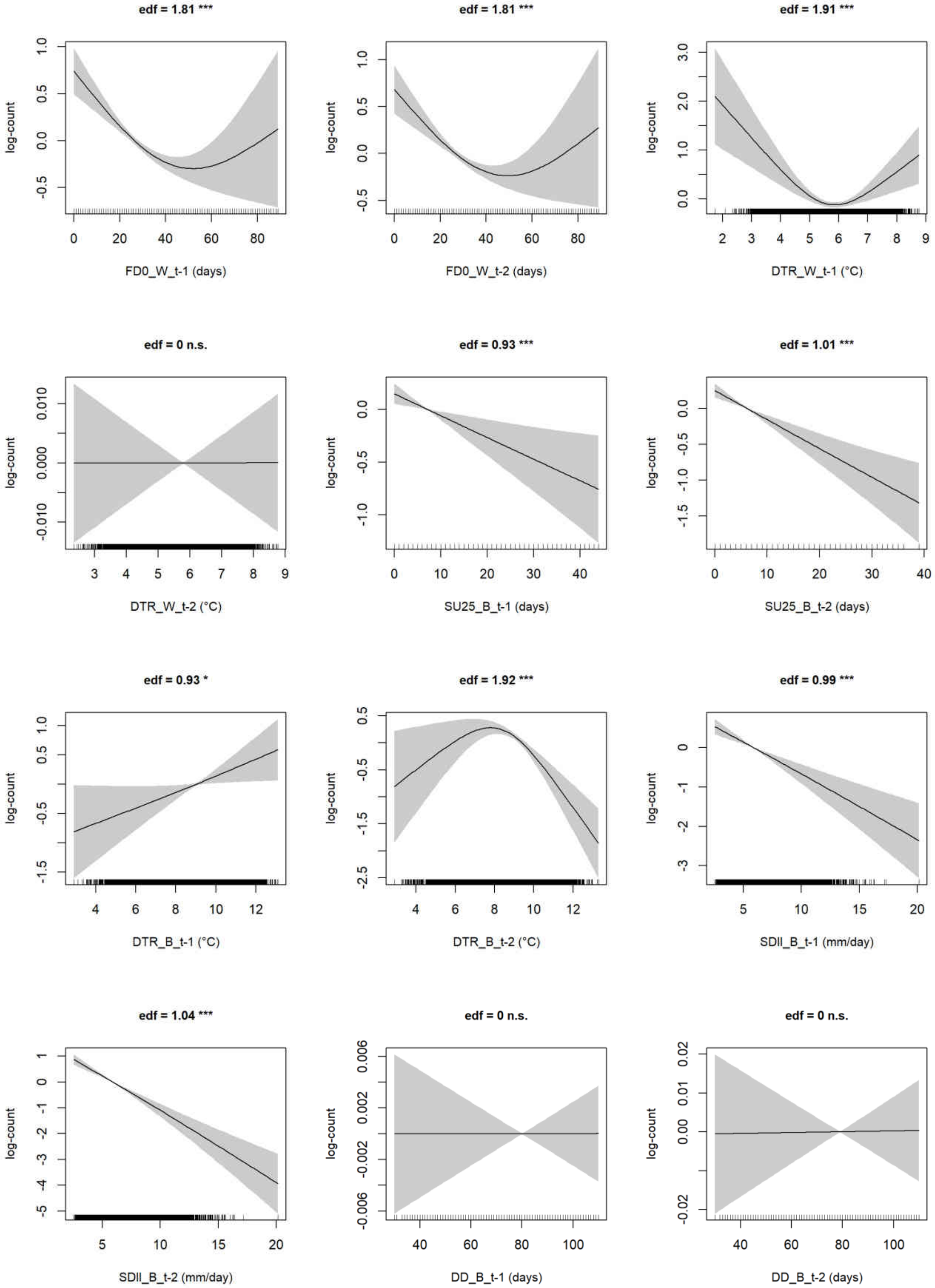
Eurasian Woodcock *Scolopax rusticola*



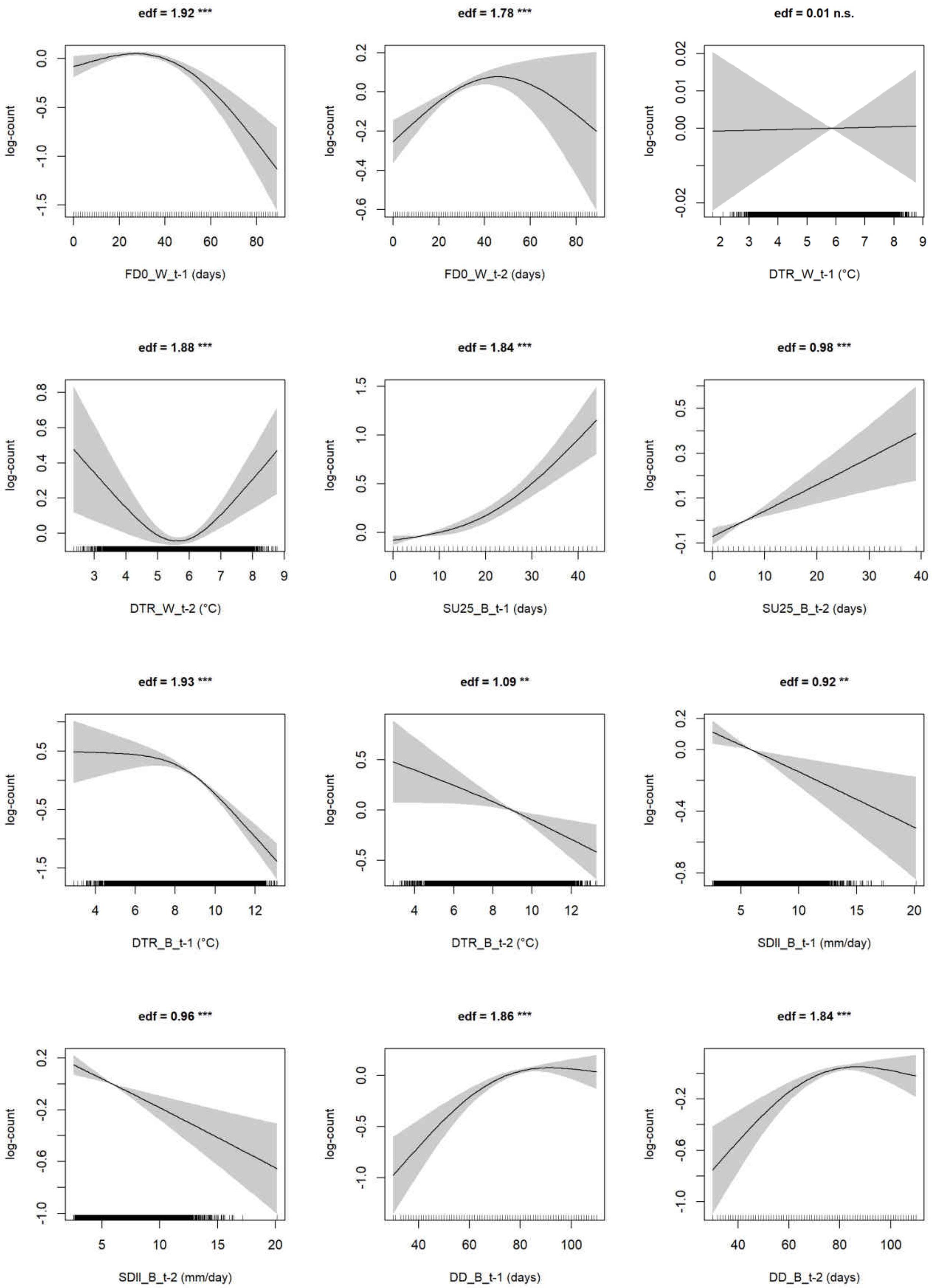
Eurasian Curlew *Numenius arquata*



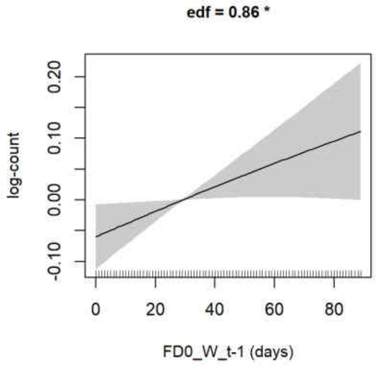
Common Redshank *Tringa totanus*

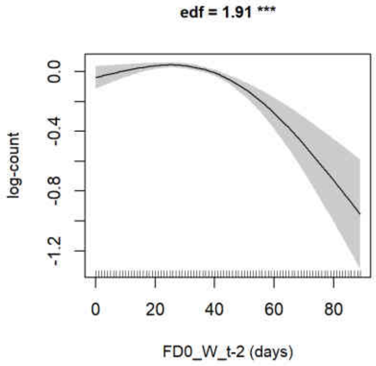


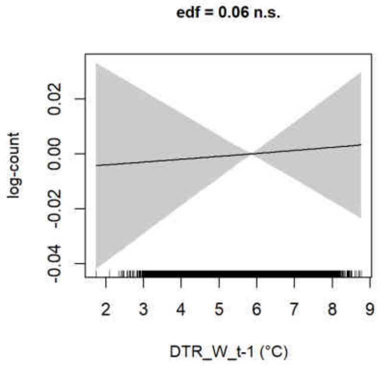
Feral Pigeon *Columba livia*

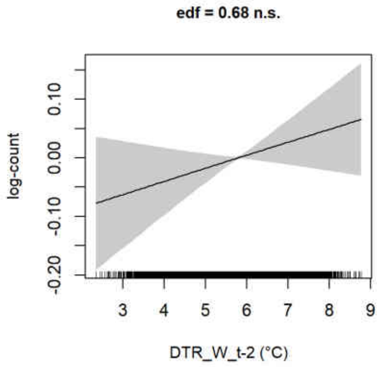


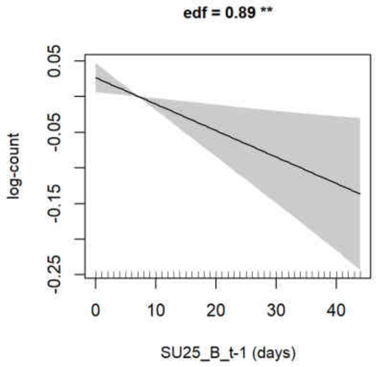
Stock Dove *Columba oenas*

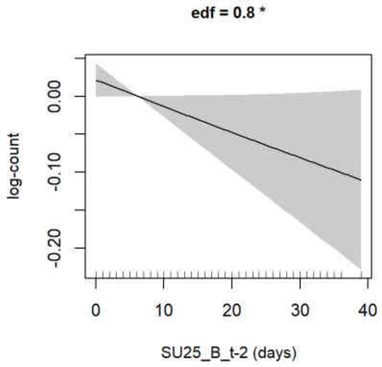

edf = 0.86 *

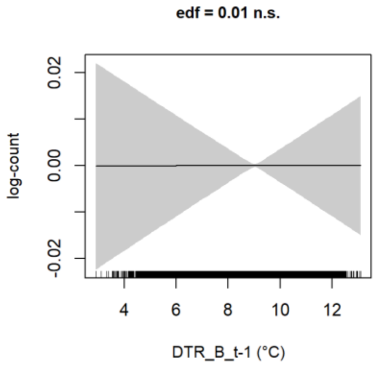

edf = 1.91 ***

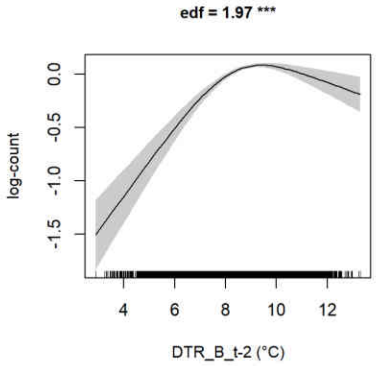

edf = 0.06 n.s.

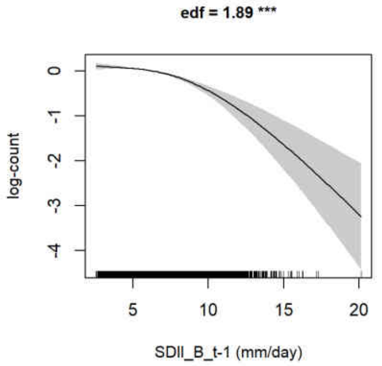

edf = 0.68 n.s.

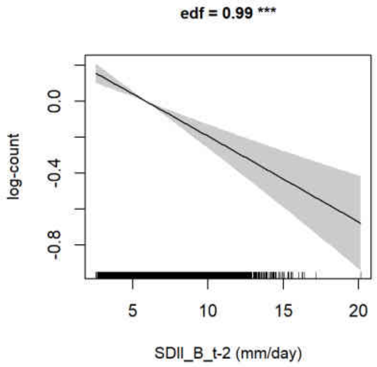

edf = 0.89 **

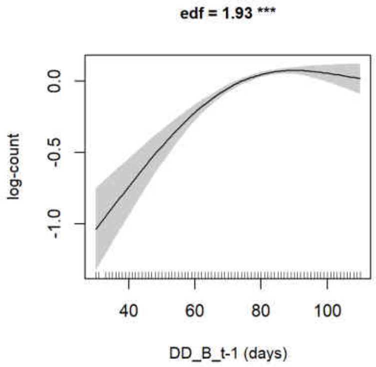

edf = 0.8 *

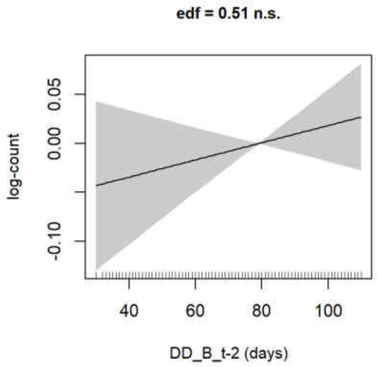

edf = 0.01 n.s.


edf = 1.97 ***

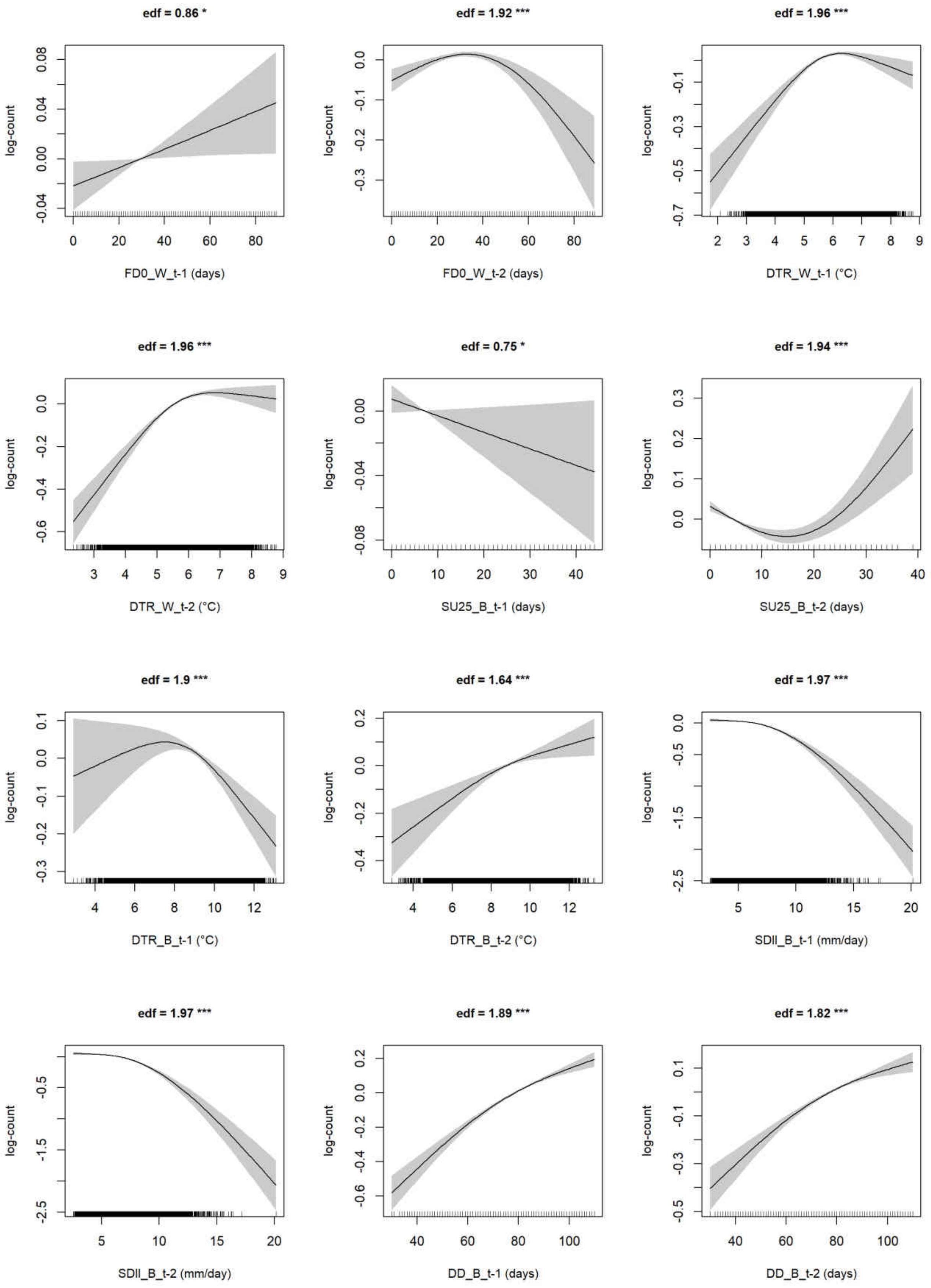

edf = 1.89 ***


edf = 0.99 ***

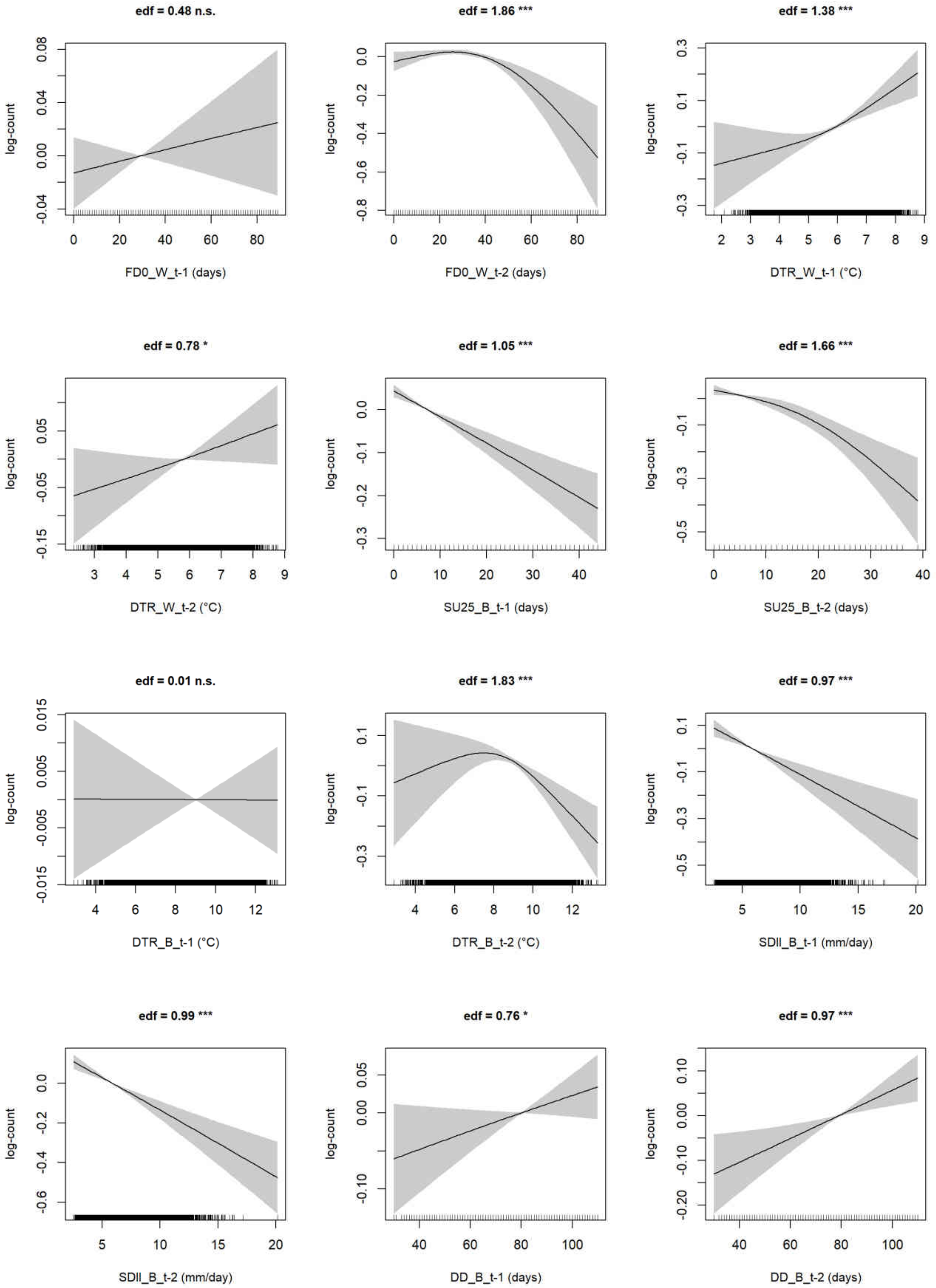

edf = 1.93 ***


edf = 0.51 n.s.

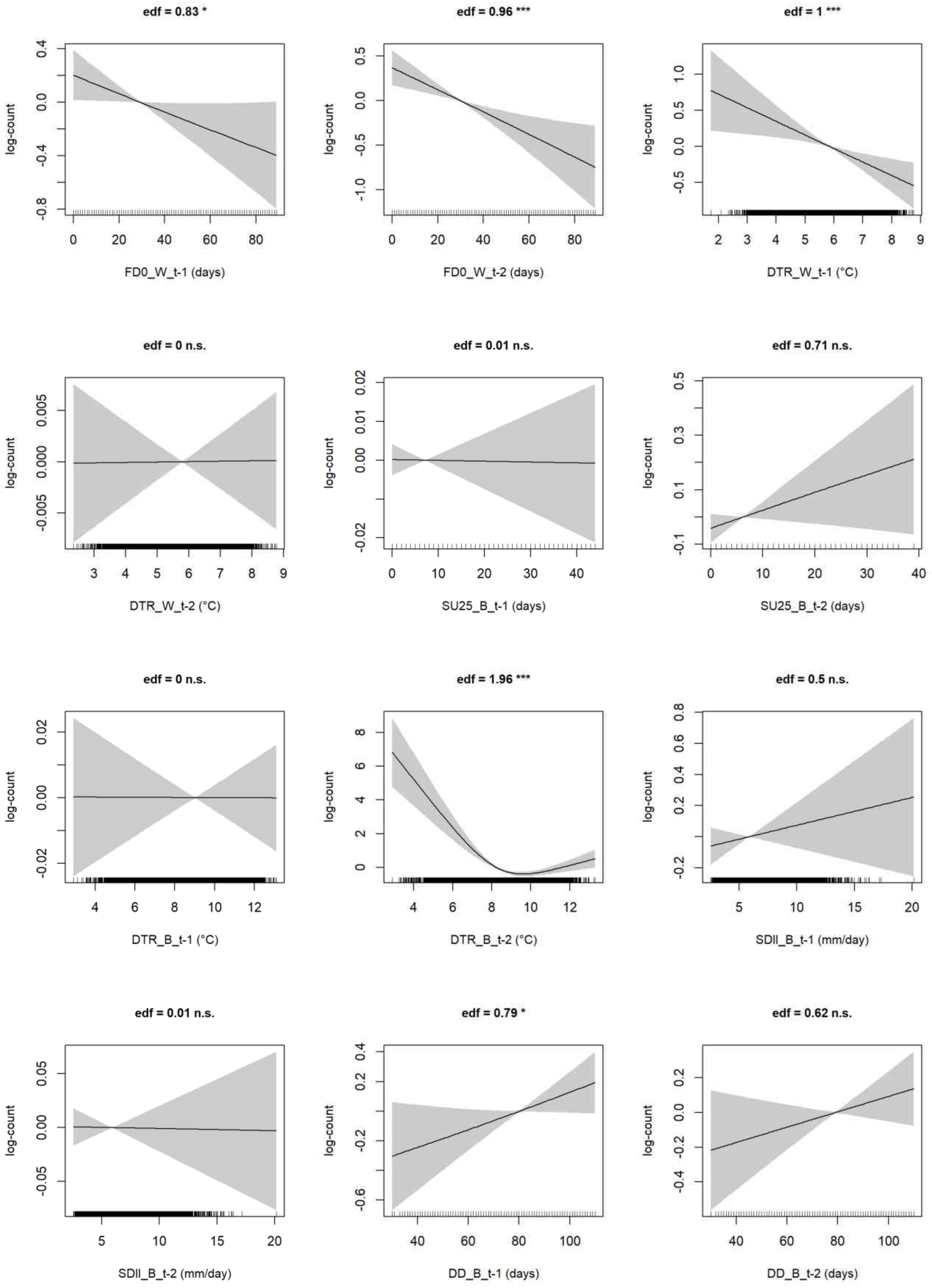
Common Wood Pigeon *Columba palumbus*



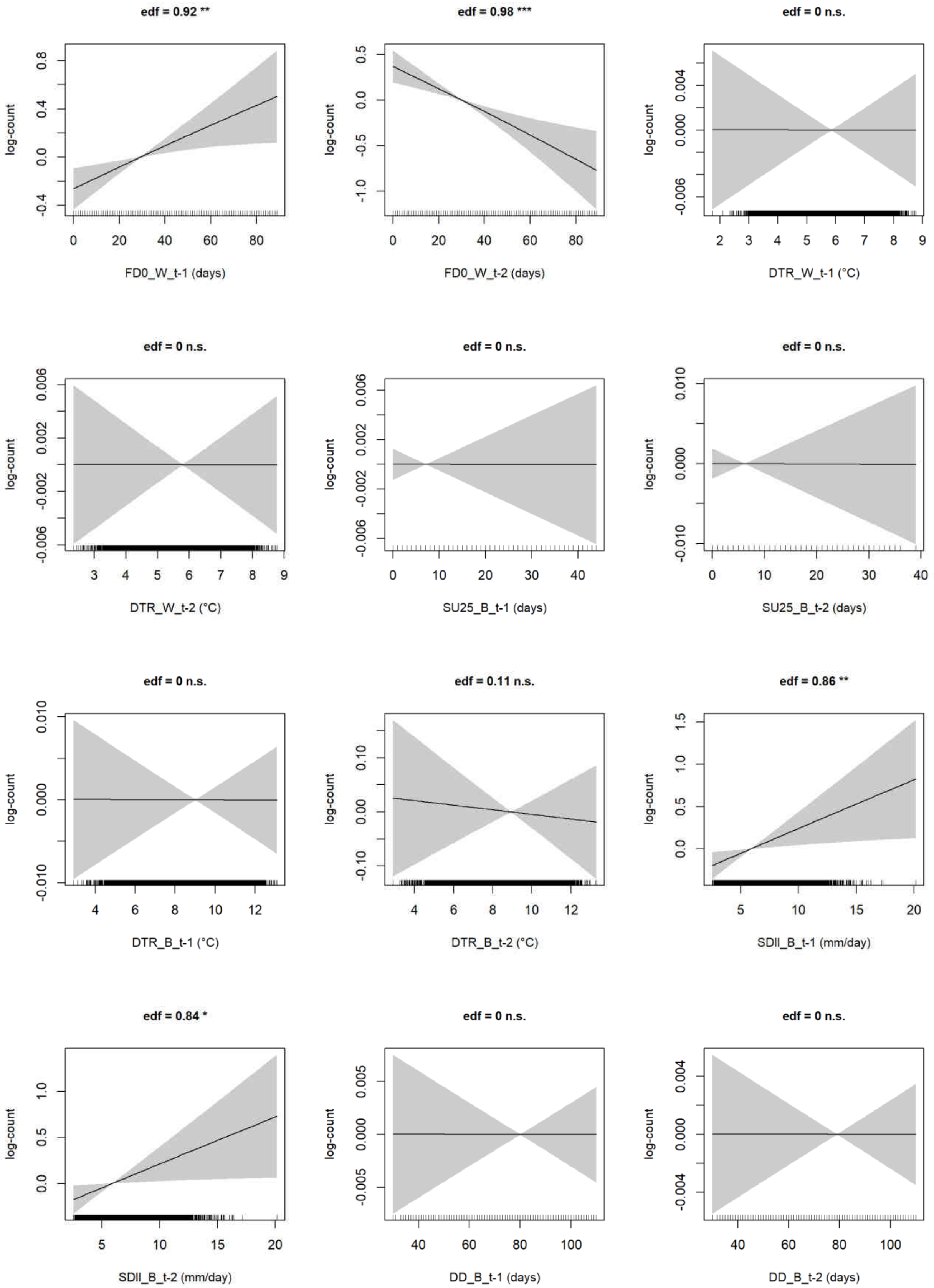
Eurasian Collared Dove *Streptopelia decaocto*



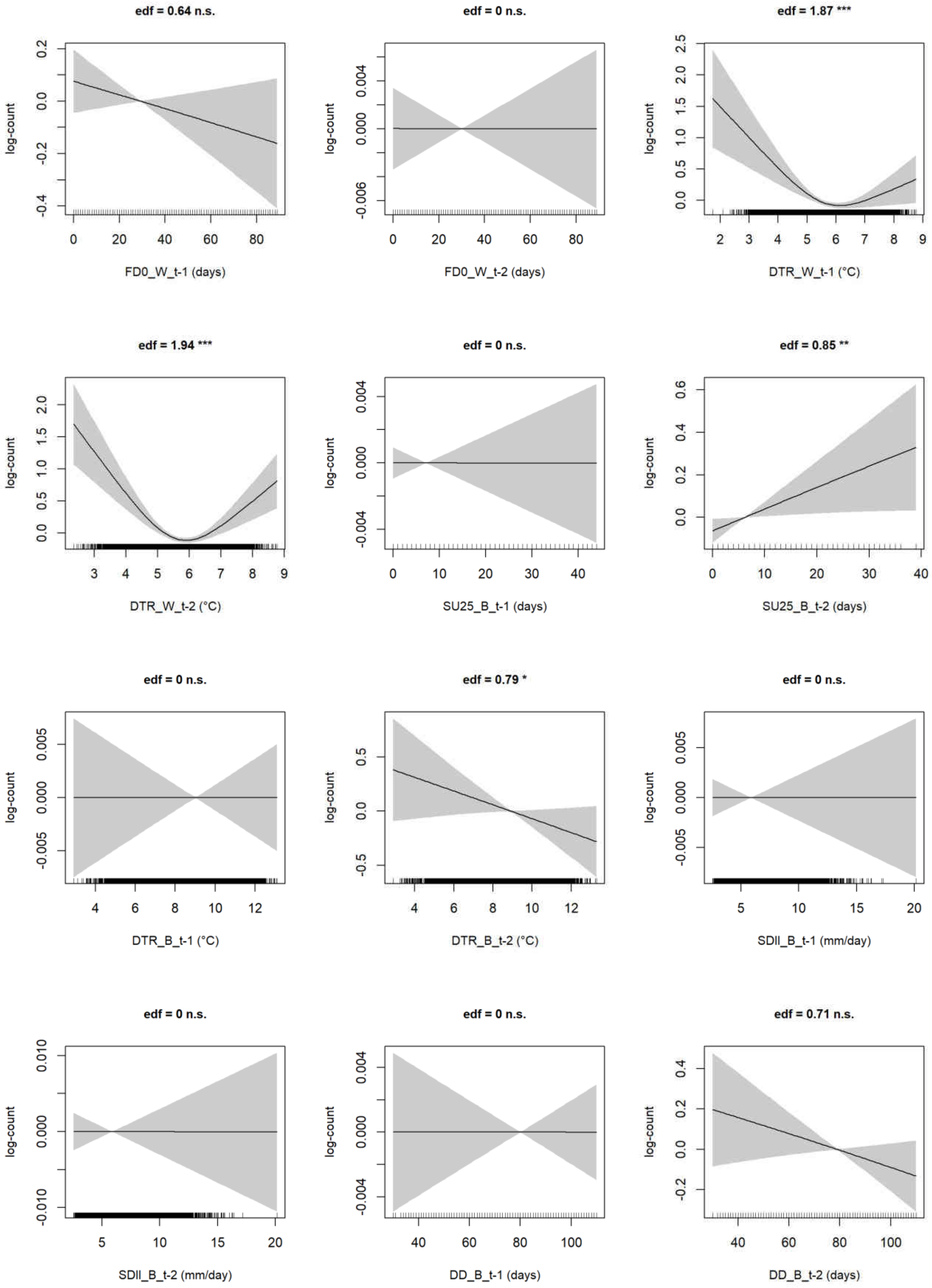
Rose-ringed Parakeet *Psittacula krameri*



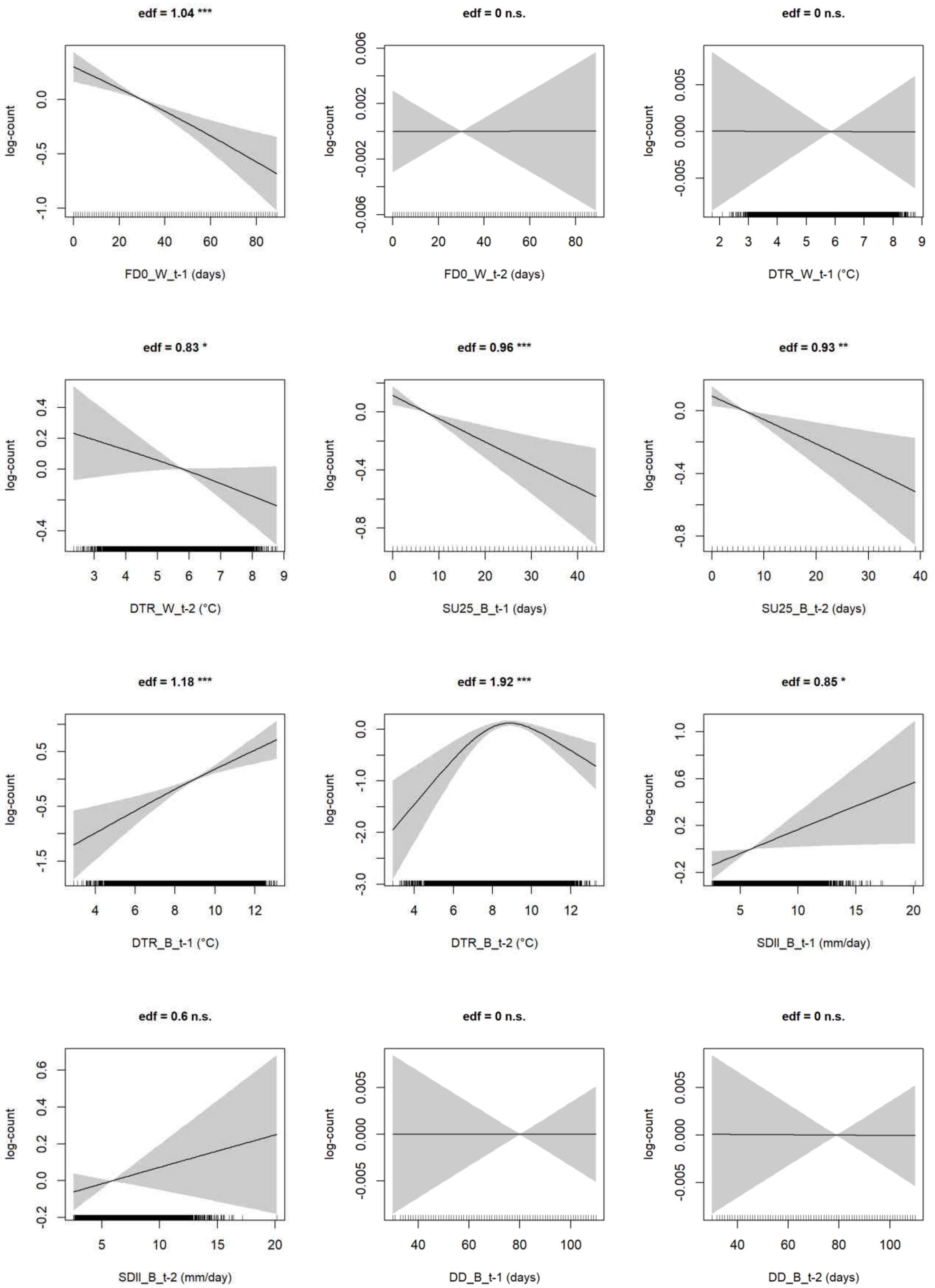
Western Barn Owl *Tyto alba*



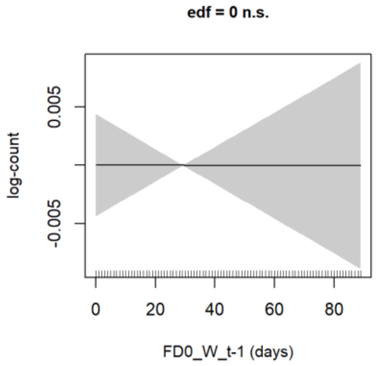
Little Owl *Athene noctua*

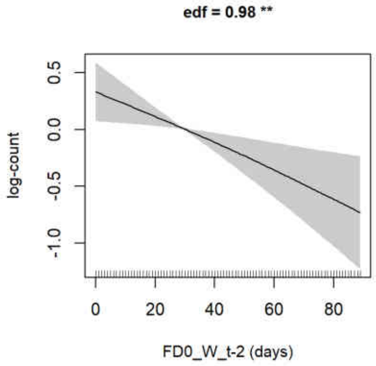


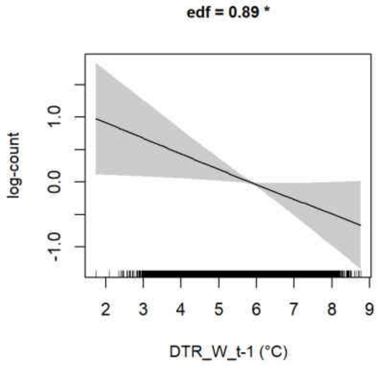
Tawny Owl *Strix aluco*

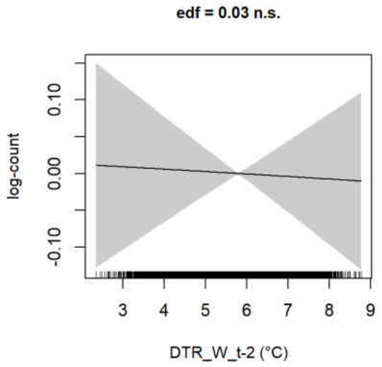


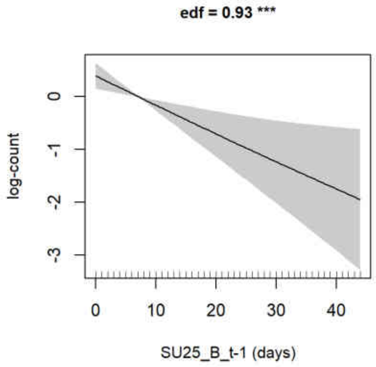
Short-eared Owl *Asio flammeus*

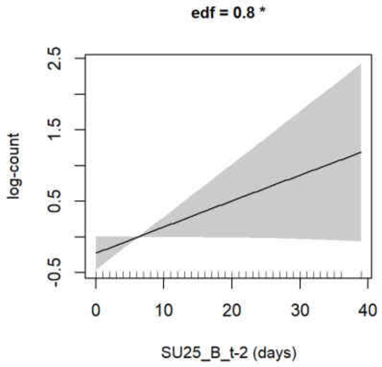


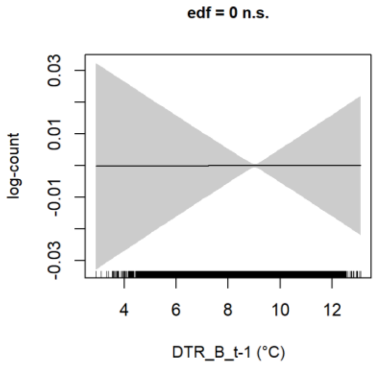


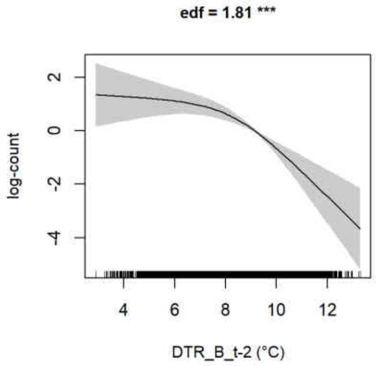


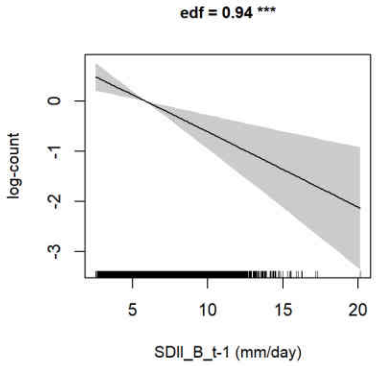


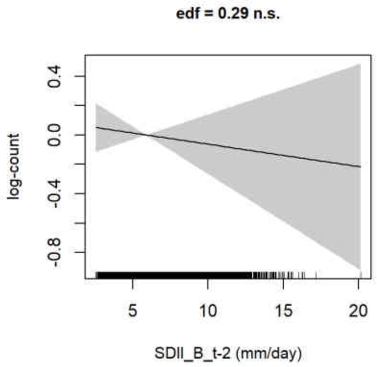


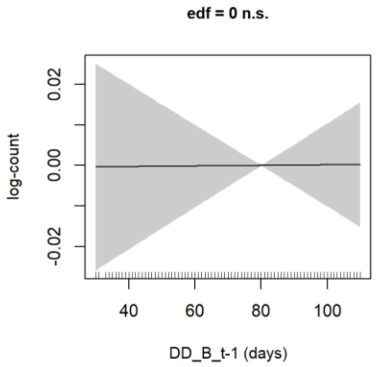


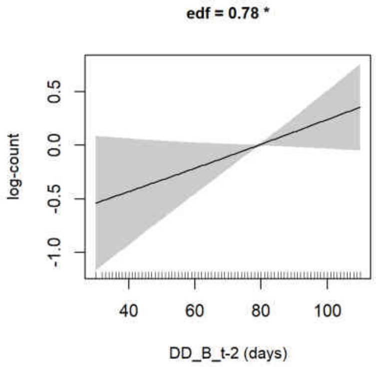




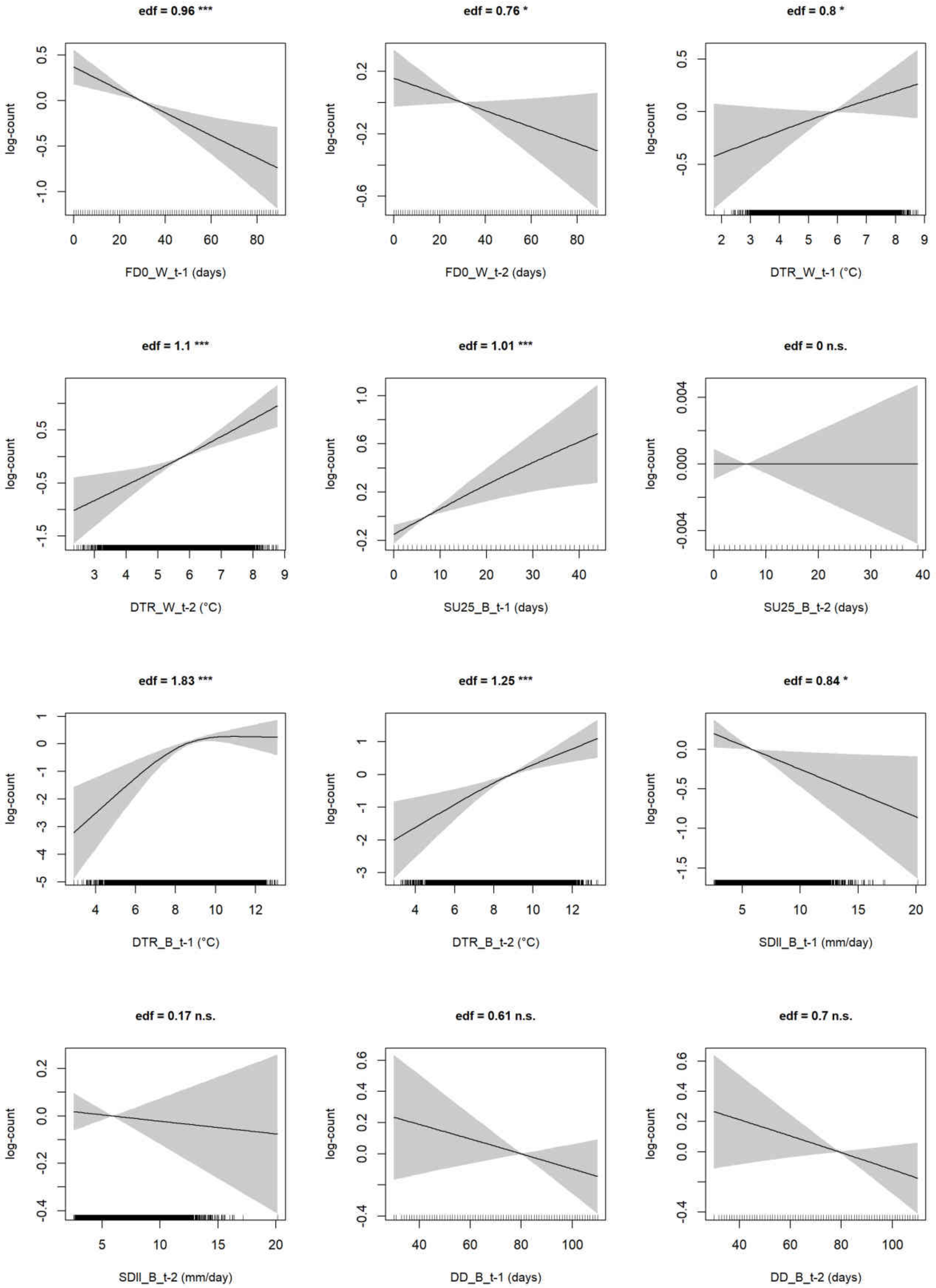




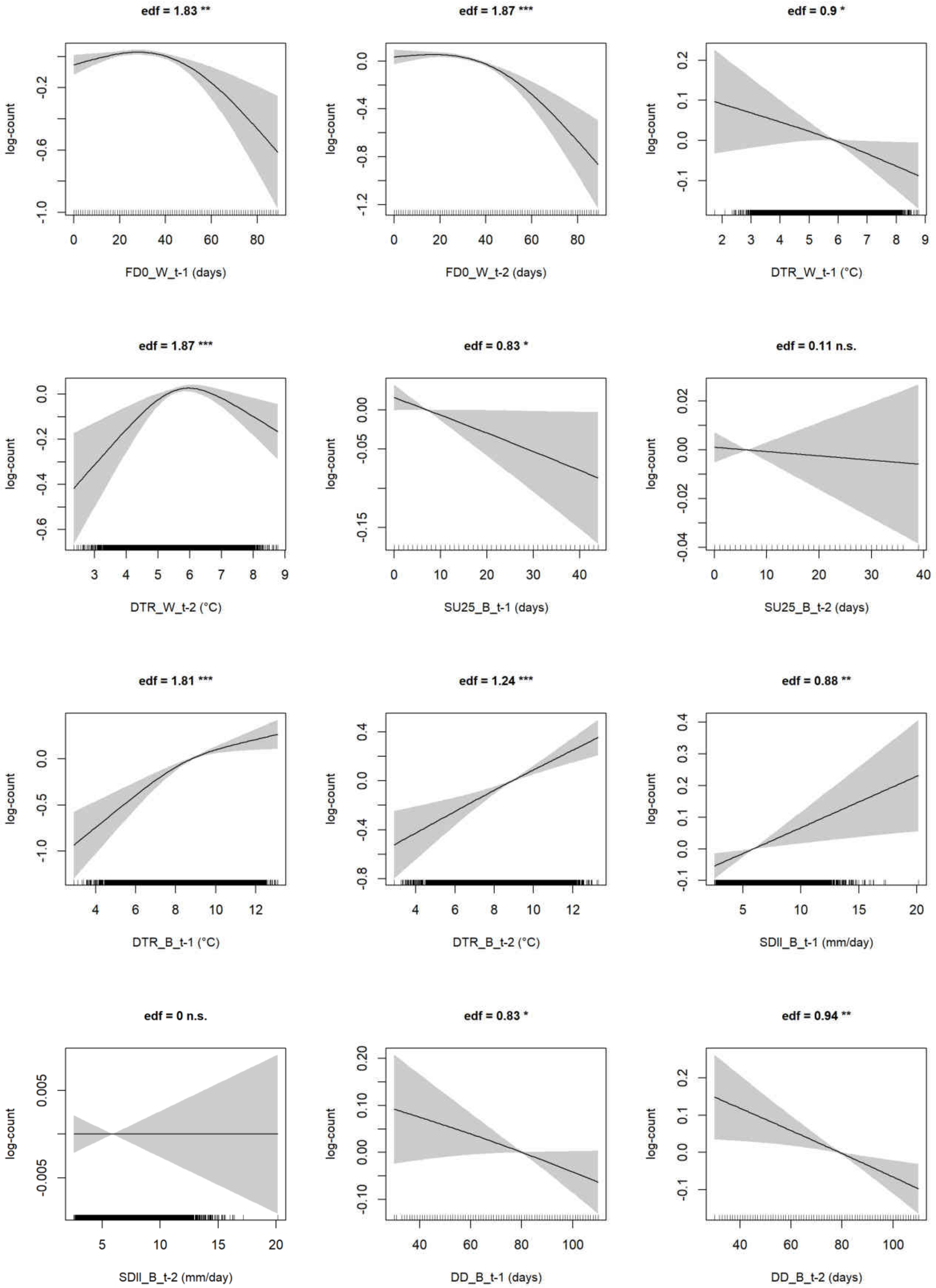




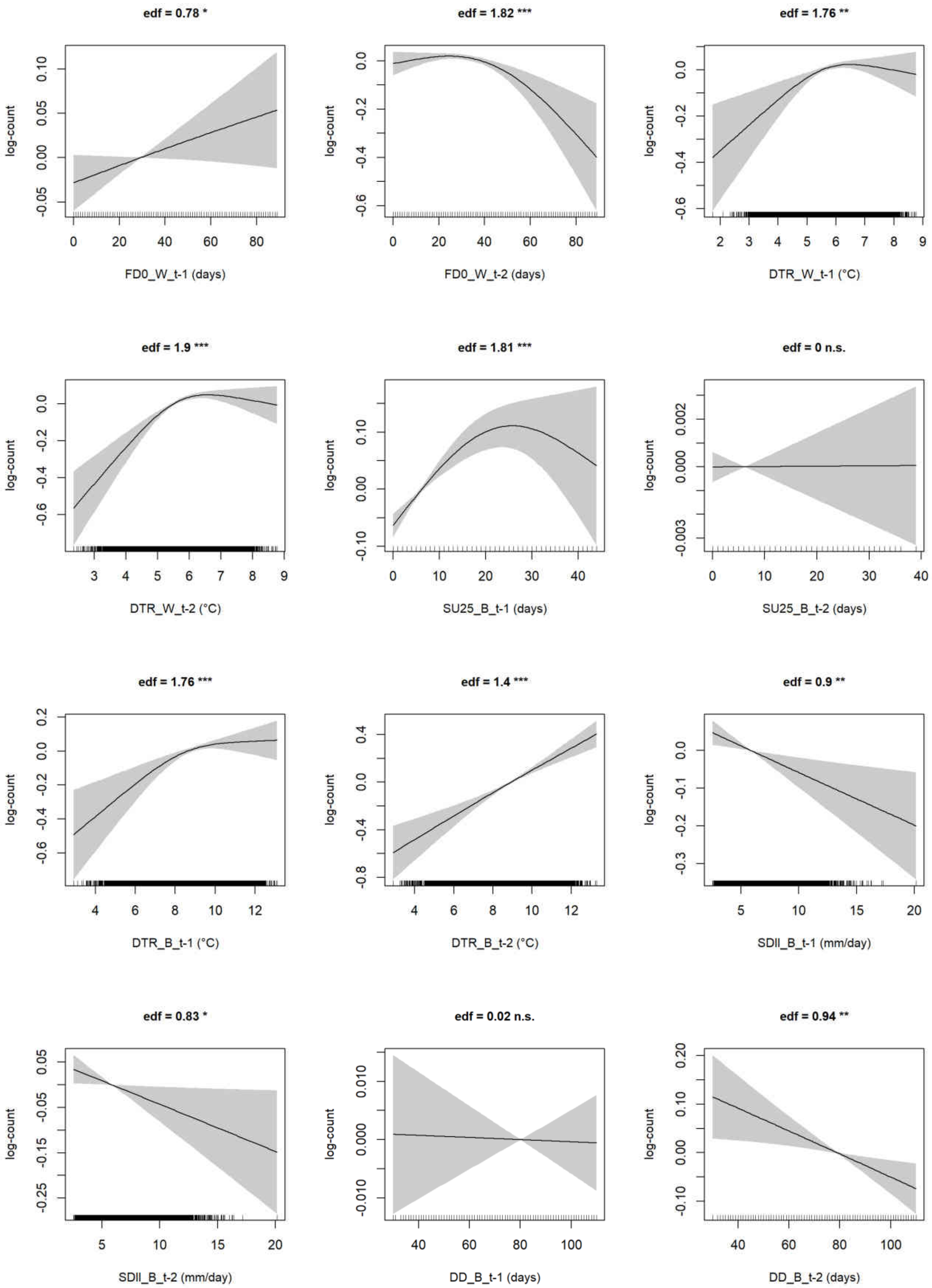
Common Kingfisher *Alcedo atthis*



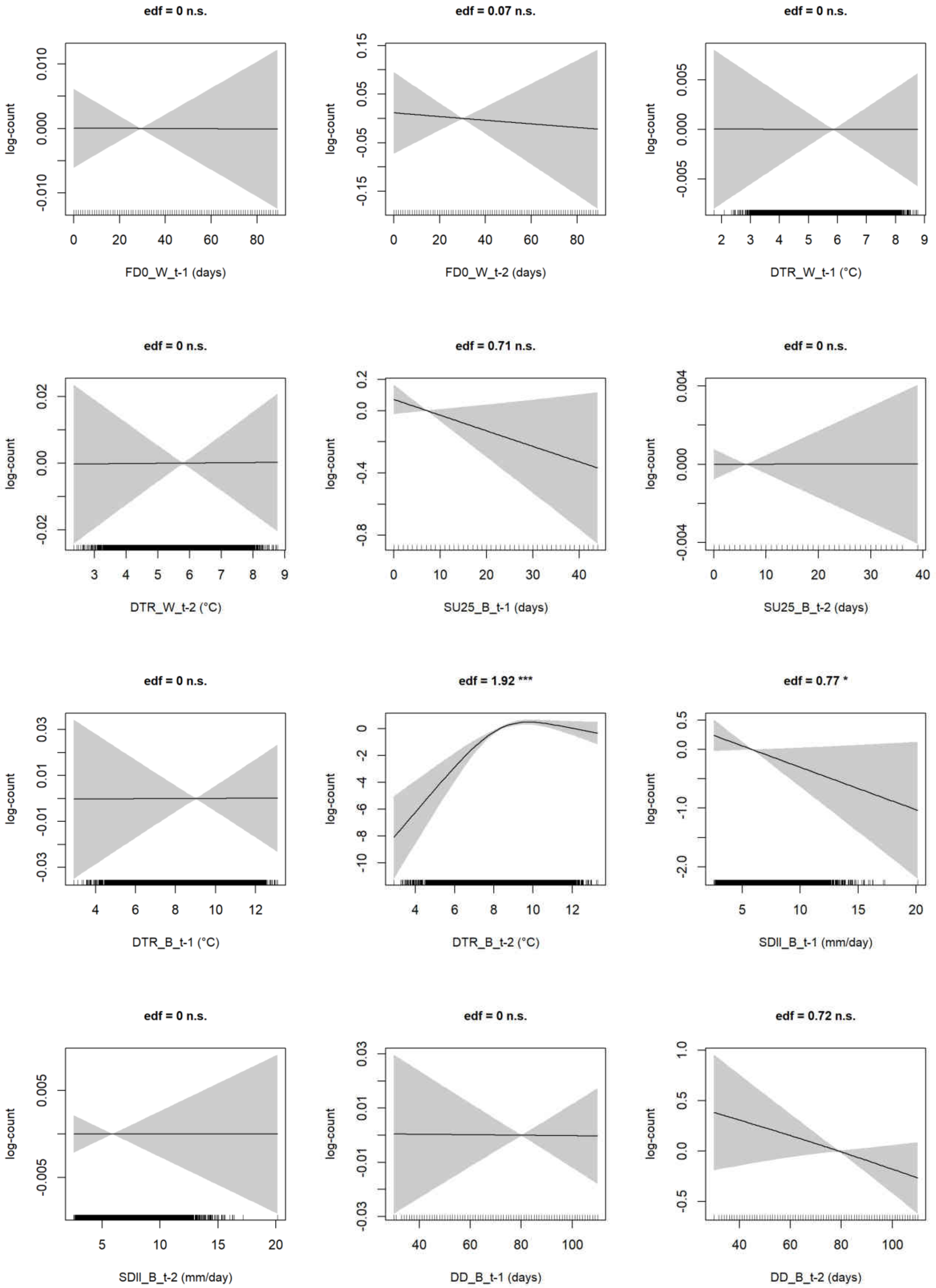
European Green Woodpecker *Picus viridis*



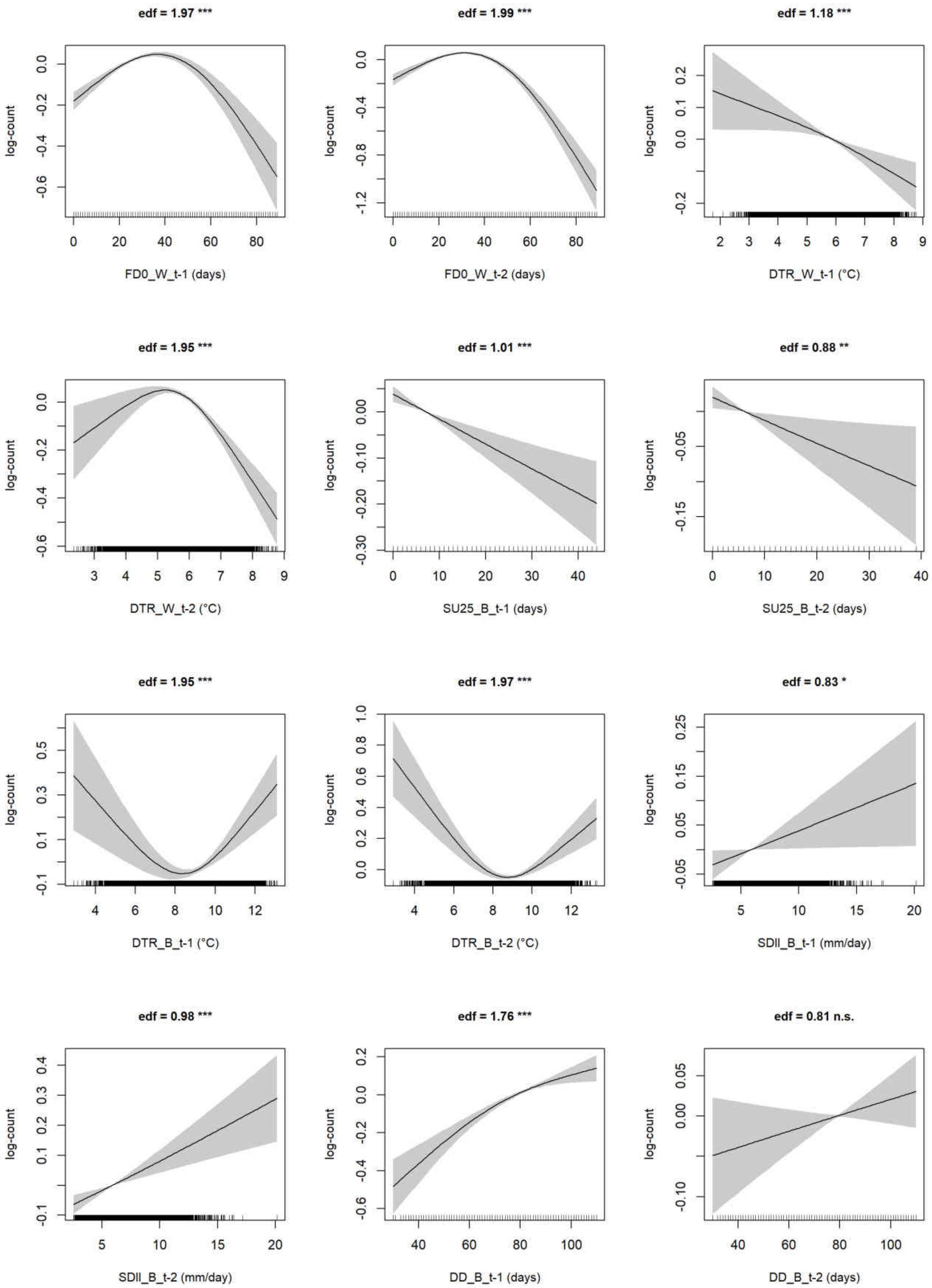
Great Spotted Woodpecker *Dendrocopos major*



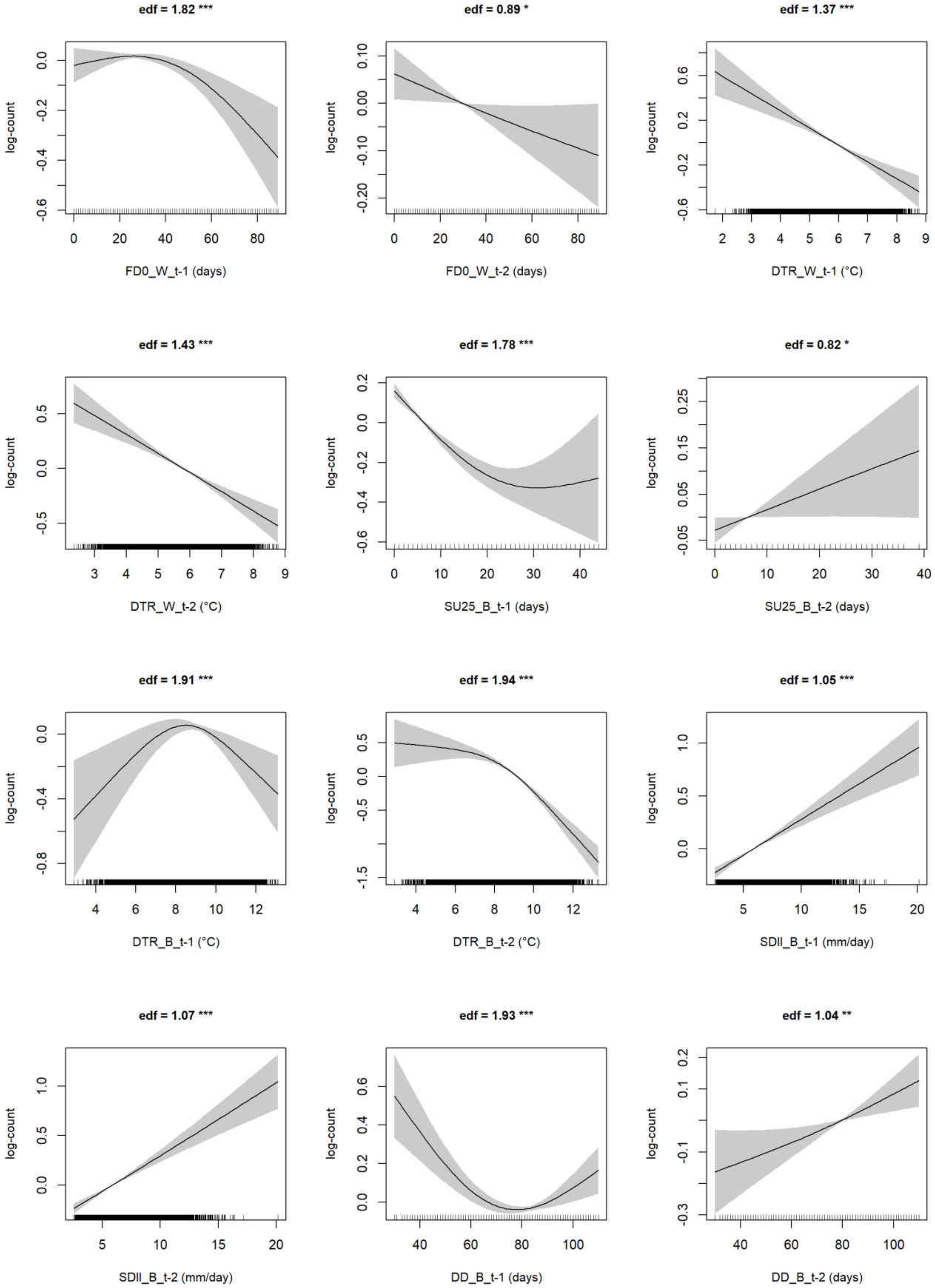
Lesser Spotted Woodpecker *Dryobates minor*



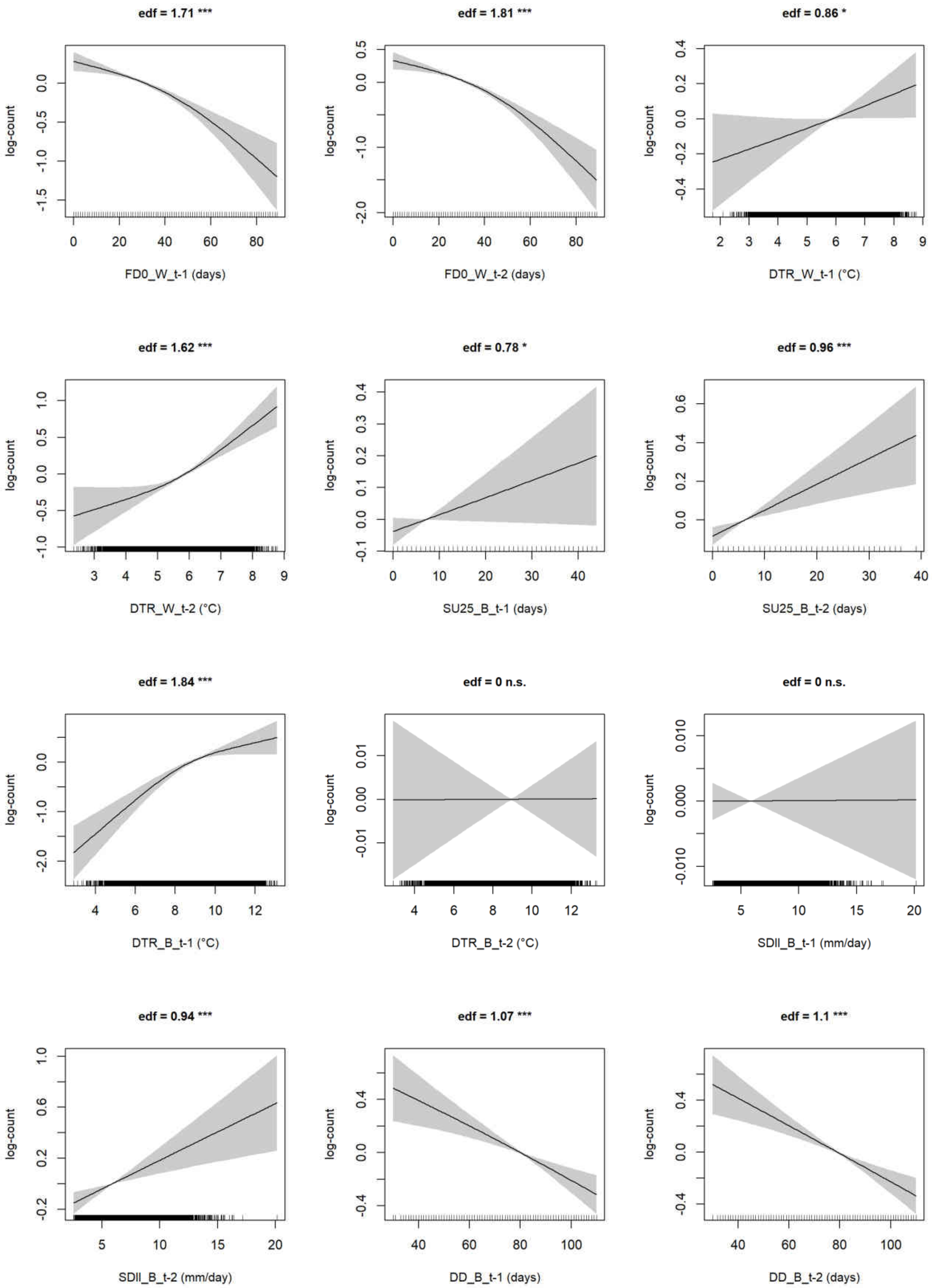
Eurasian Skylark *Alauda arvensis*



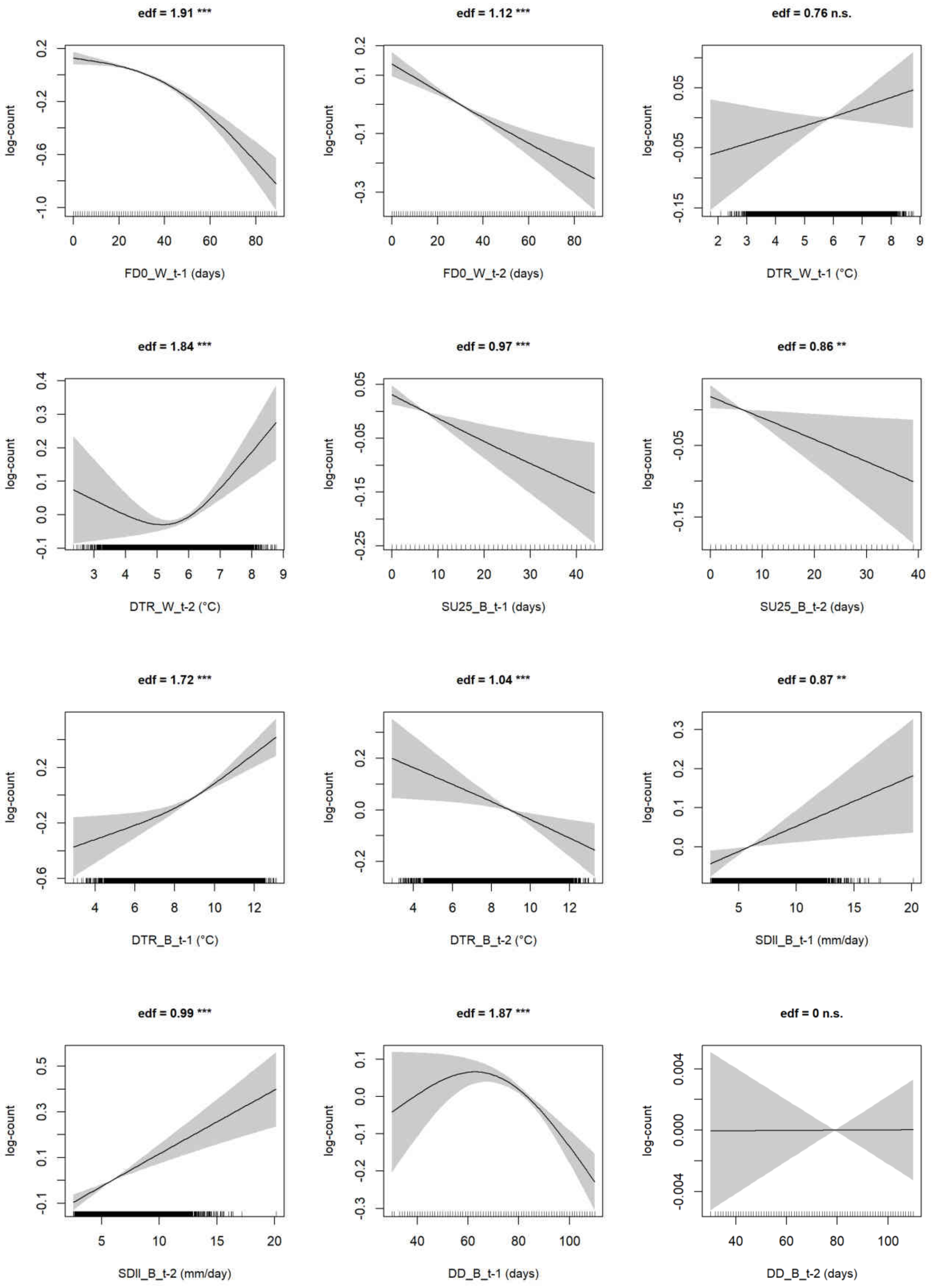
Meadow Pipit *Anthus pratensis*



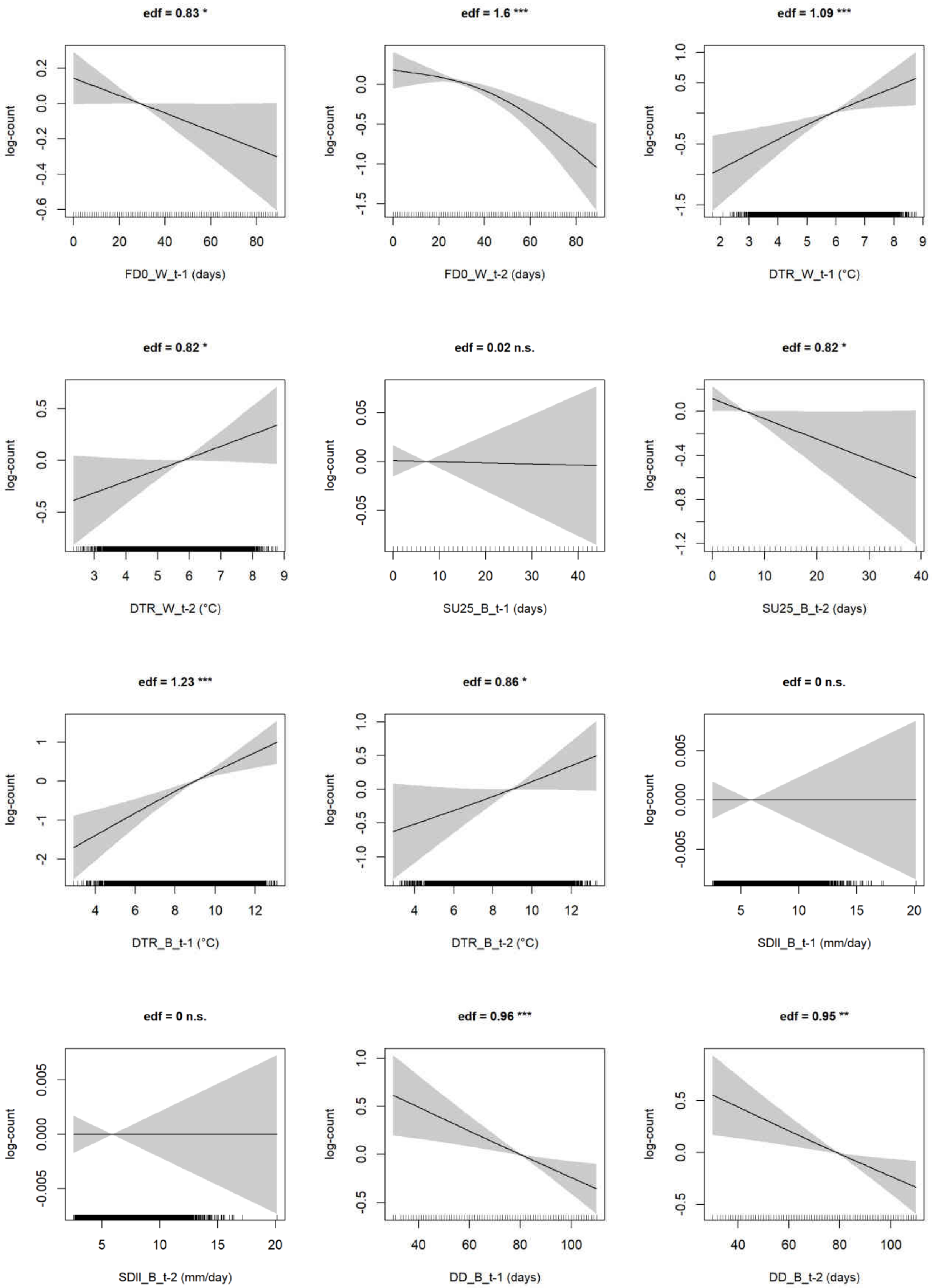
Grey Wagtail *Motacilla cinerea*



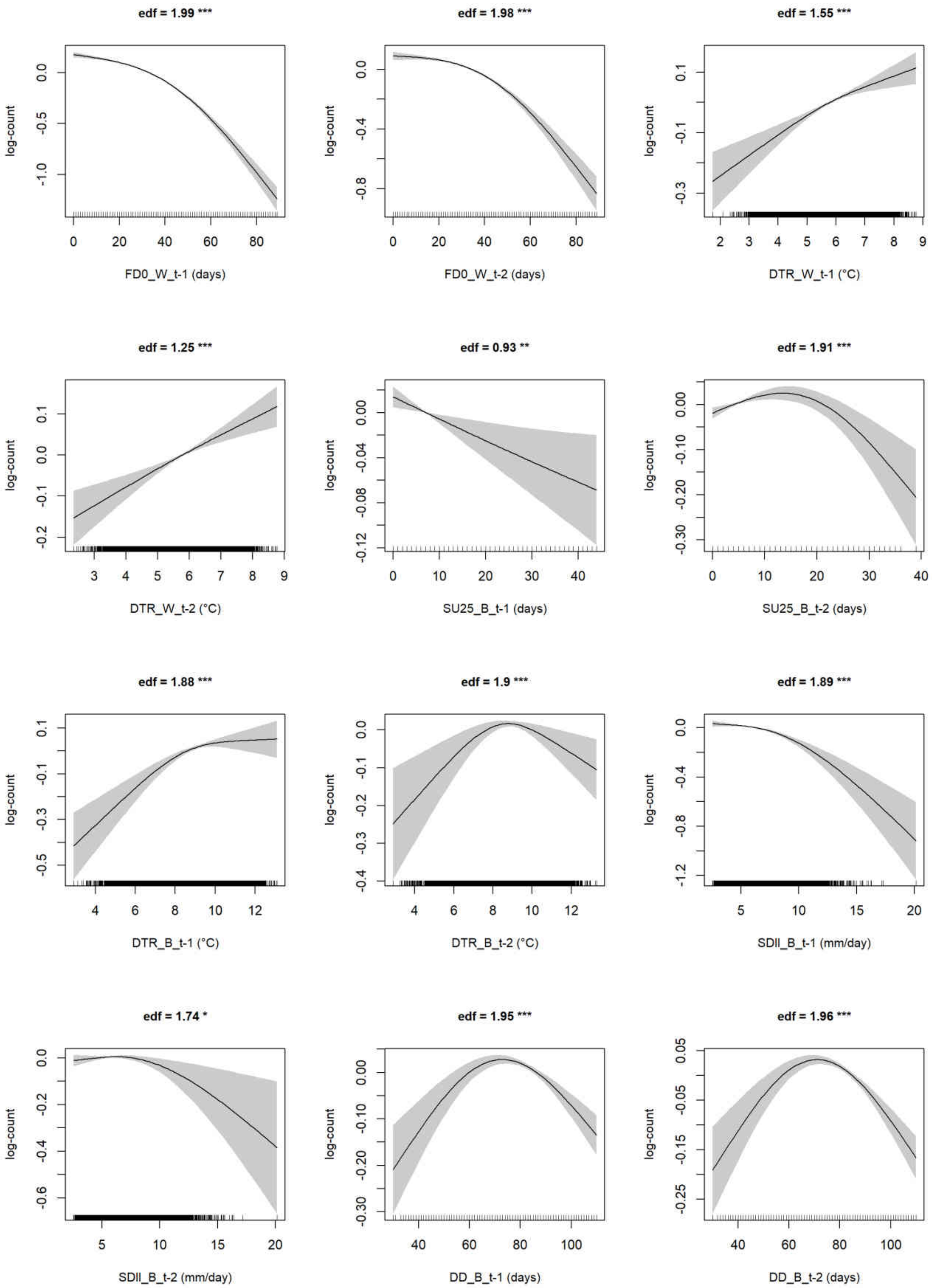
White Wagtail *Motacilla alba*



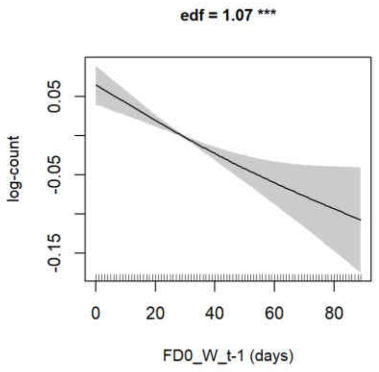
White-throated Dipper *Cinclus cinclus*

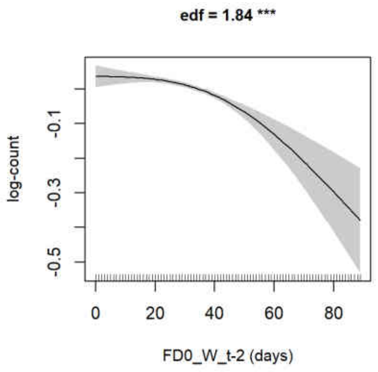


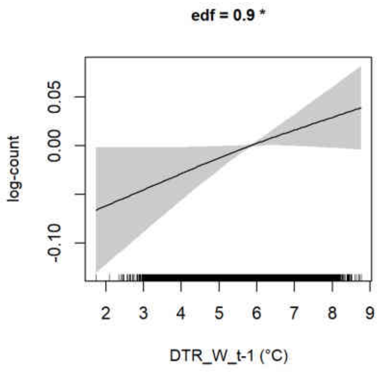
Eurasian Wren *Troglodytes troglodytes*

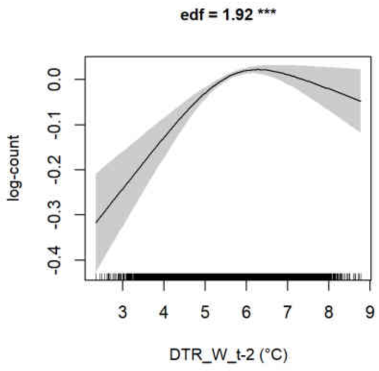


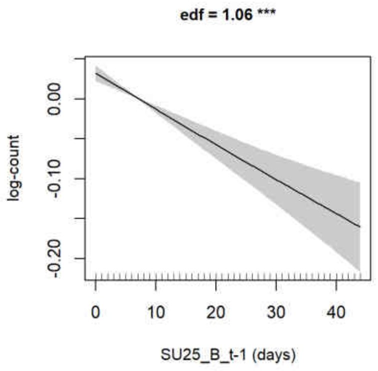
Dunnock *Prunella modularis*

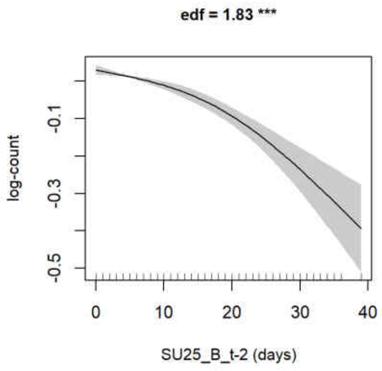


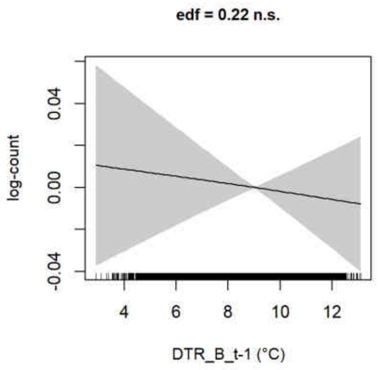


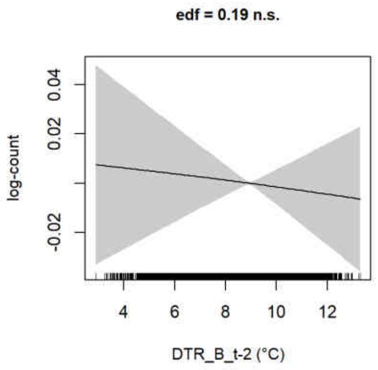


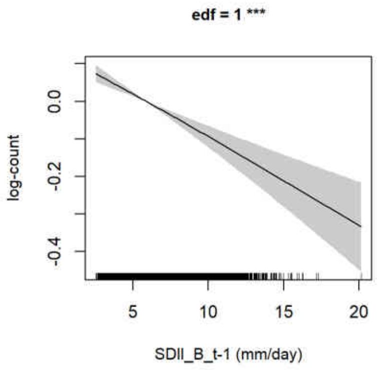


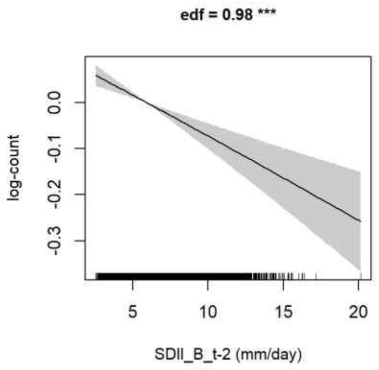


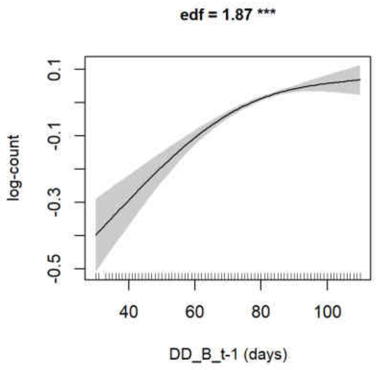


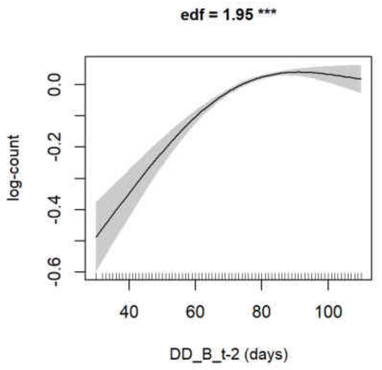




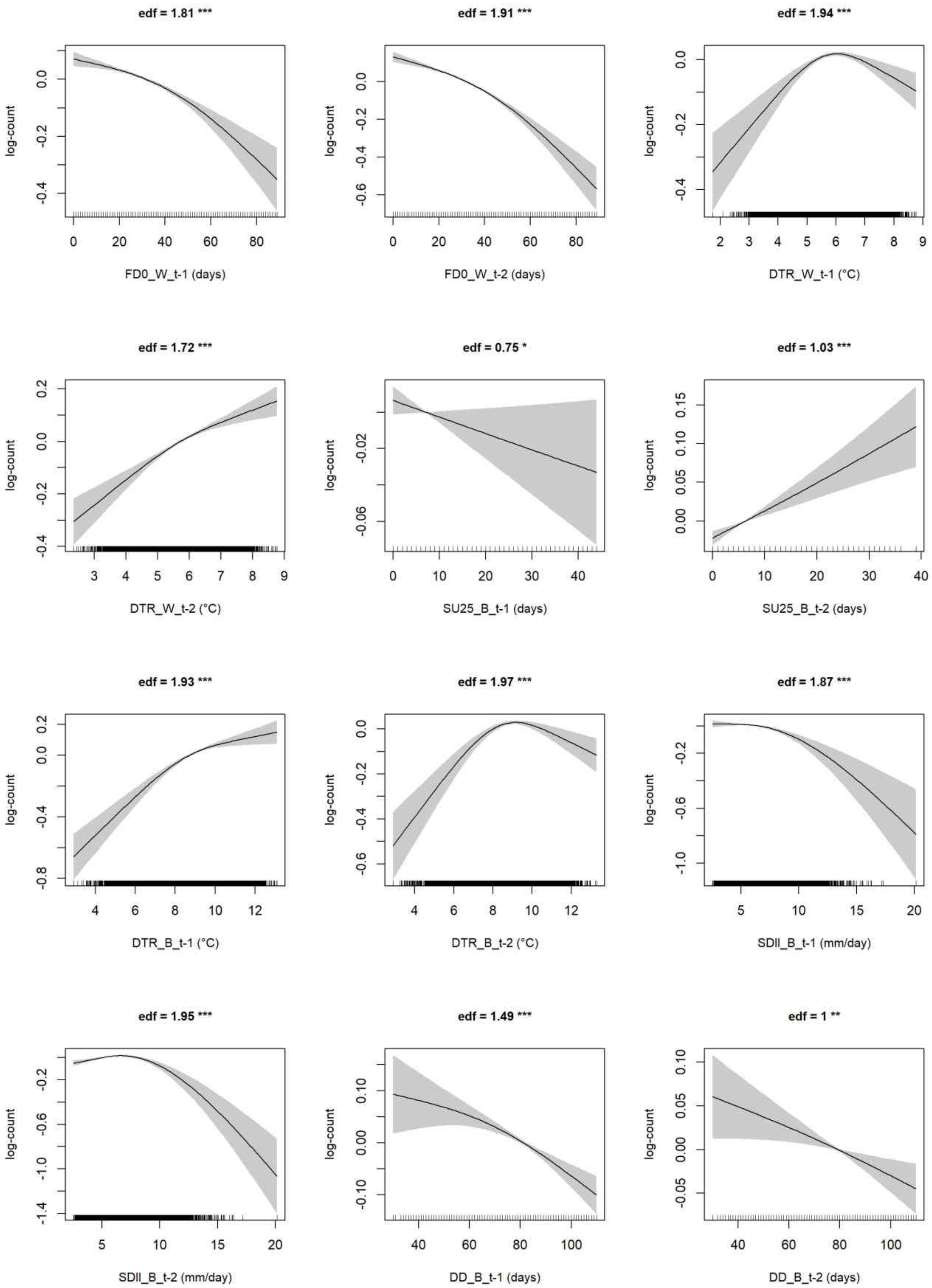




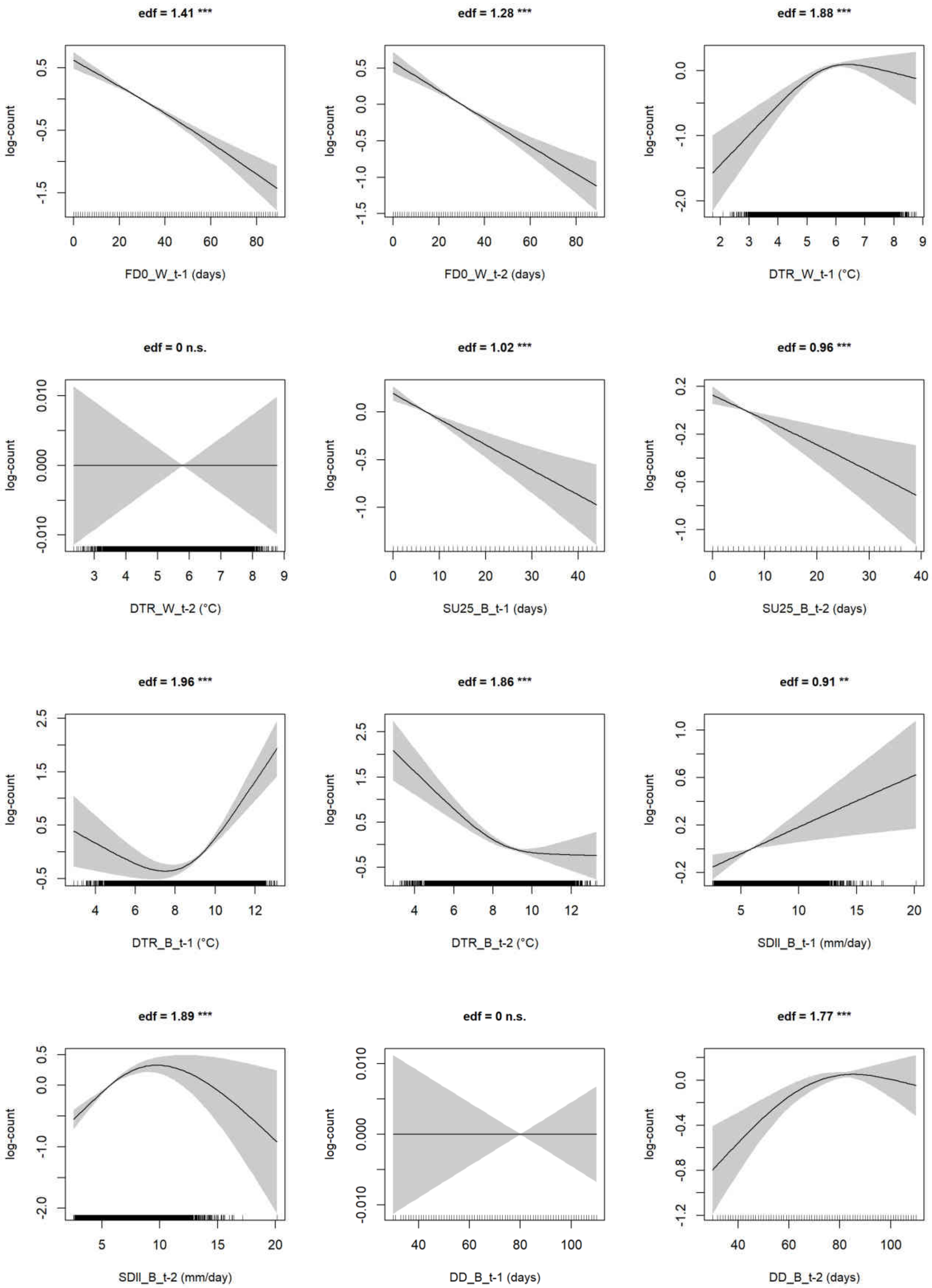




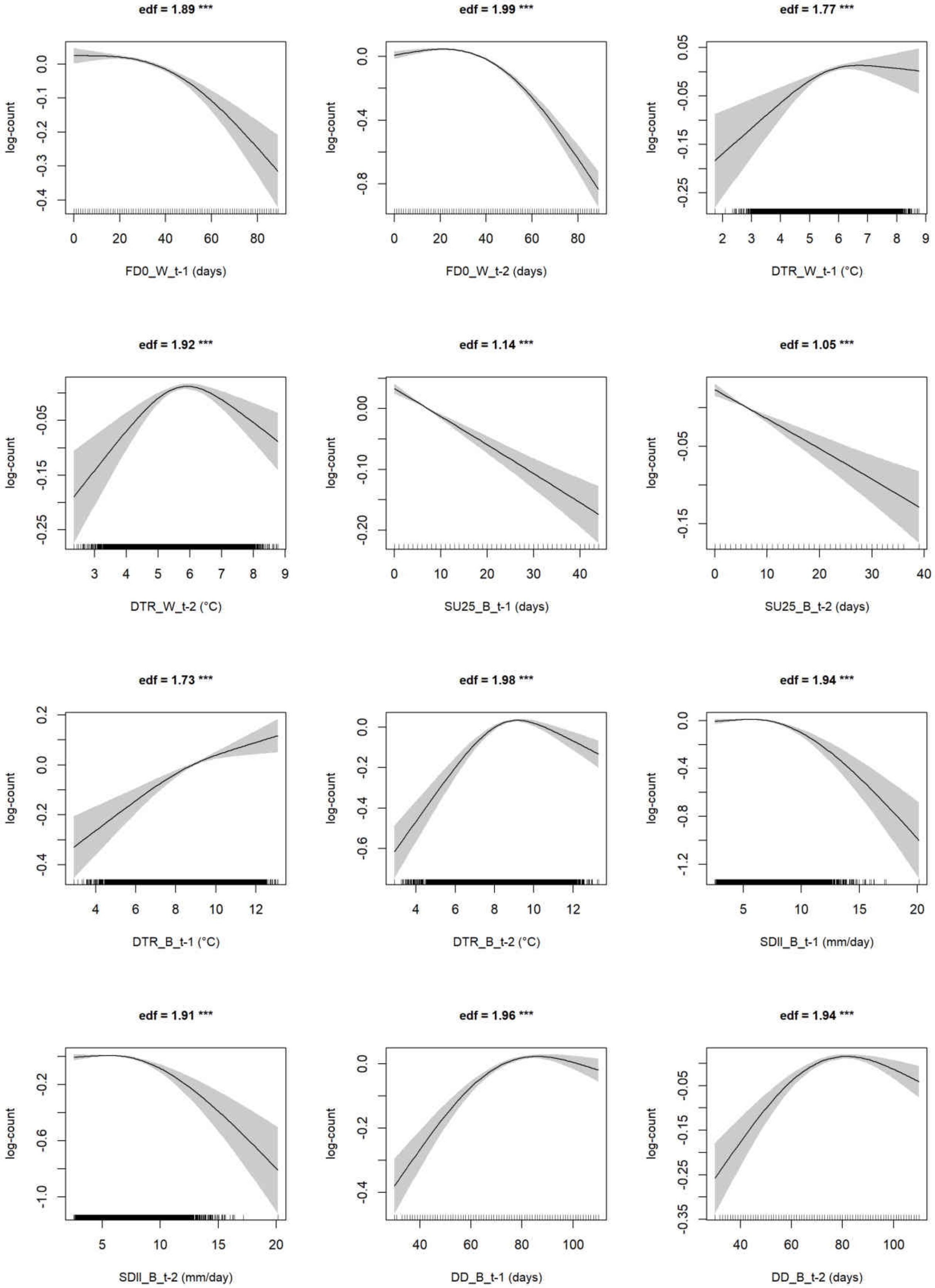
European Robin *Erithacus rubecula*



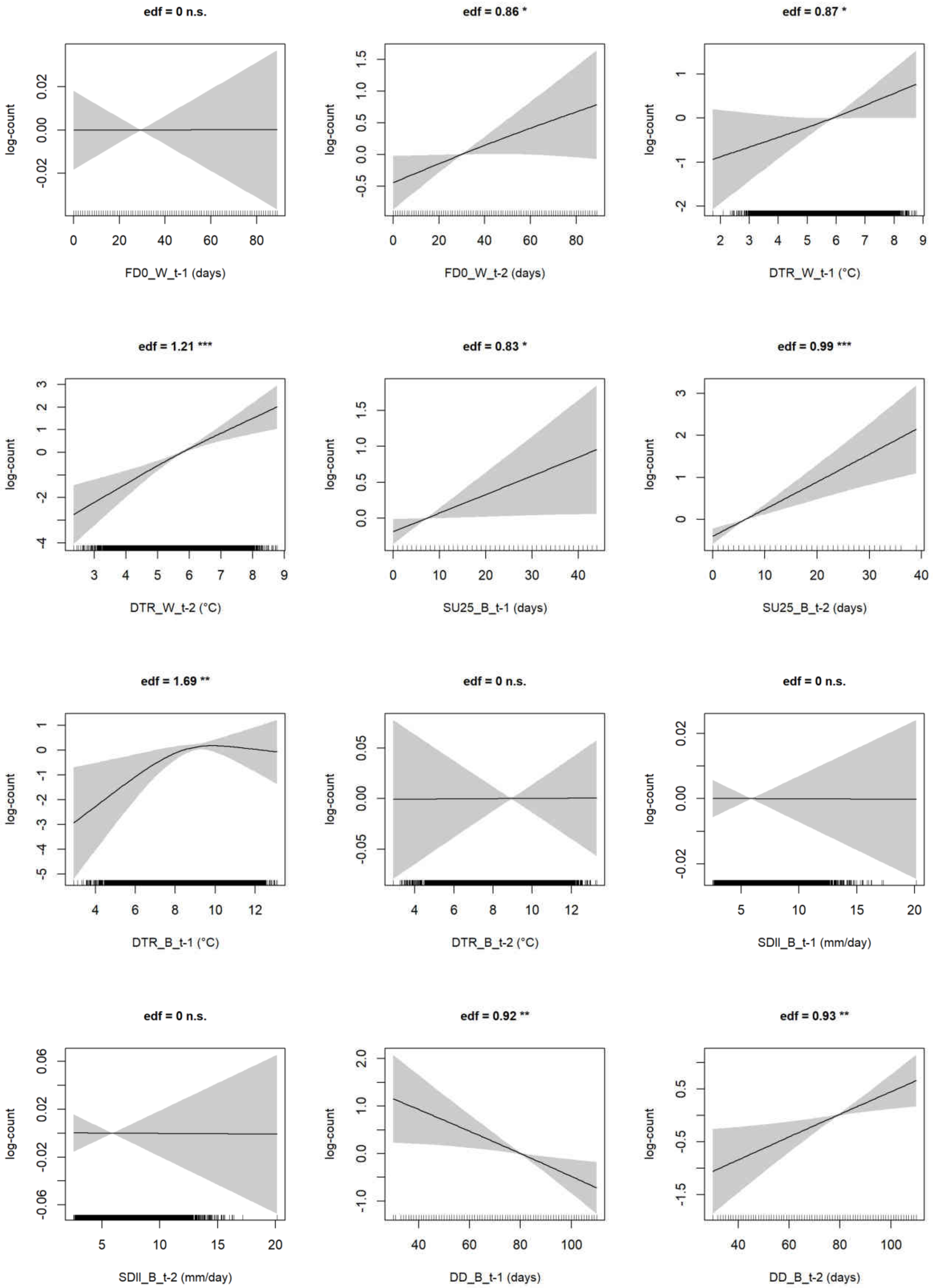
European Stonechat *Saxicola rubicola*



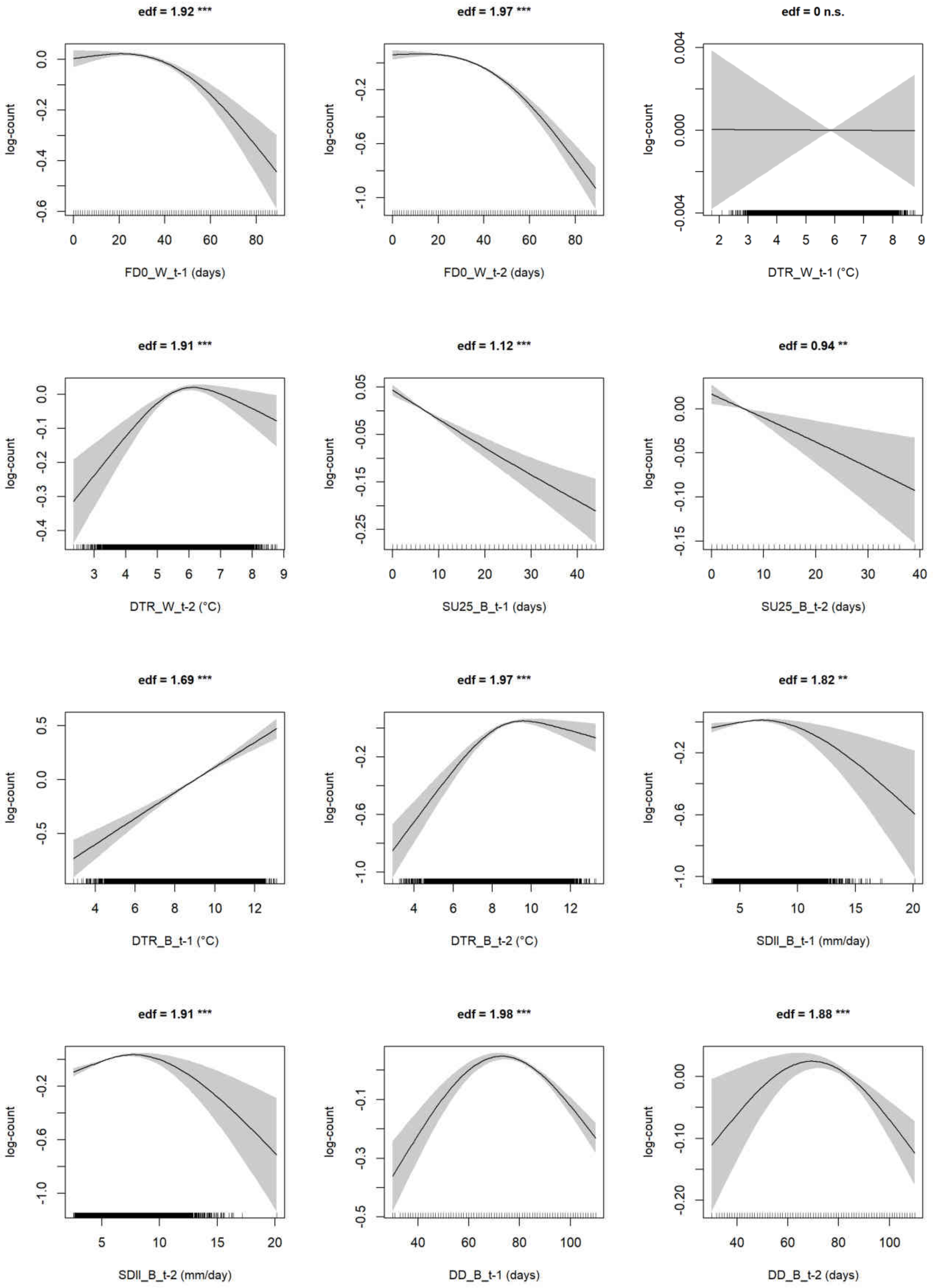
Common Blackbird *Turdus merula*



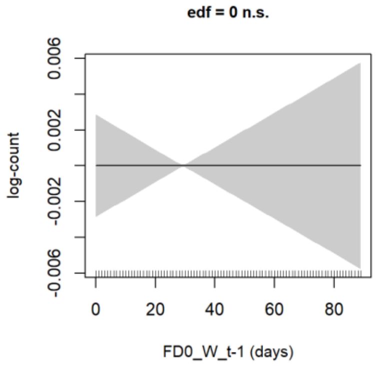
Fieldfare *Turdus pilaris*

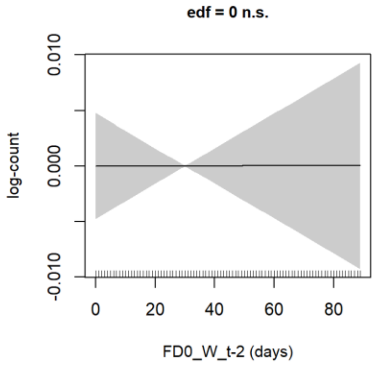


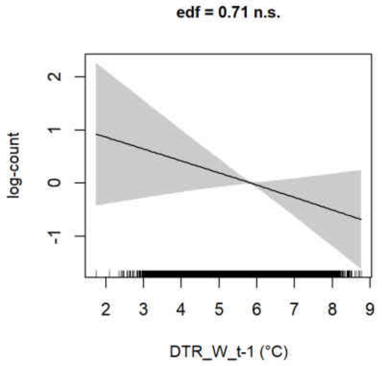
Song Thrush *Turdus philomelos*

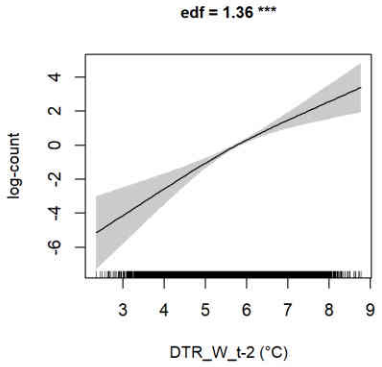


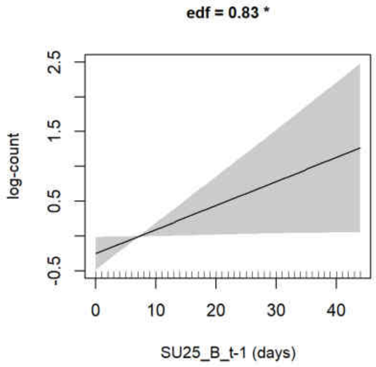
Redwing *Turdus iliacus*

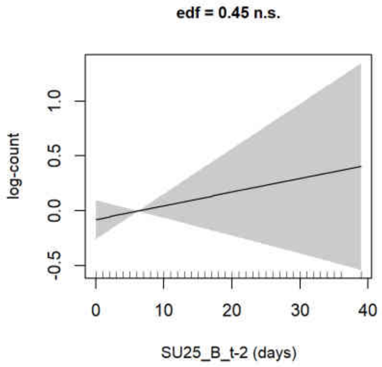


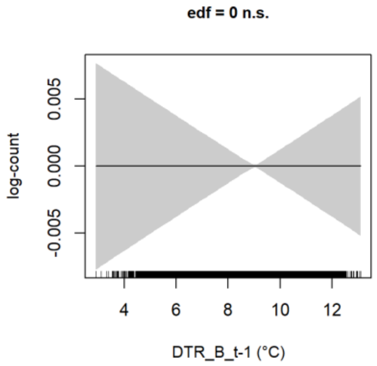


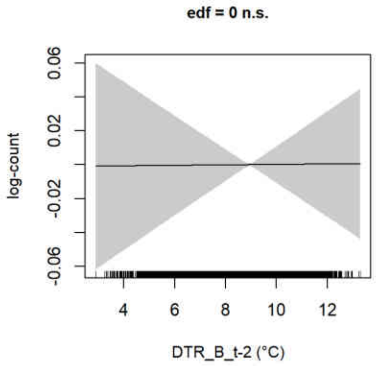


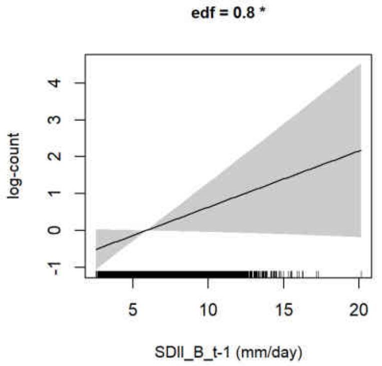


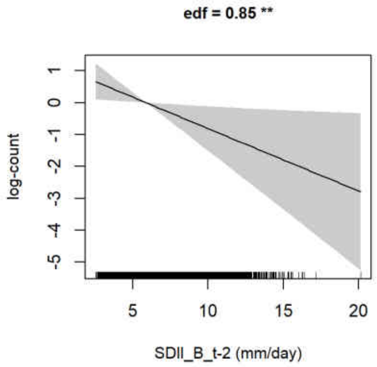


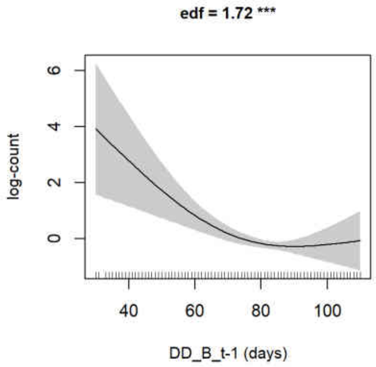


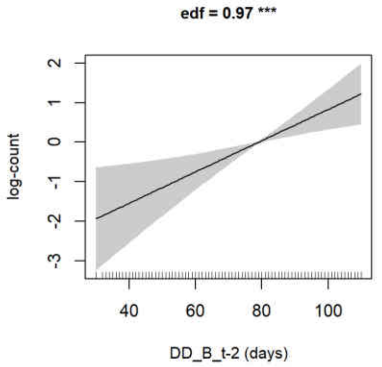




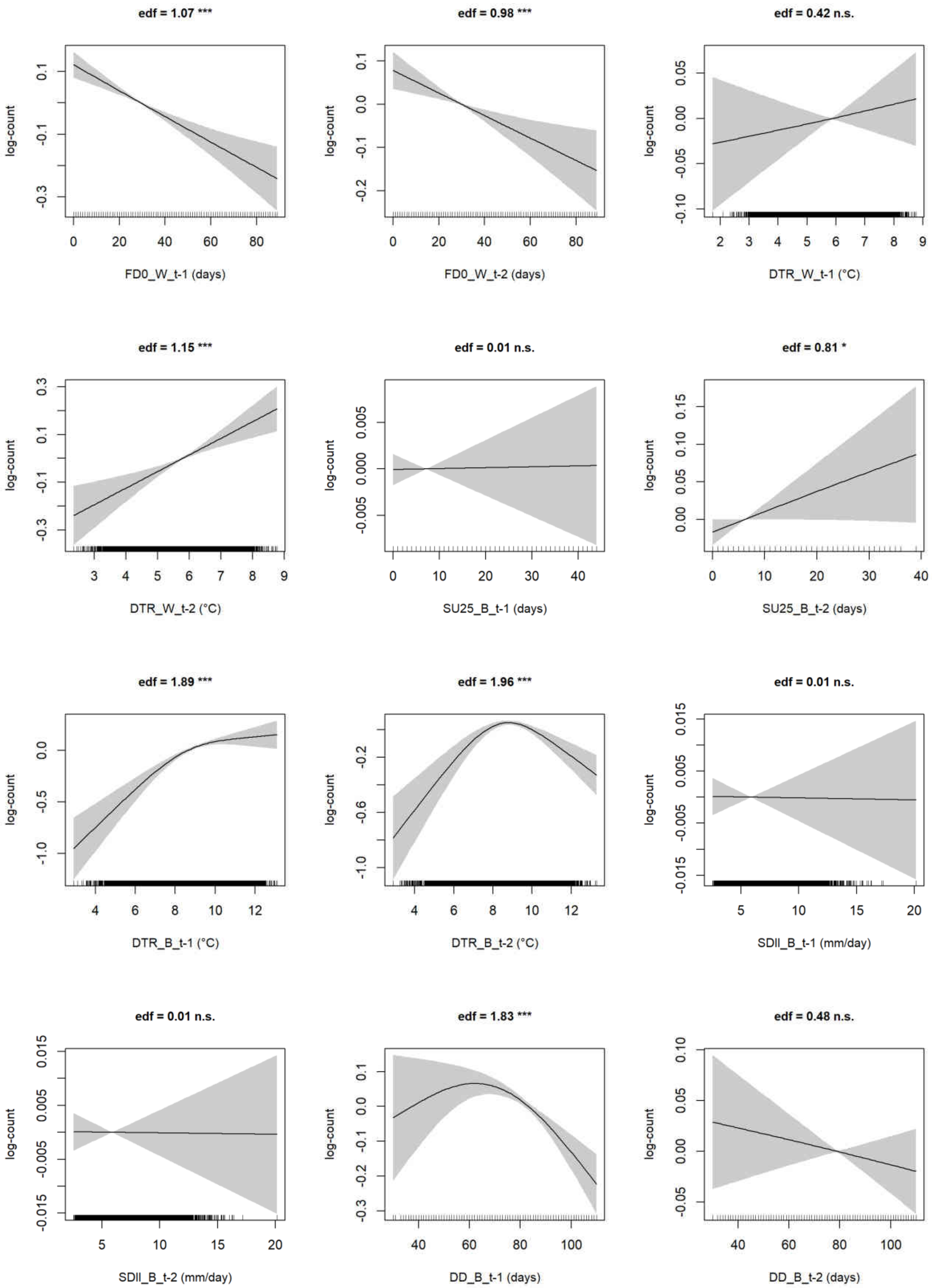




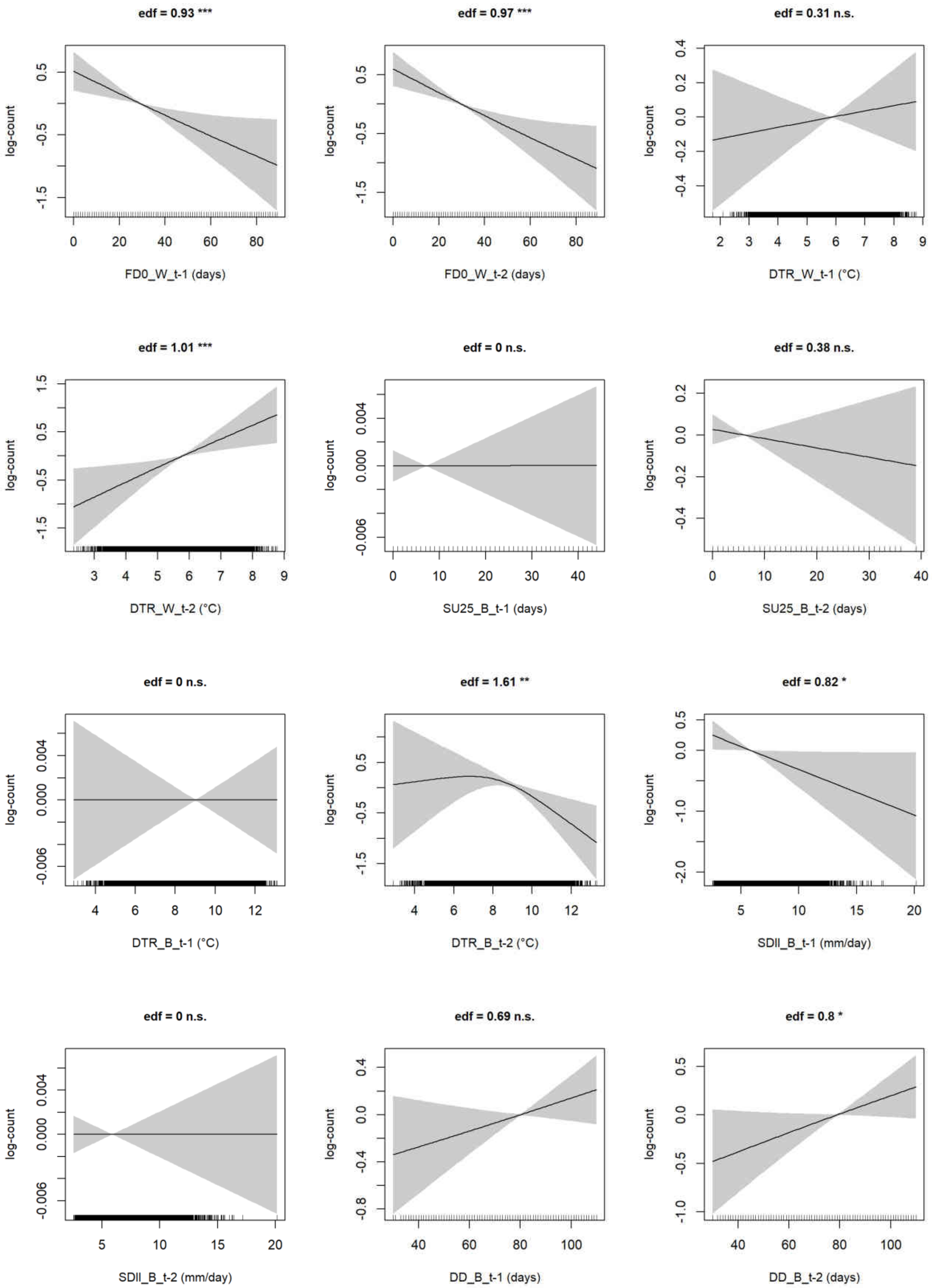




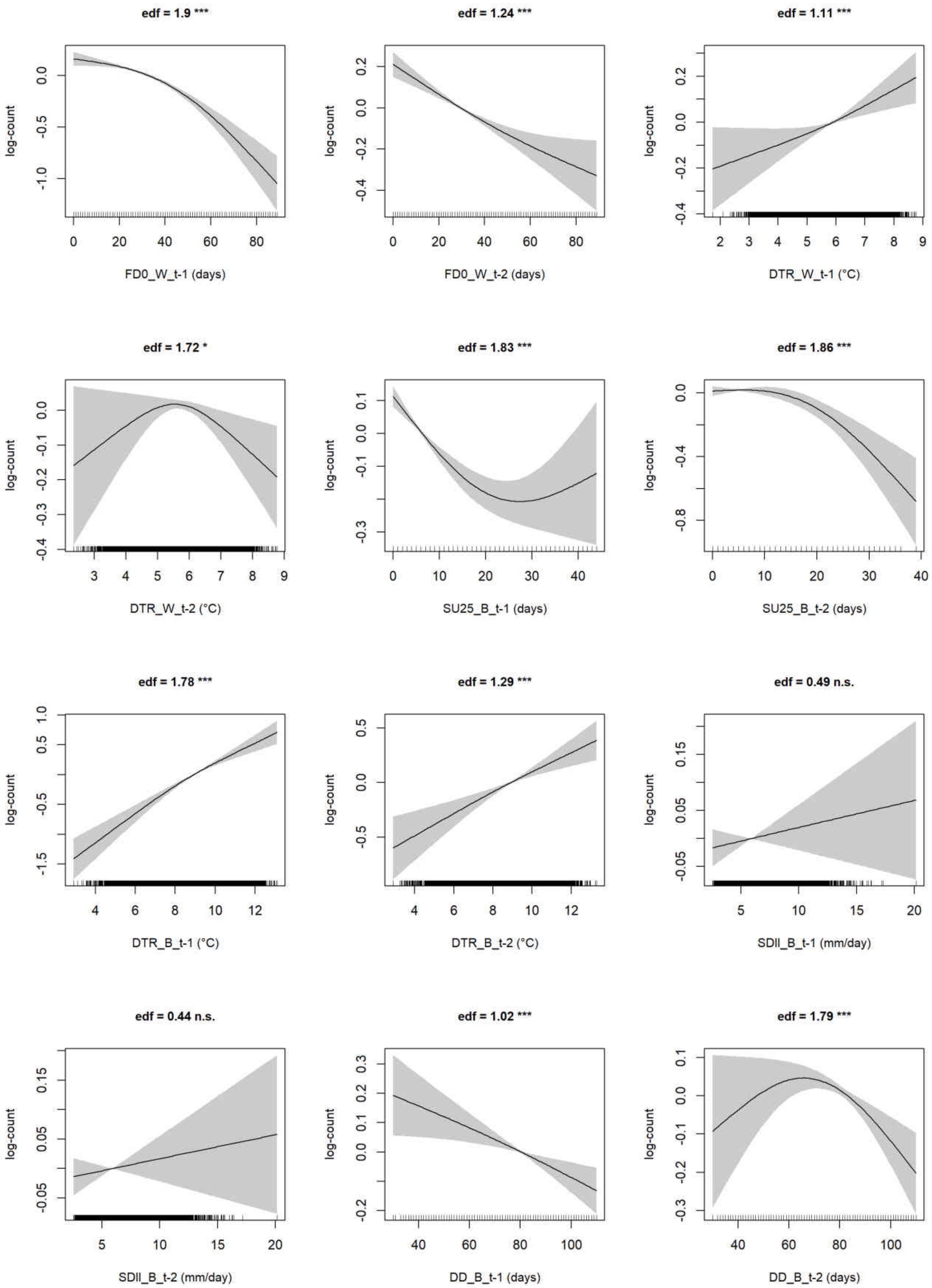
Mistle Thrush *Turdus viscivorus*



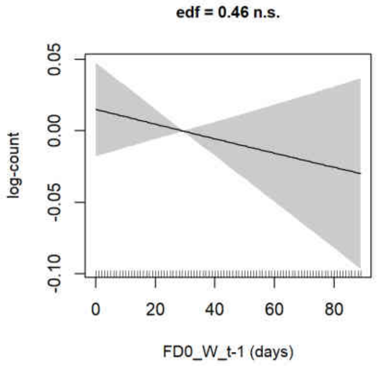
Cetti's Warbler *Cettia cetti*

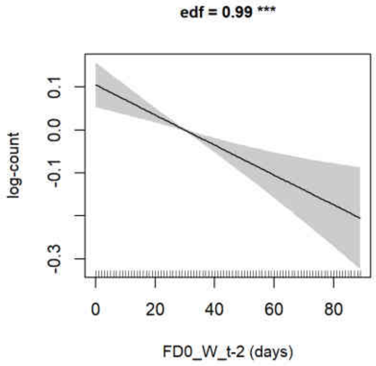


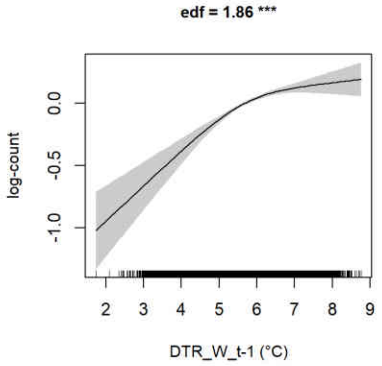
Goldcrest *Regulus regulus*

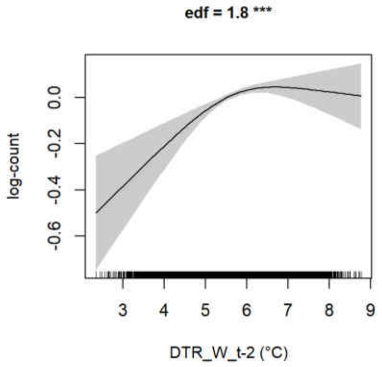


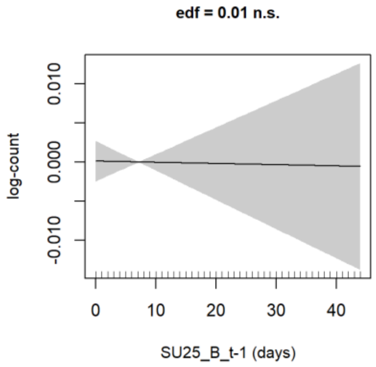
Long-tailed Tit *Aegithalos caudatus*

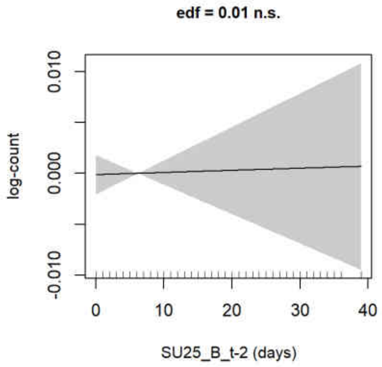

edf = 0.46 n.s.

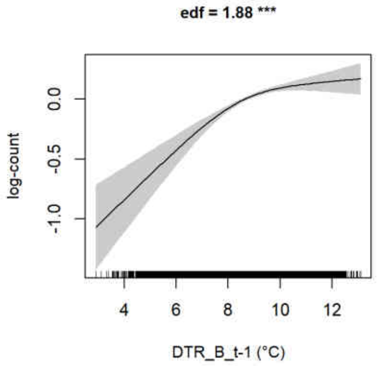

edf = 0.99 ***

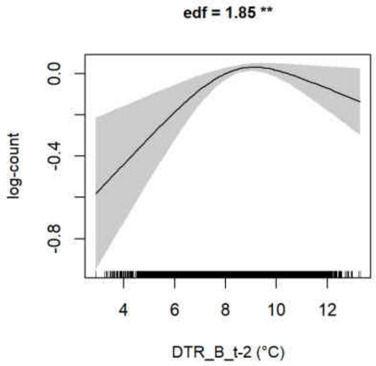

edf = 1.86 ***

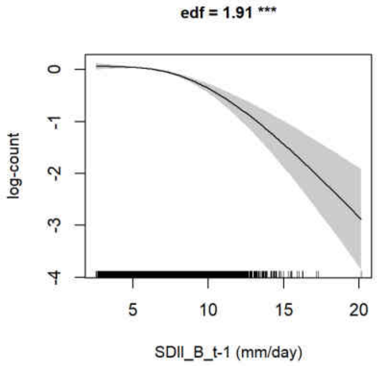

edf = 1.8 ***

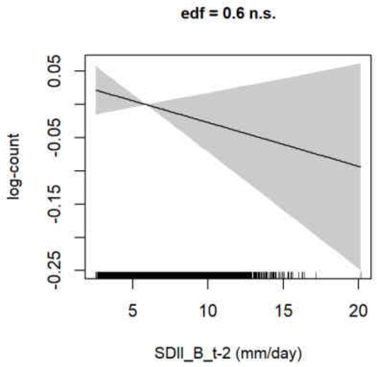

edf = 0.01 n.s.

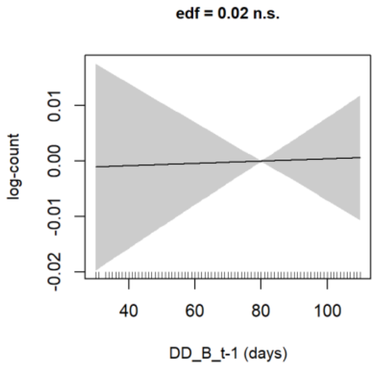

edf = 0.01 n.s.

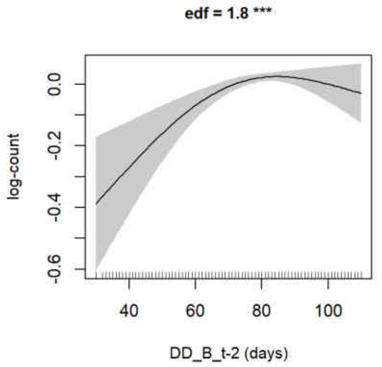

edf = 1.88 ***


edf = 1.85 **

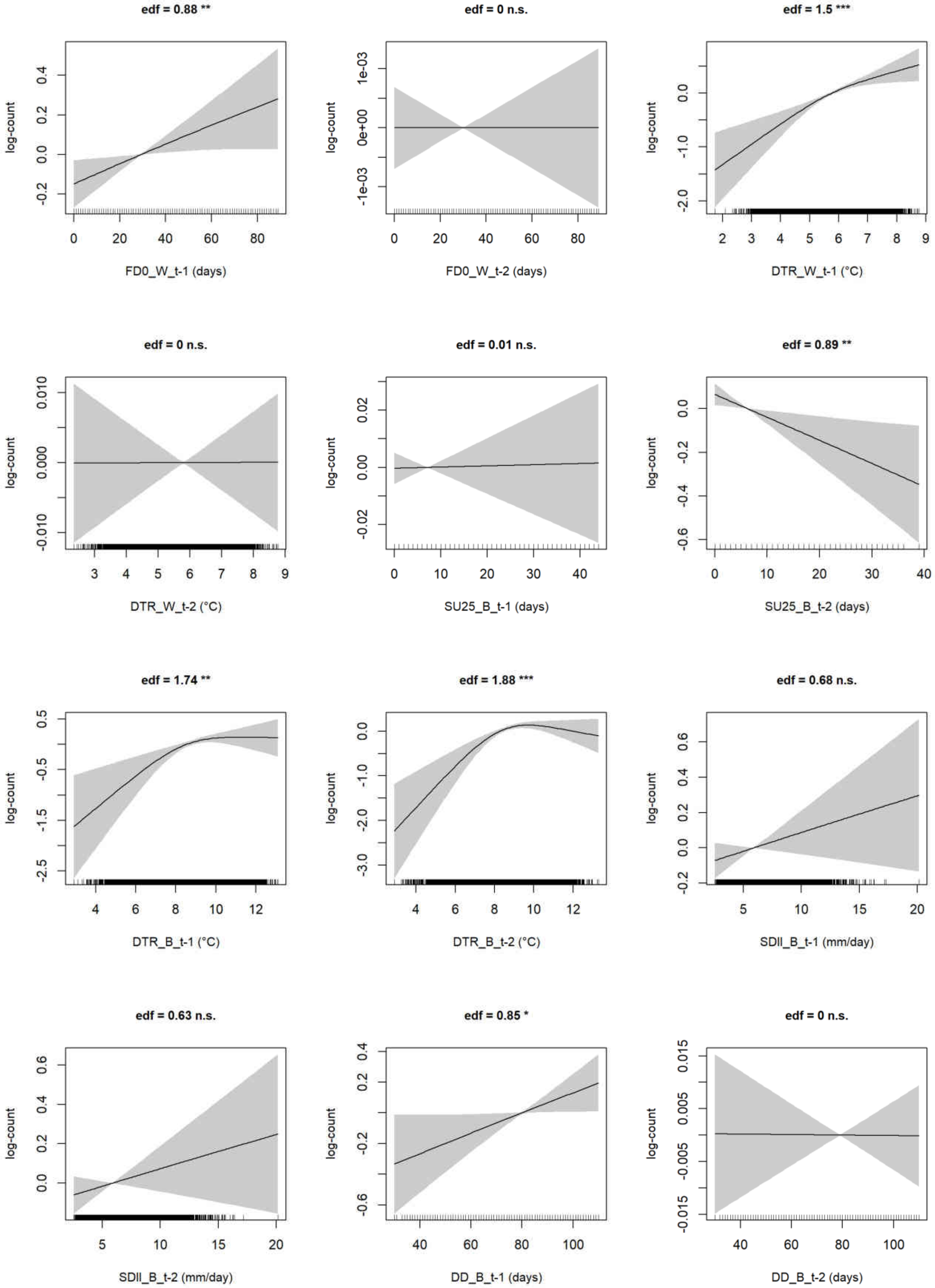

edf = 1.91 ***


edf = 0.6 n.s.

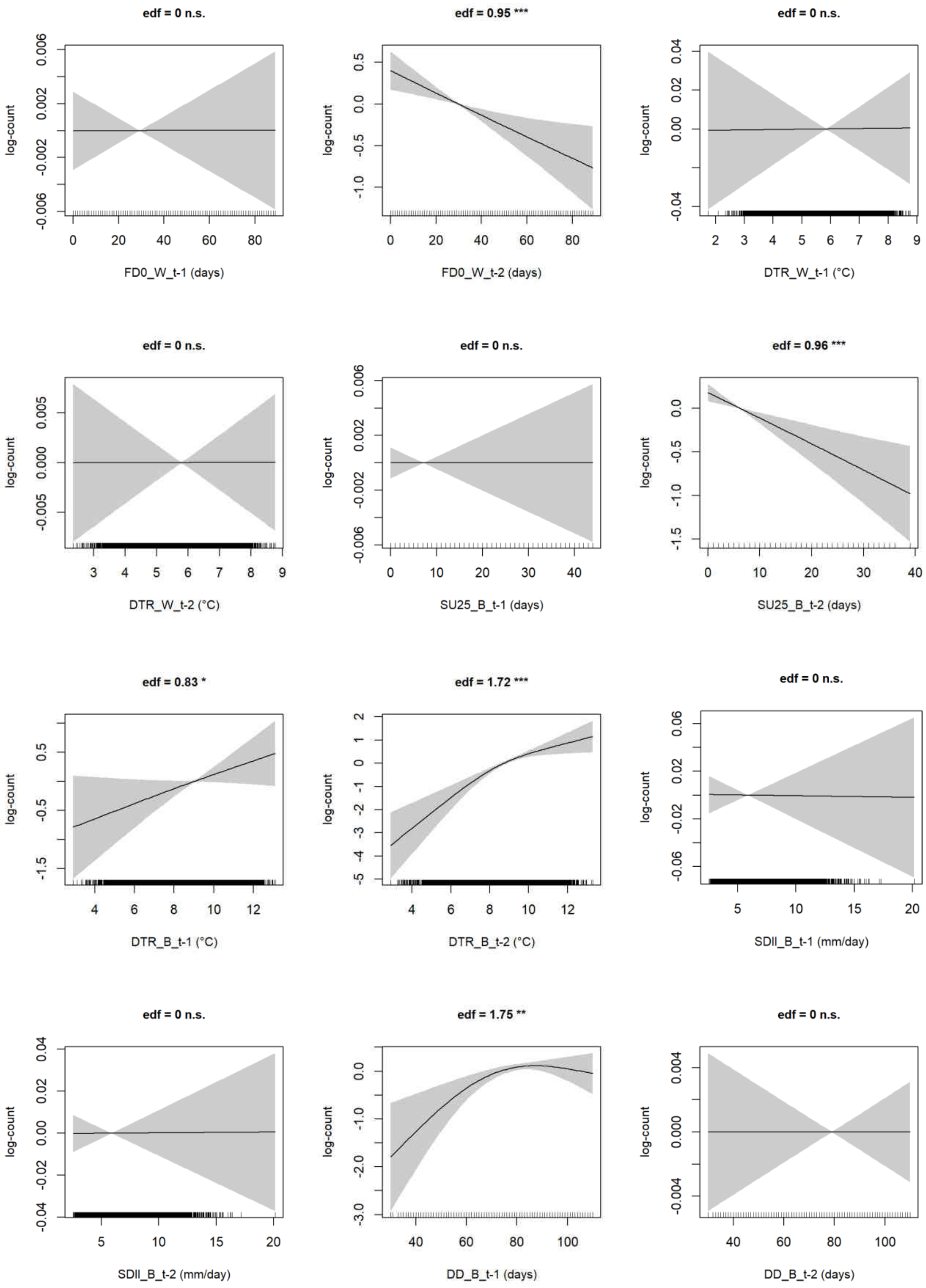

edf = 0.02 n.s.


edf = 1.8 ***

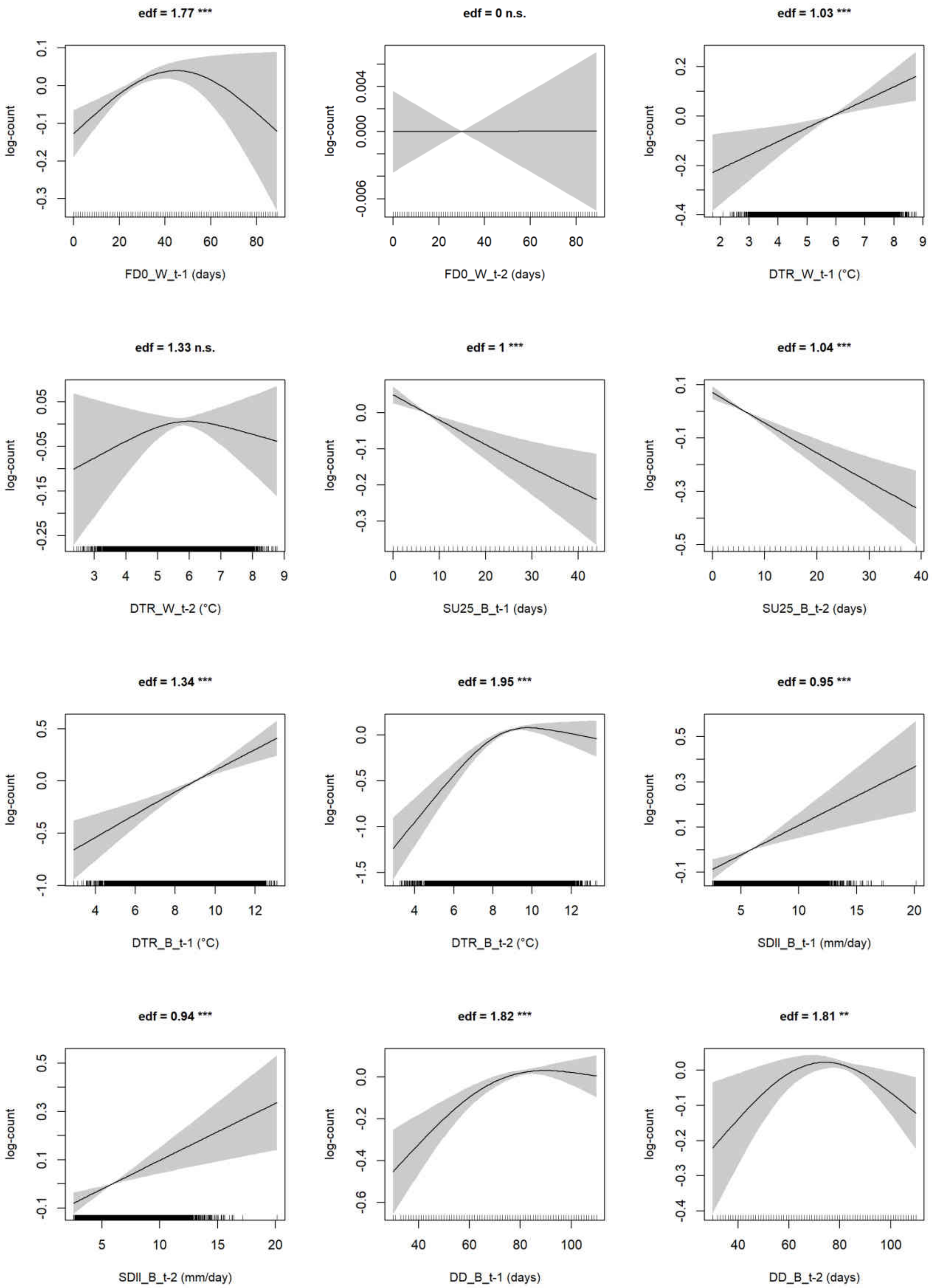
Marsh Tit *Poecile palustris*



Willow Tit *Poecile montanus*



Coal Tit *Periparus ater*



edf = 1.77 ***

edf = 0 n.s.

edf = 1.03 ***

edf = 1.33 n.s.

edf = 1 ***

edf = 1.04 ***

edf = 1.34 ***

edf = 1.95 ***

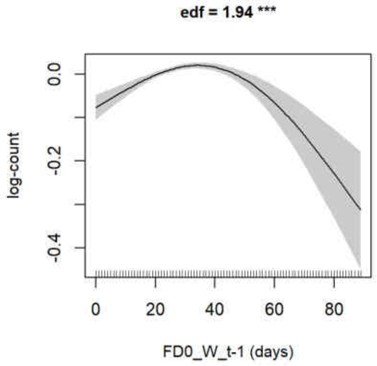
edf = 0.95 ***

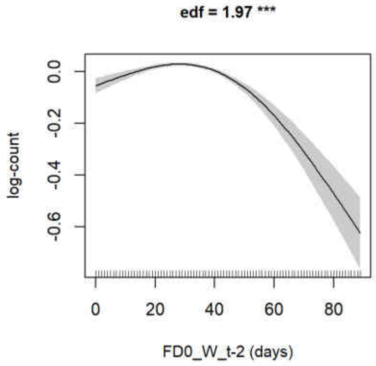
edf = 0.94 ***

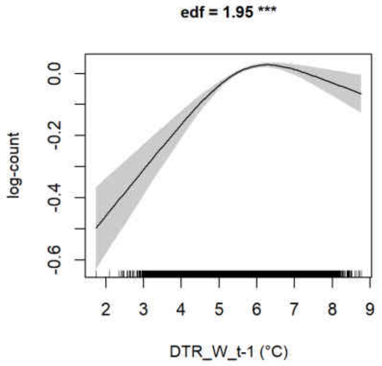
edf = 1.82 ***

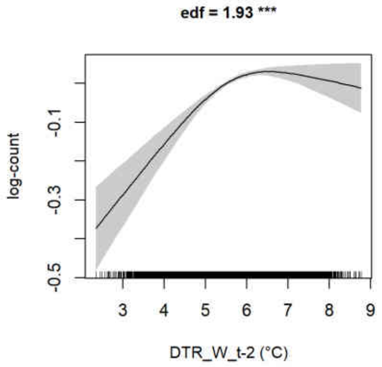
edf = 1.81 **

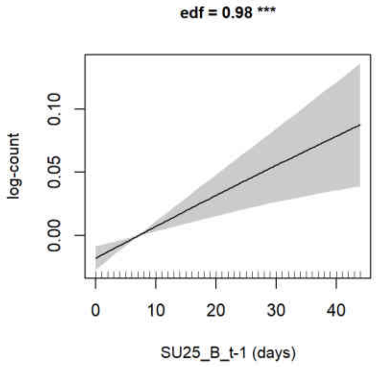
Eurasian Blue Tit *Cyanistes caeruleus*

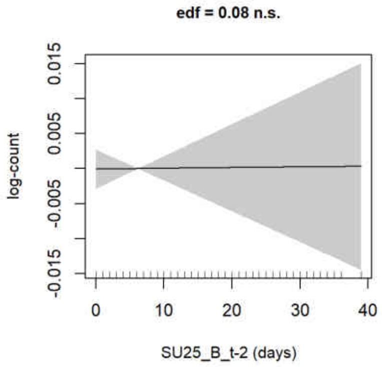


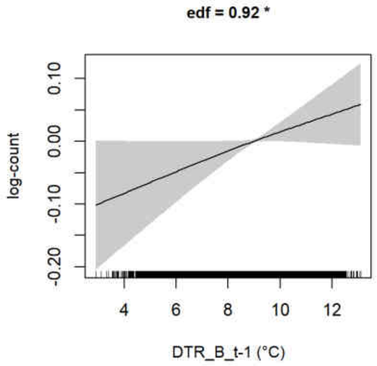


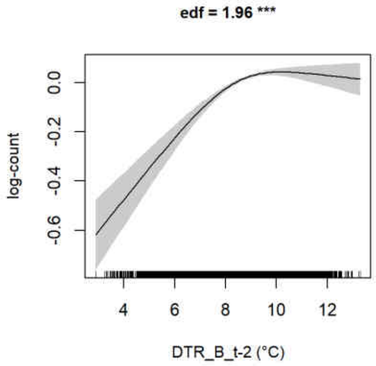


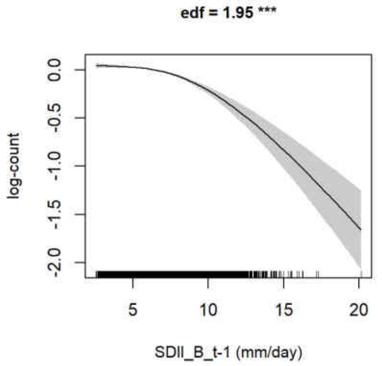


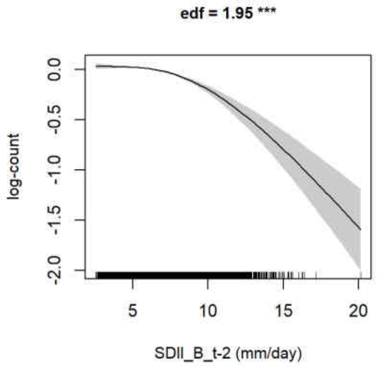


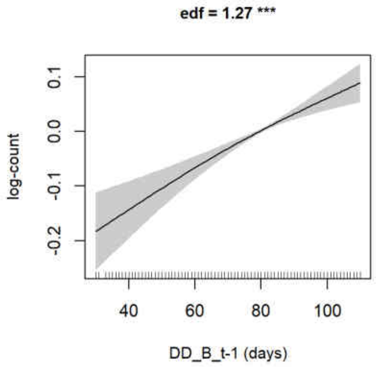


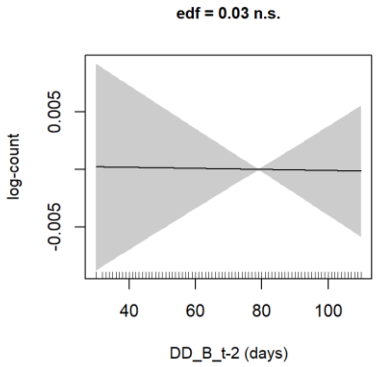




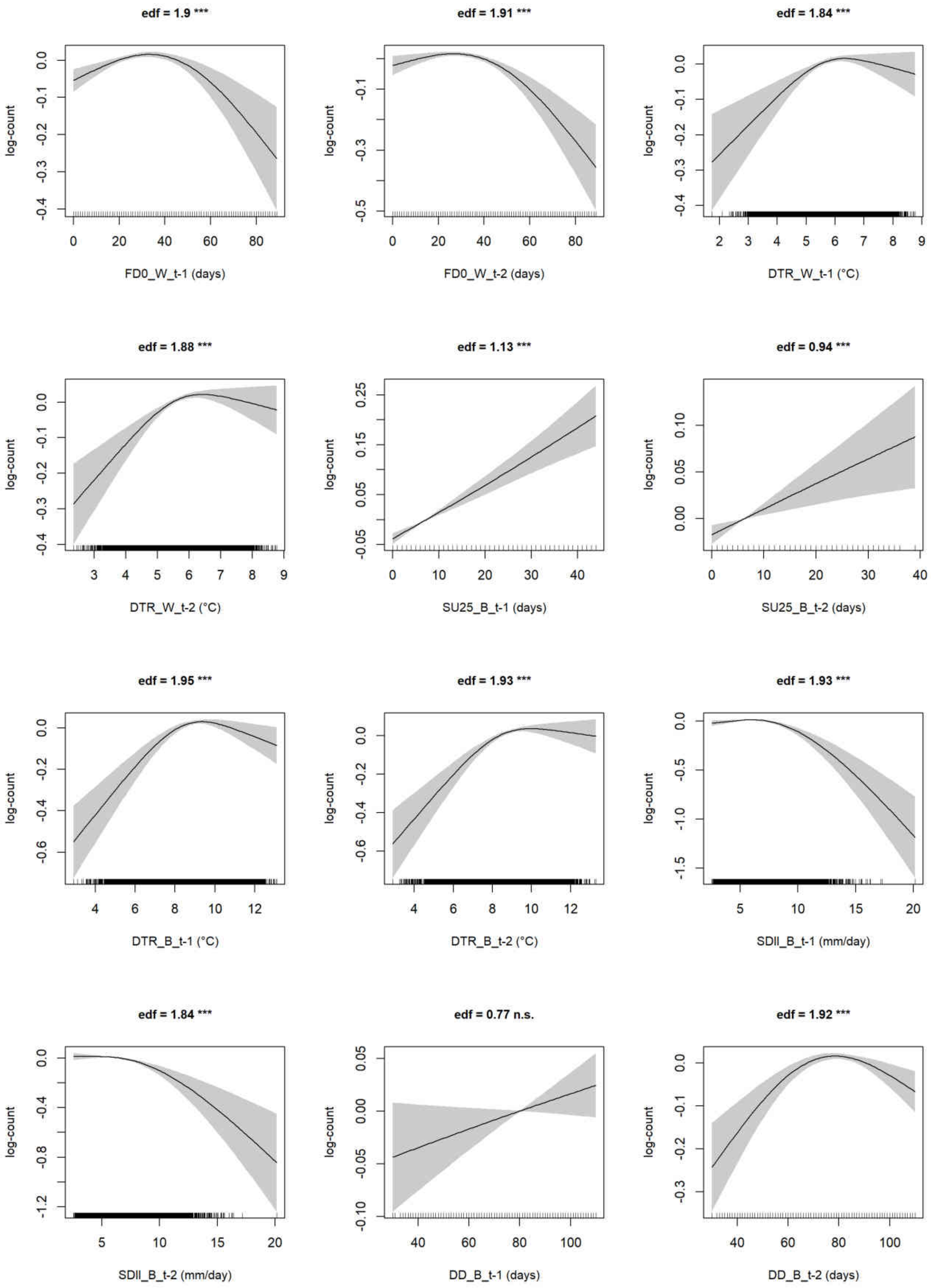




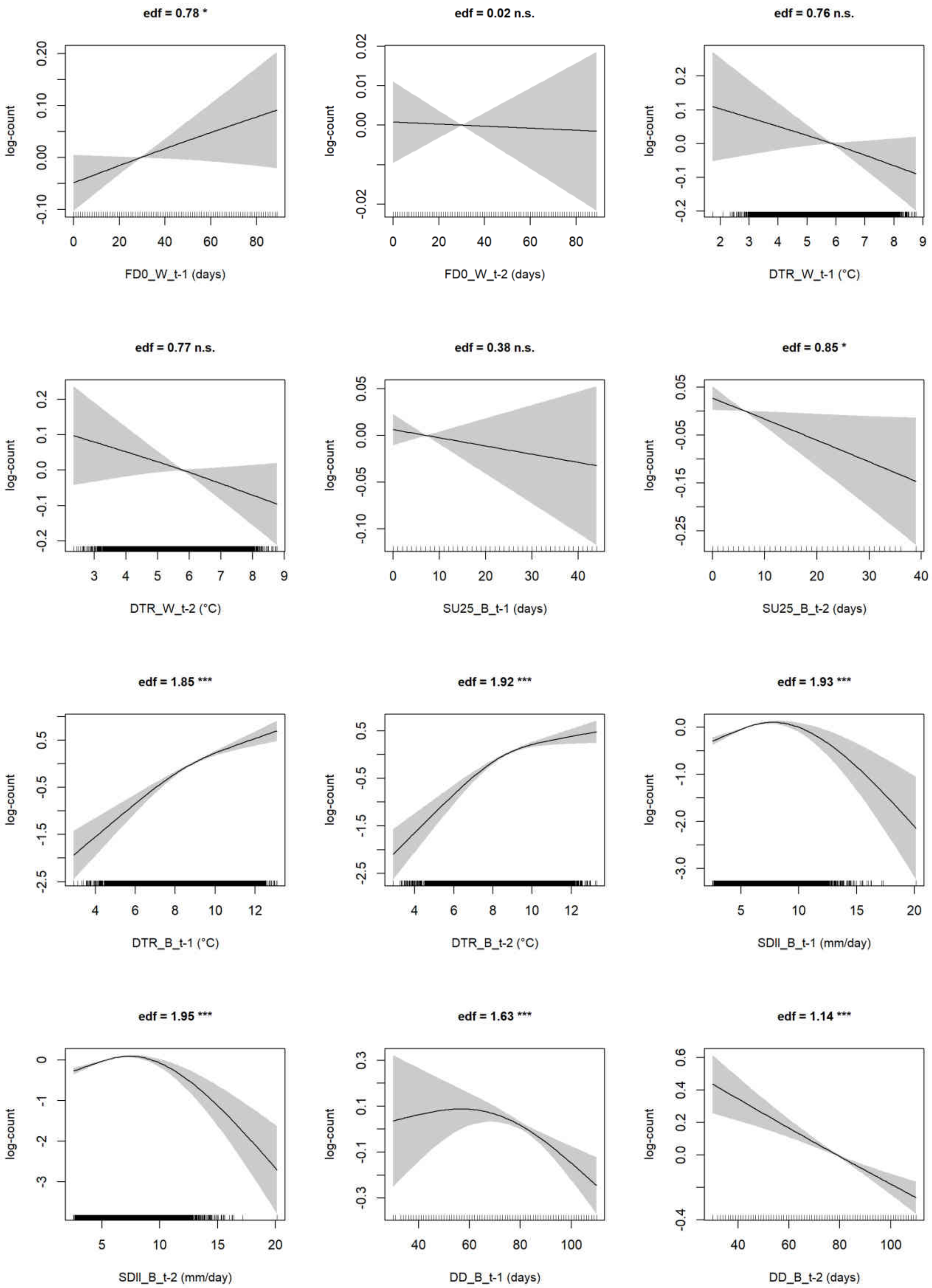




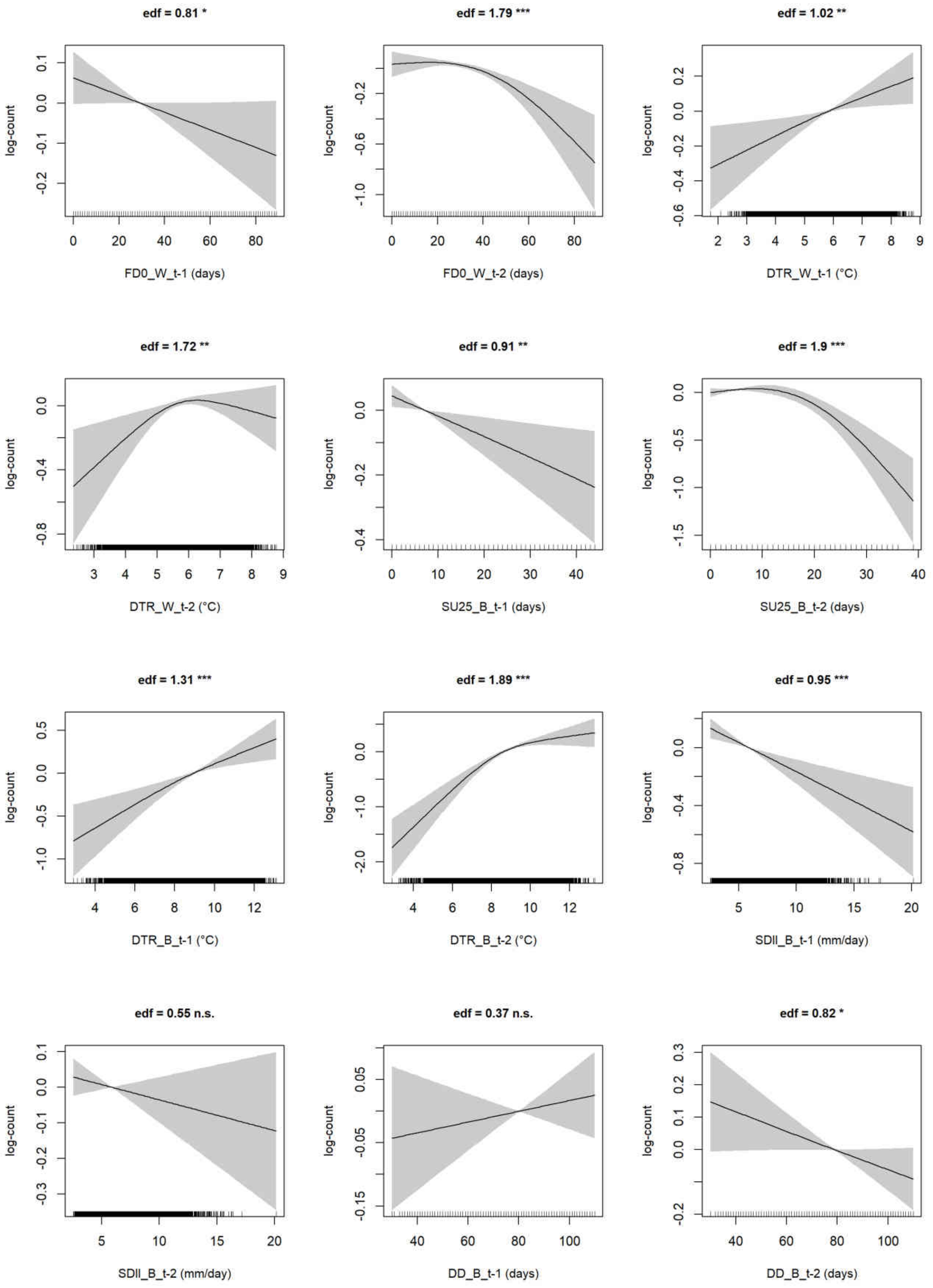
Great Tit *Parus major*



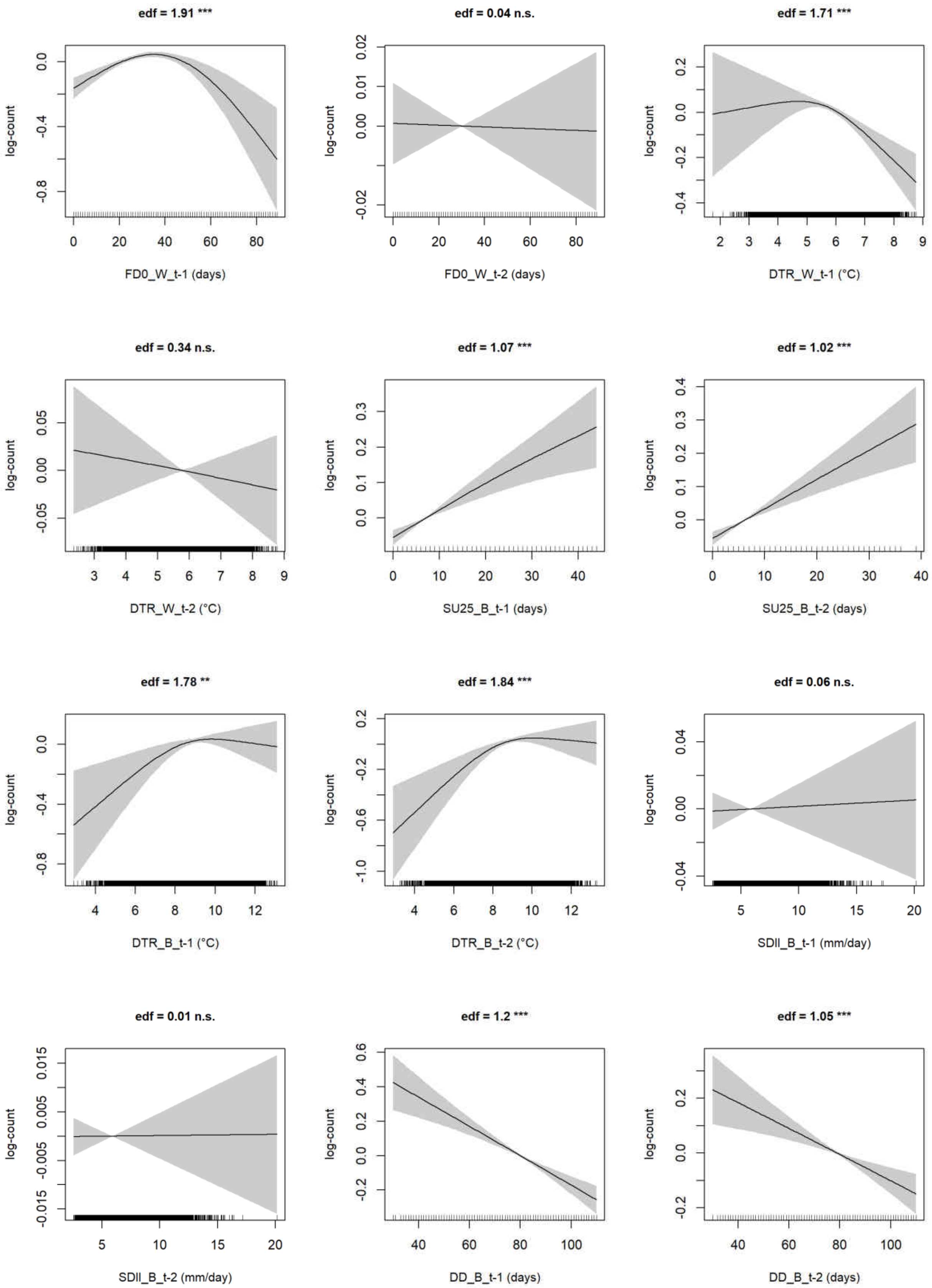
Eurasian Nuthatch *Sitta europaea*



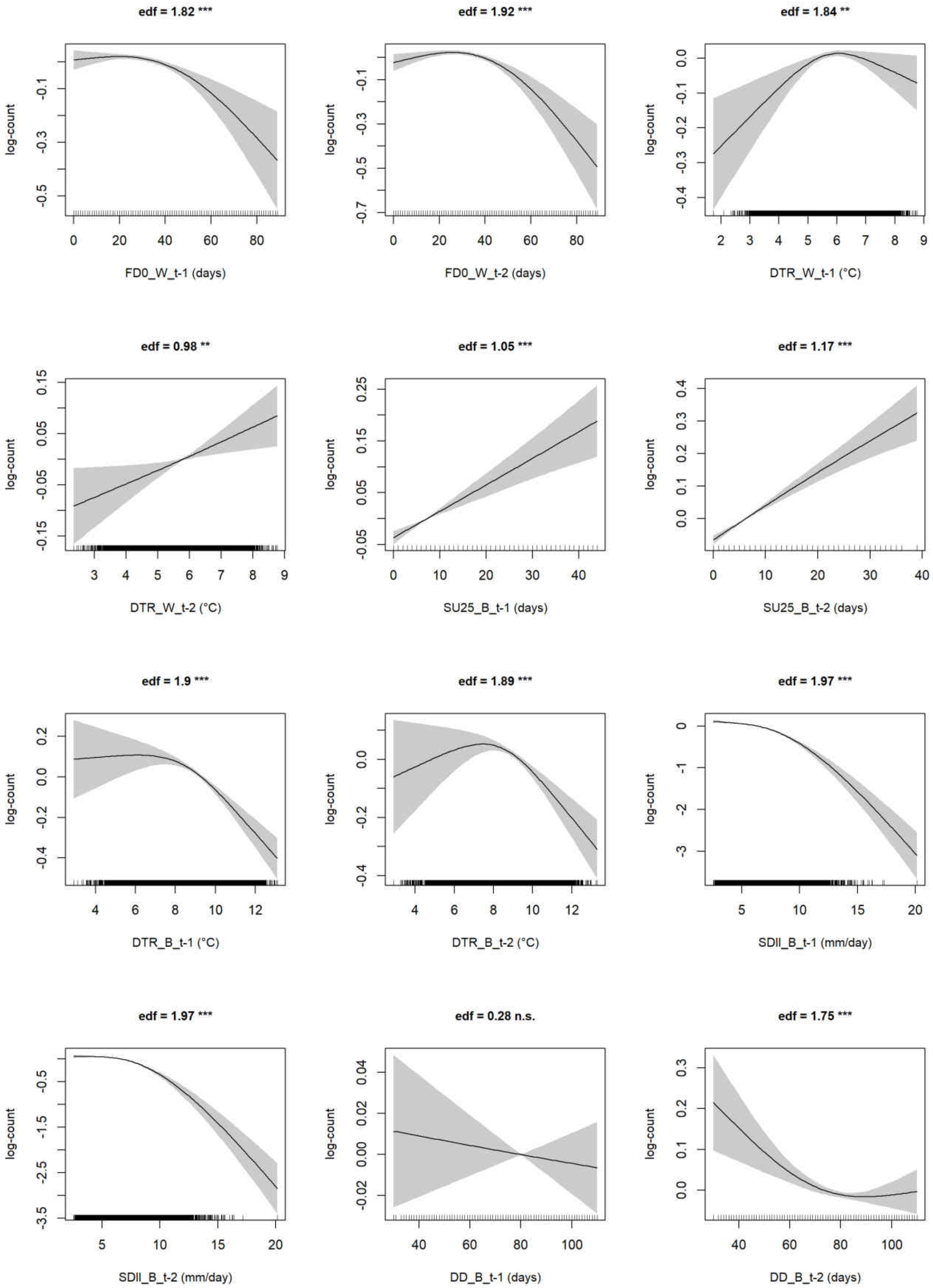
Eurasian Treecreeper *Certhia familiaris*



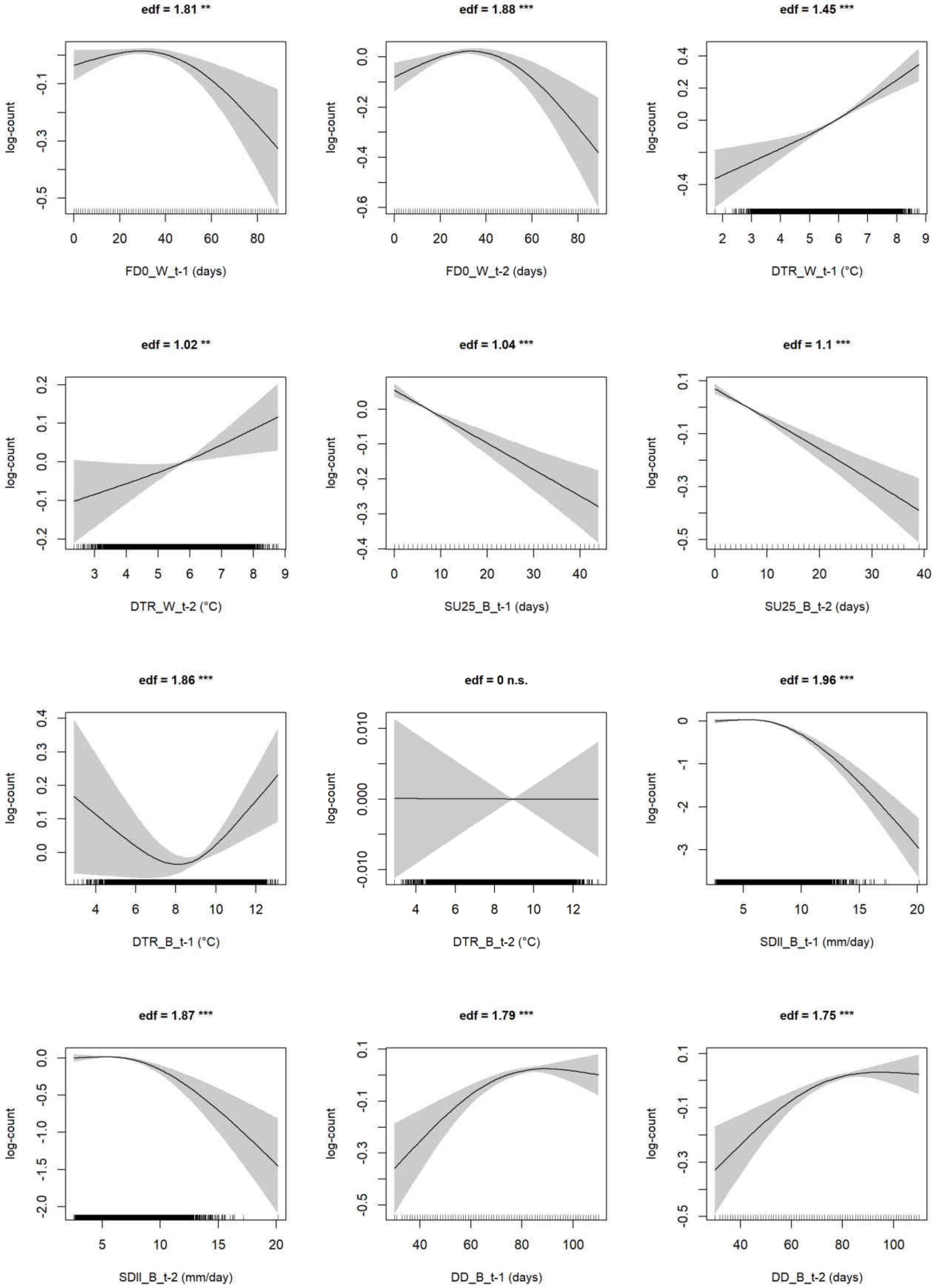
Eurasian Jay *Garrulus glandarius*



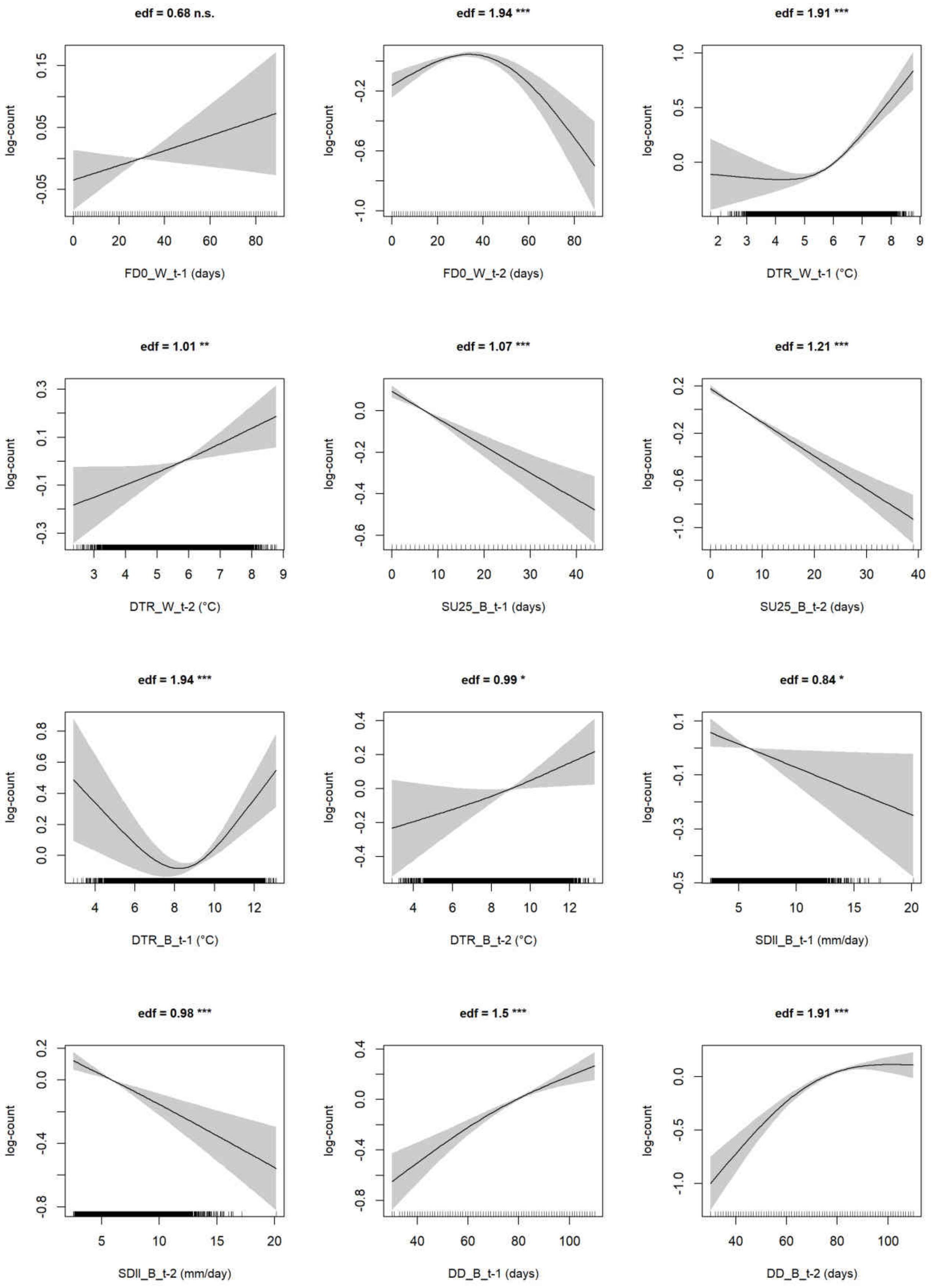
Eurasian Magpie *Pica pica*



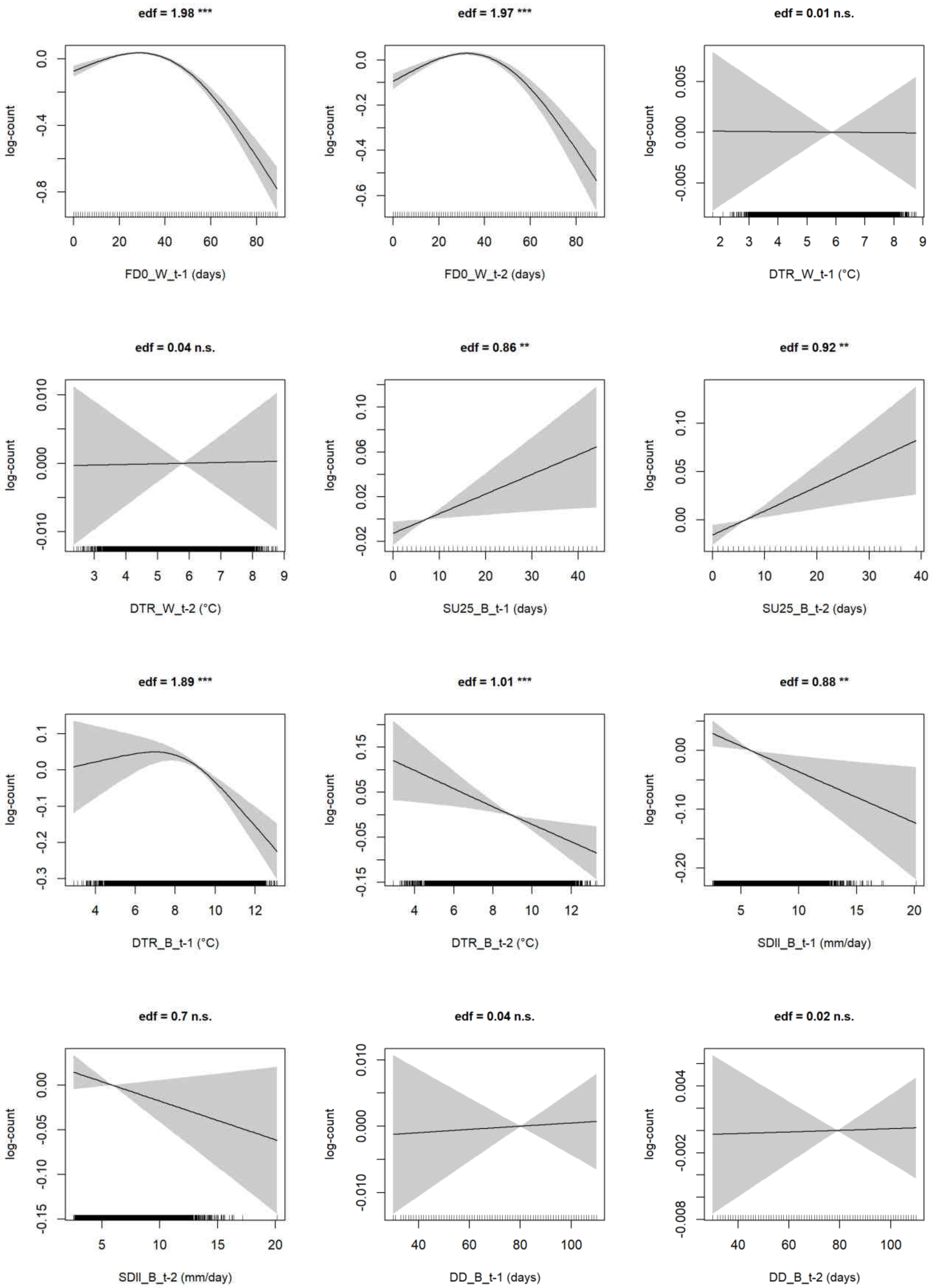
Western Jackdaw *Coloeus monedula*



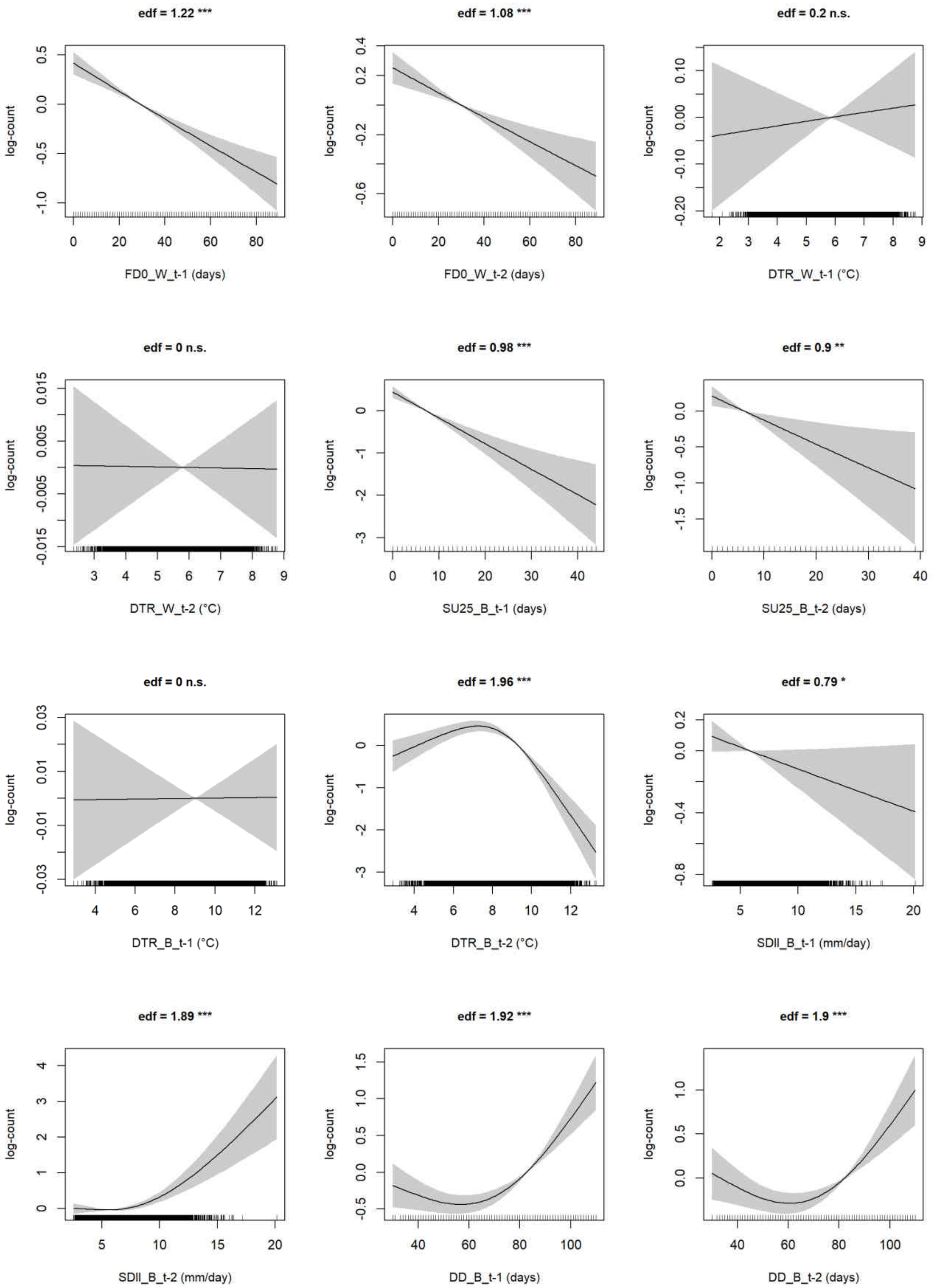
Rook *Corvus frugilegus*



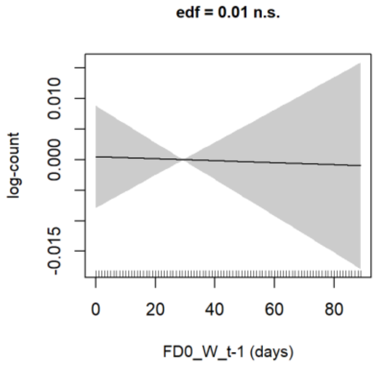
Carrion Crow *Corvus corone*

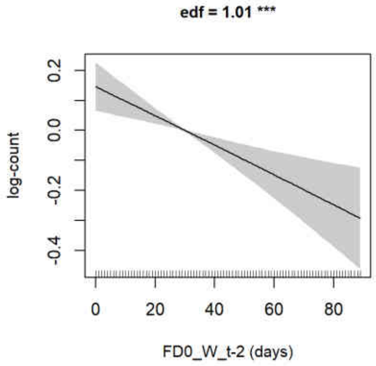


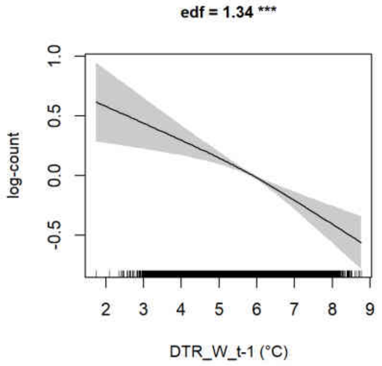
Hooded Crow *Corvus cornix*

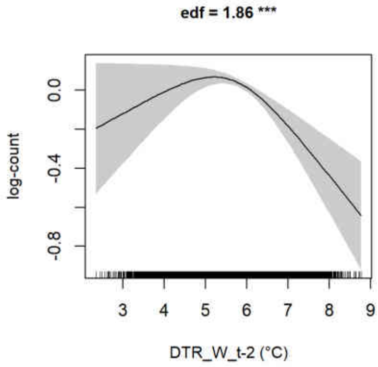


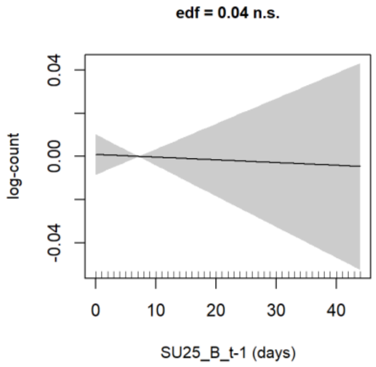
Northern Raven *Corvus corax*

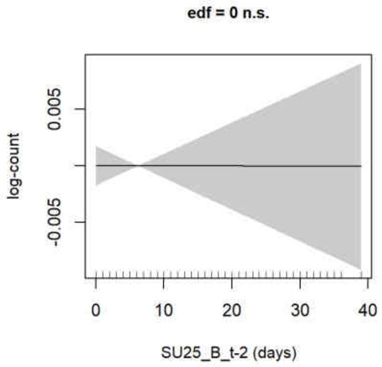


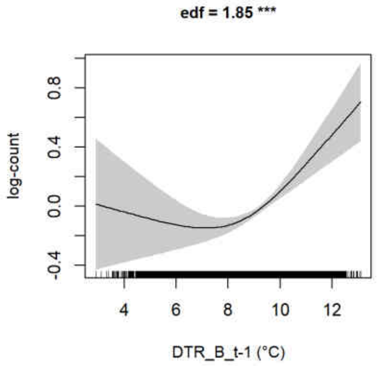


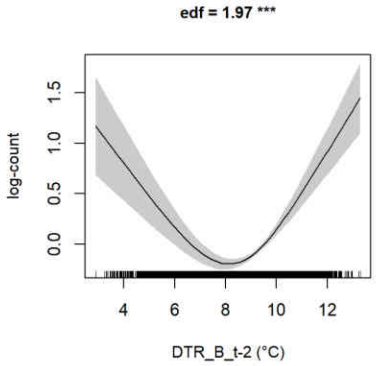


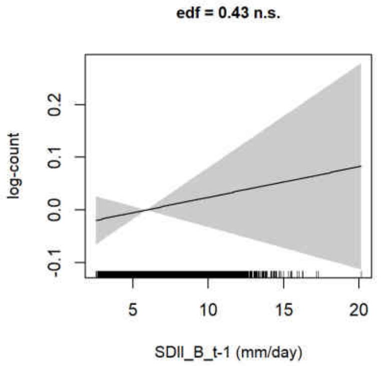


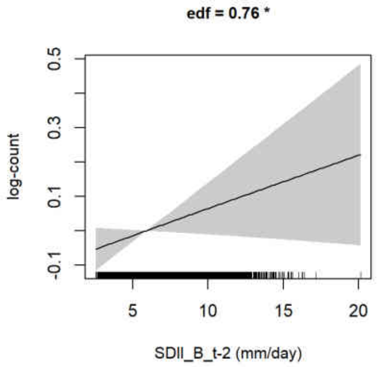


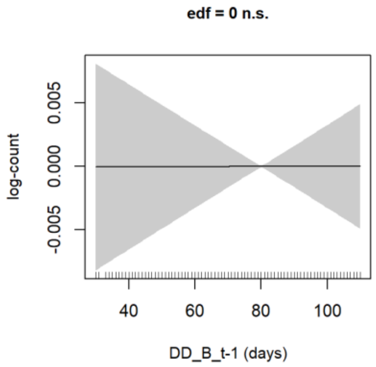


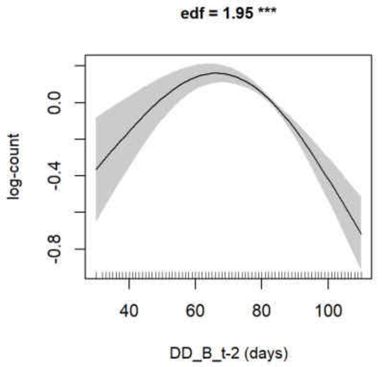




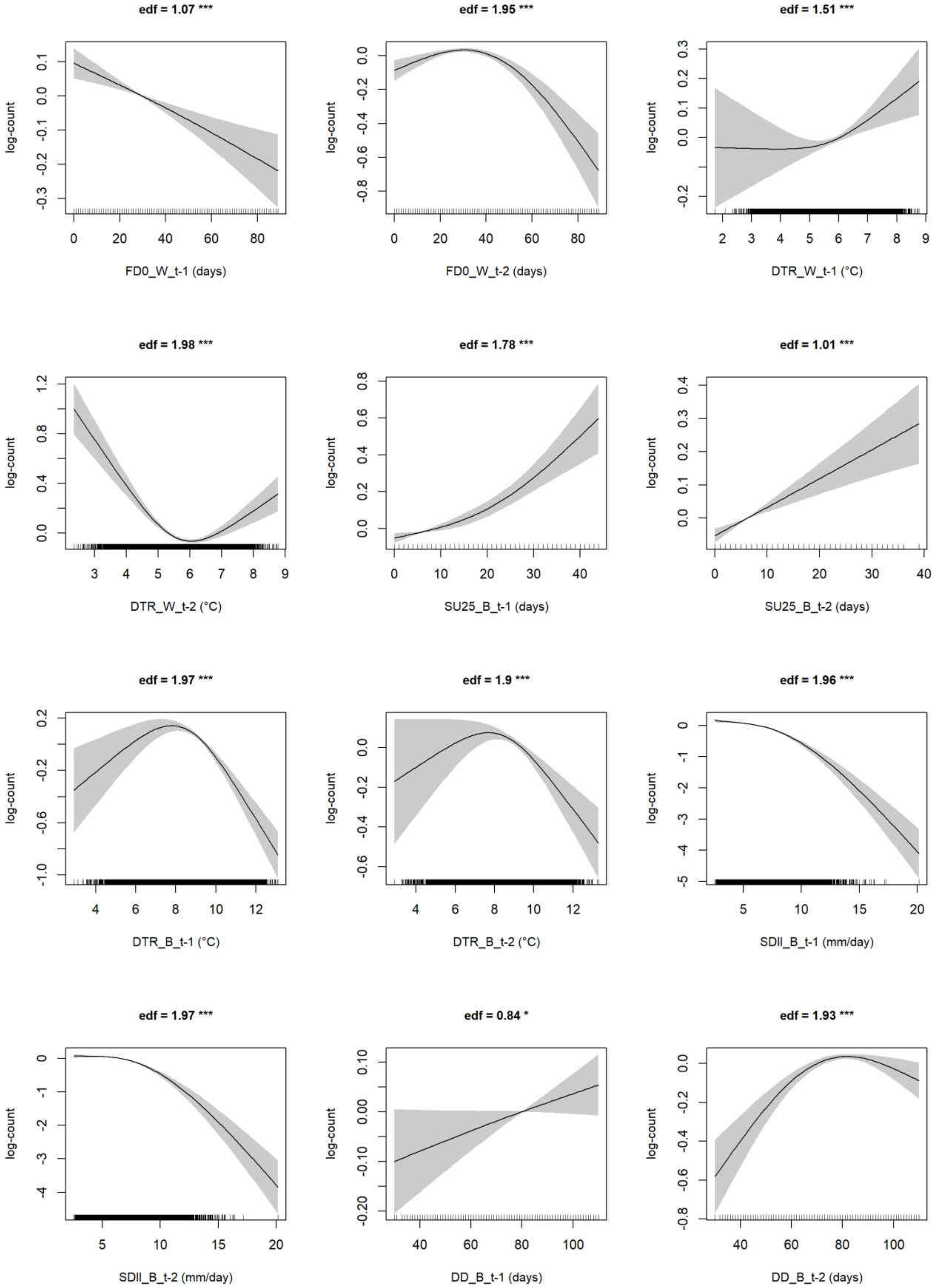




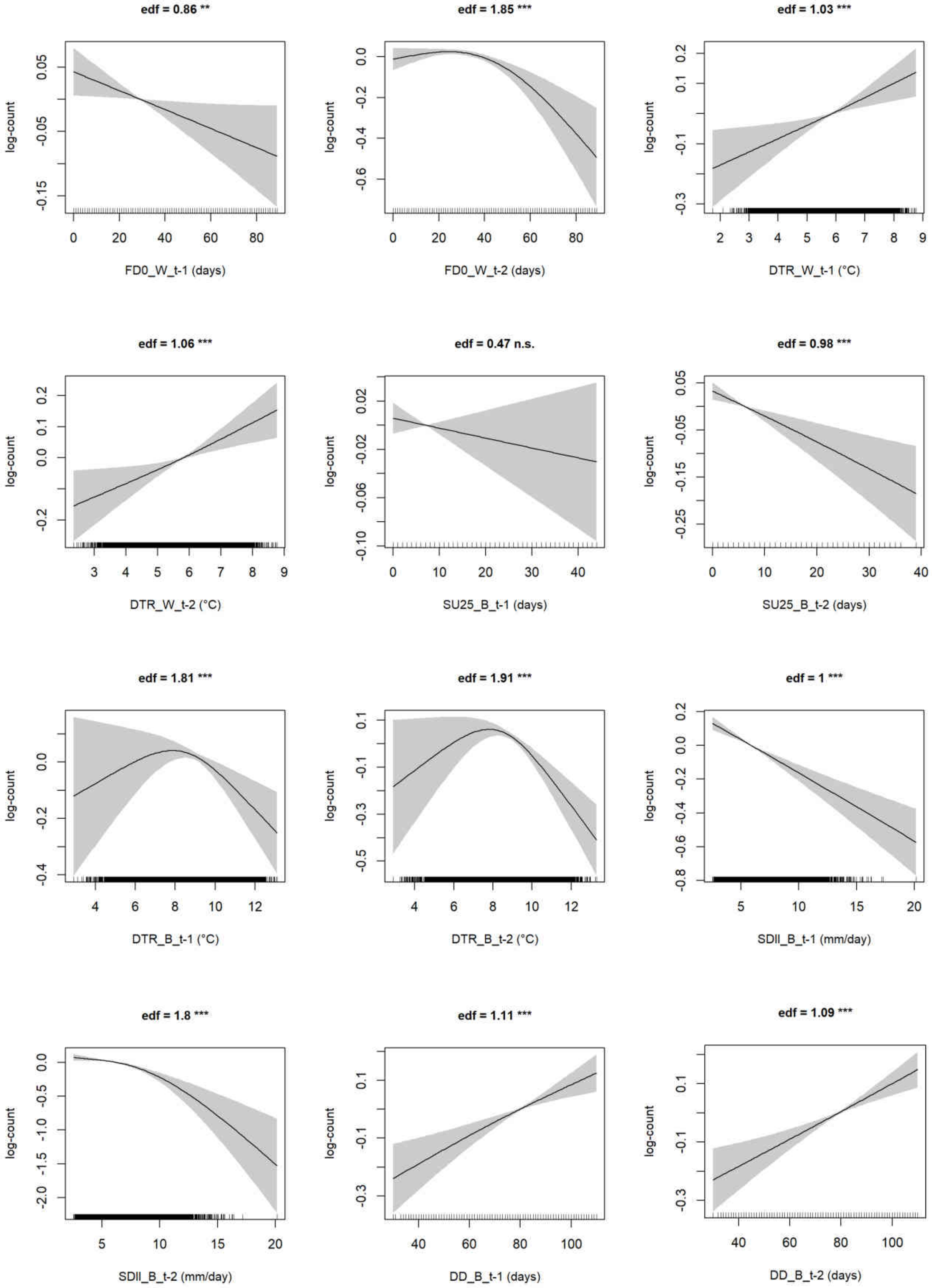




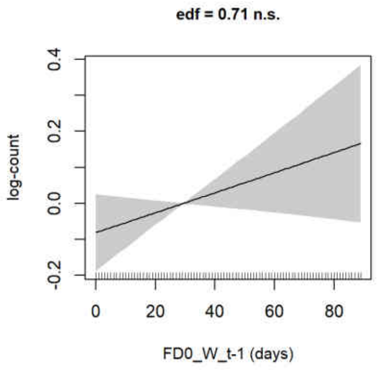
Common Starling *Sturnus vulgaris*

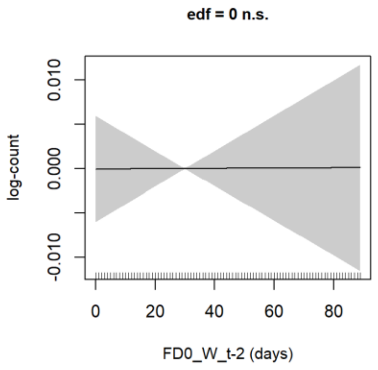


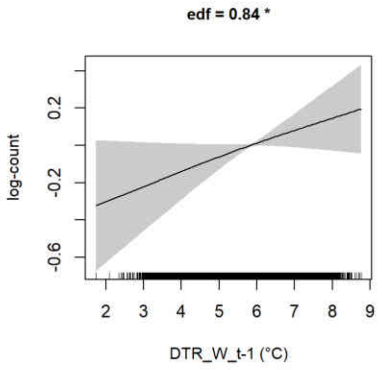
House Sparrow *Passer domesticus*

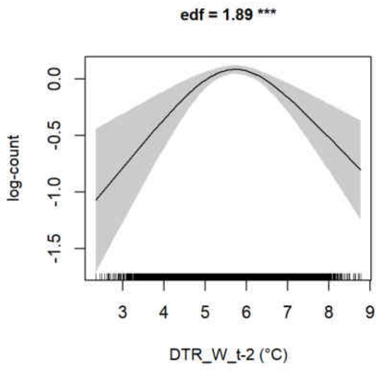


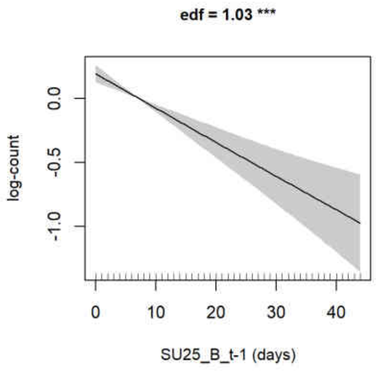
Eurasian Tree Sparrow *Passer montanus*

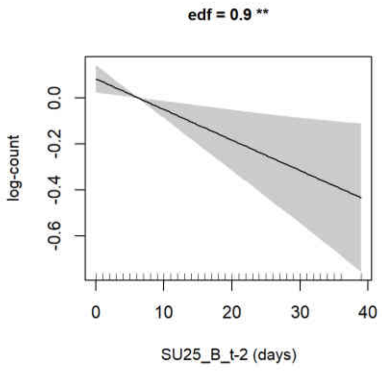


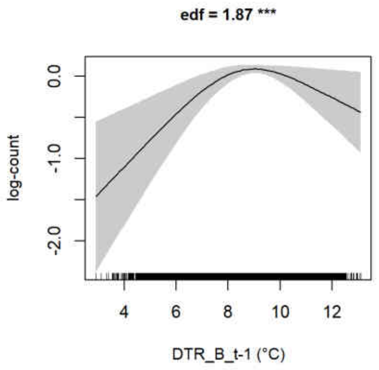


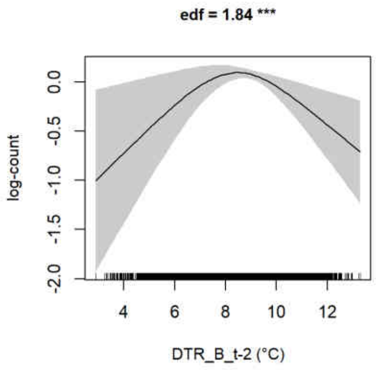


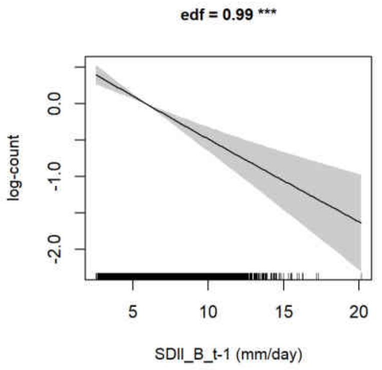


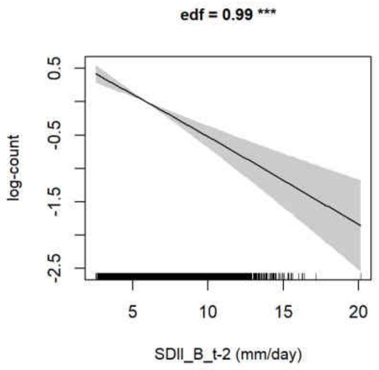


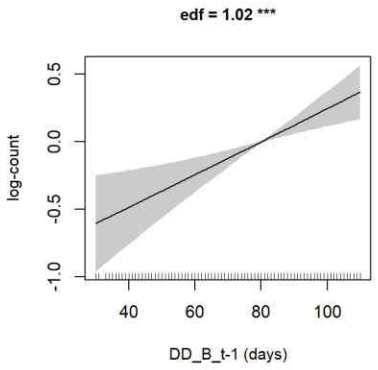


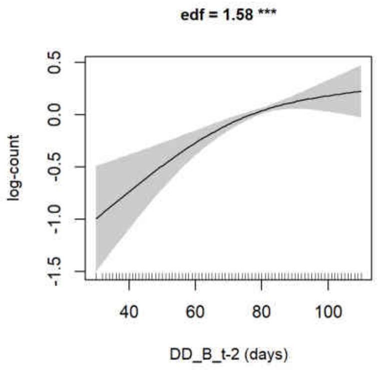




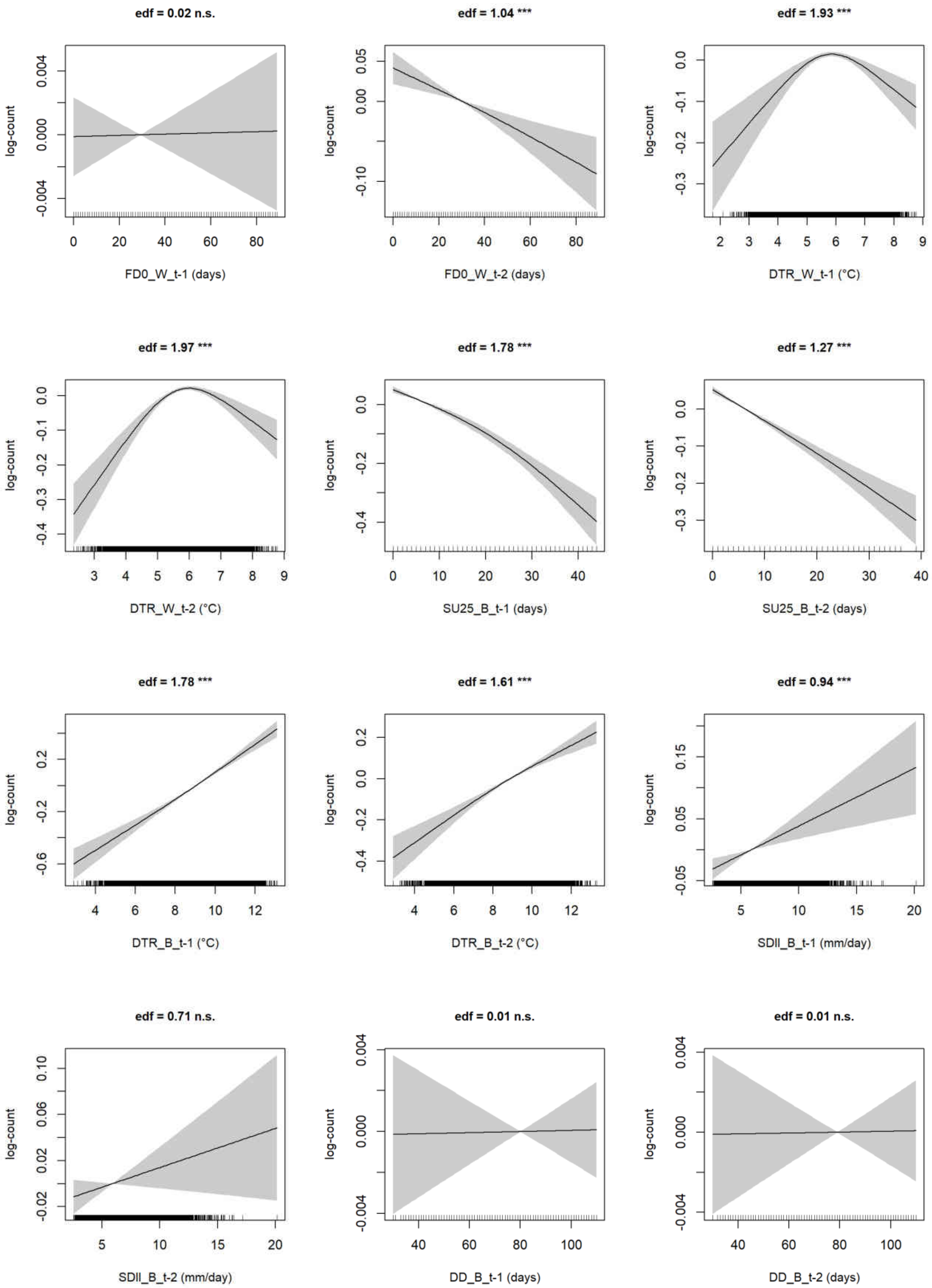




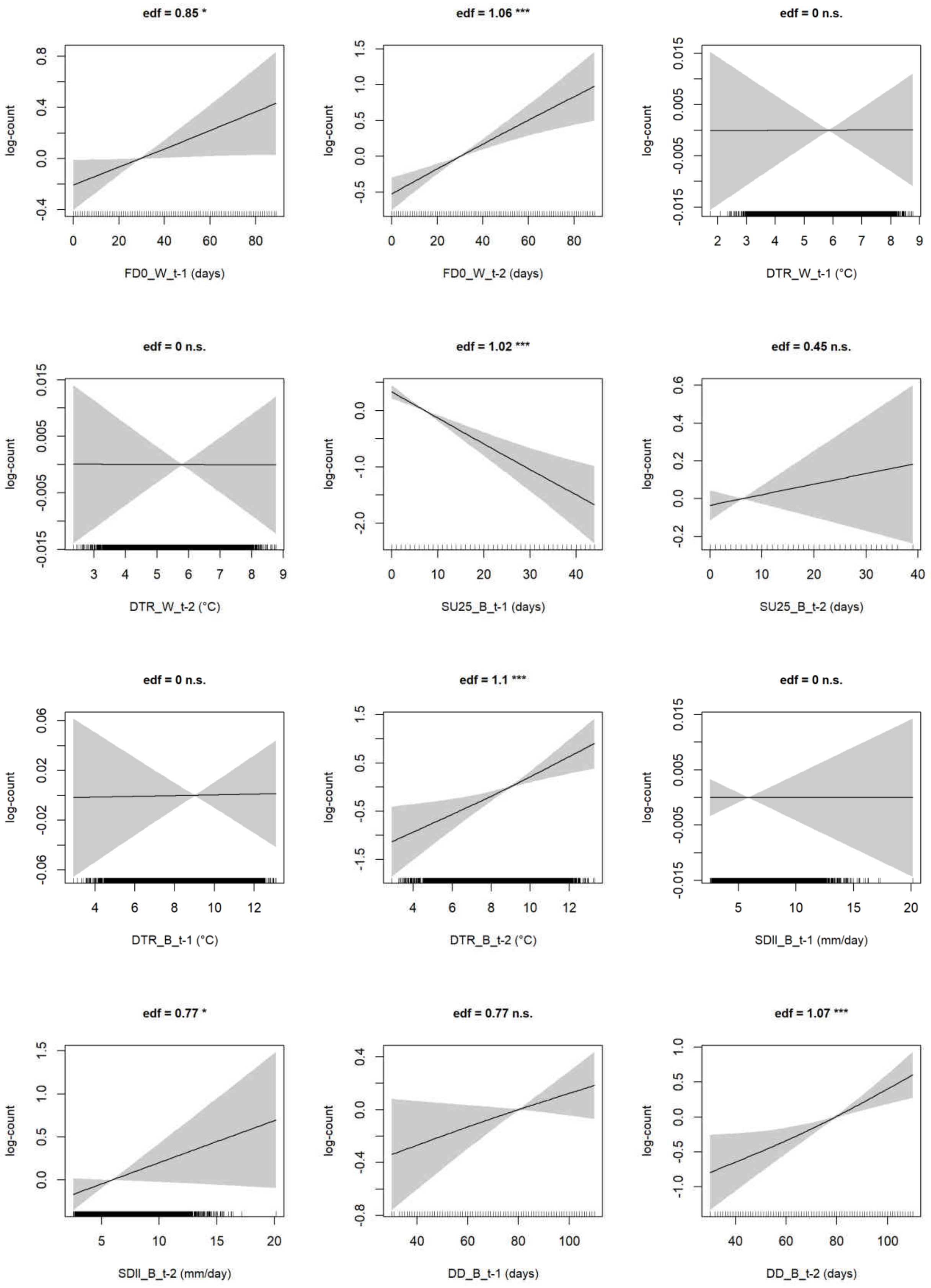




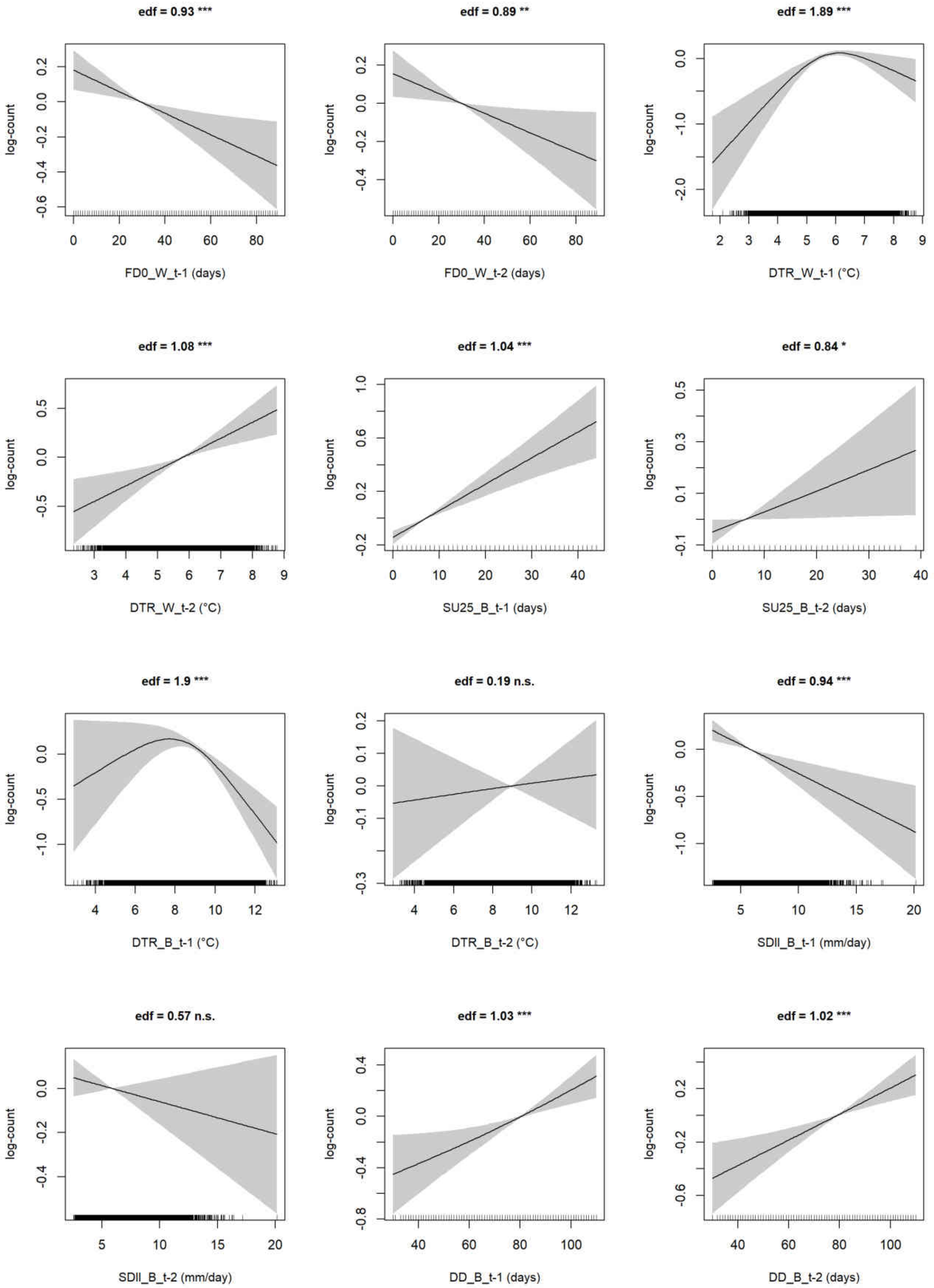
Common Chaffinch *Fringilla coelebs*



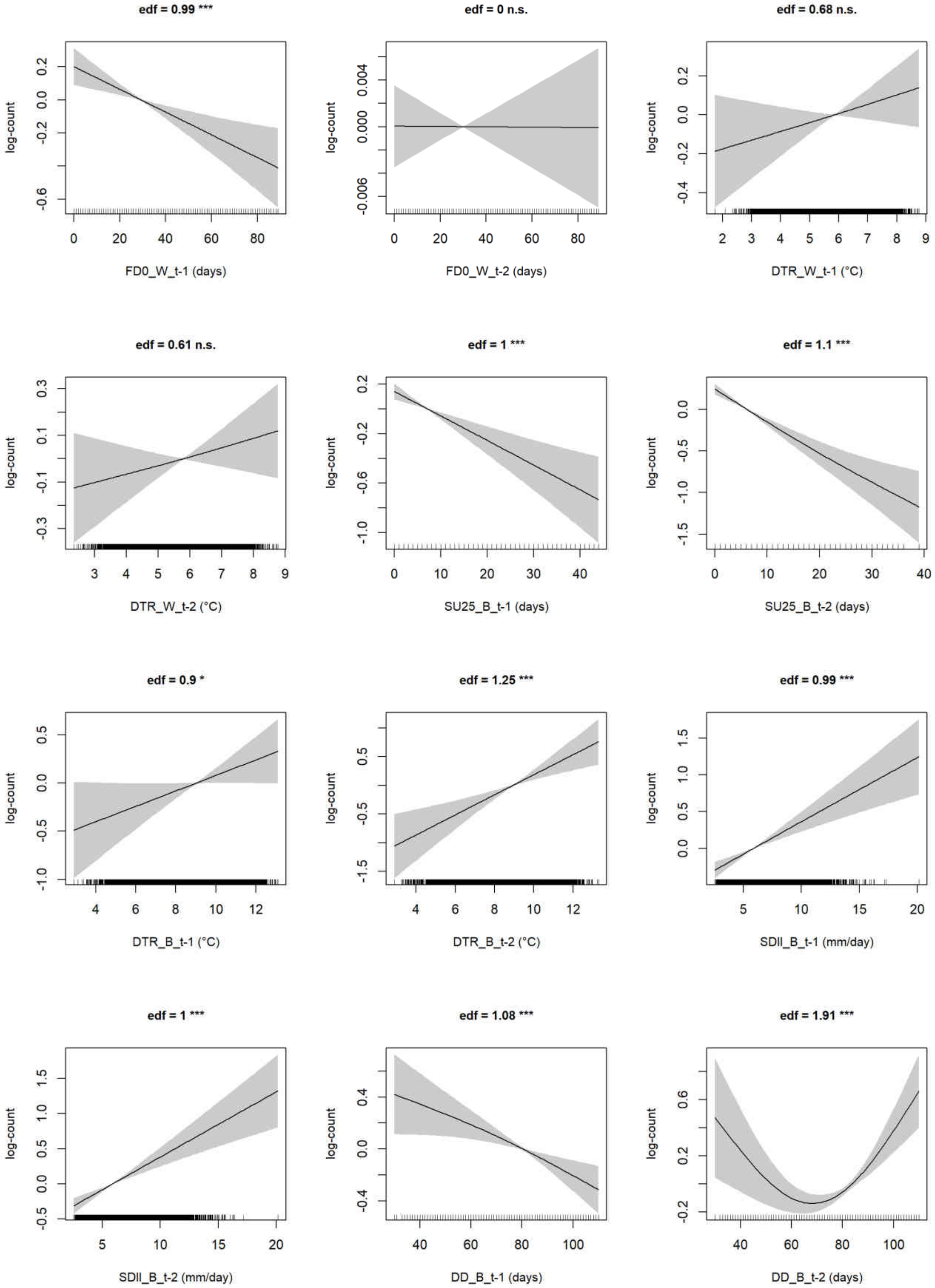
European Greenfinch *Chloris chloris*



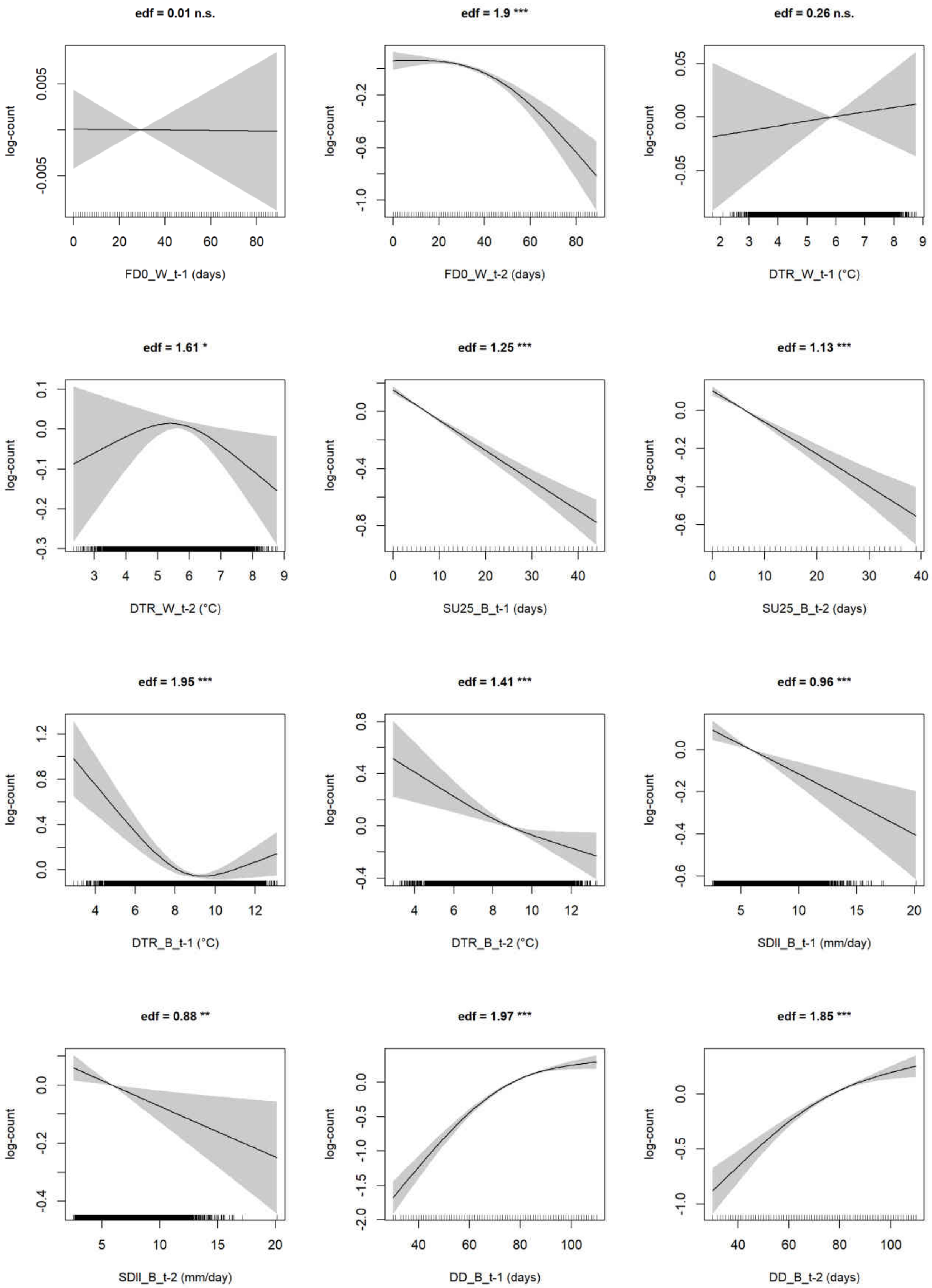
European Goldfinch *Carduelis carduelis*



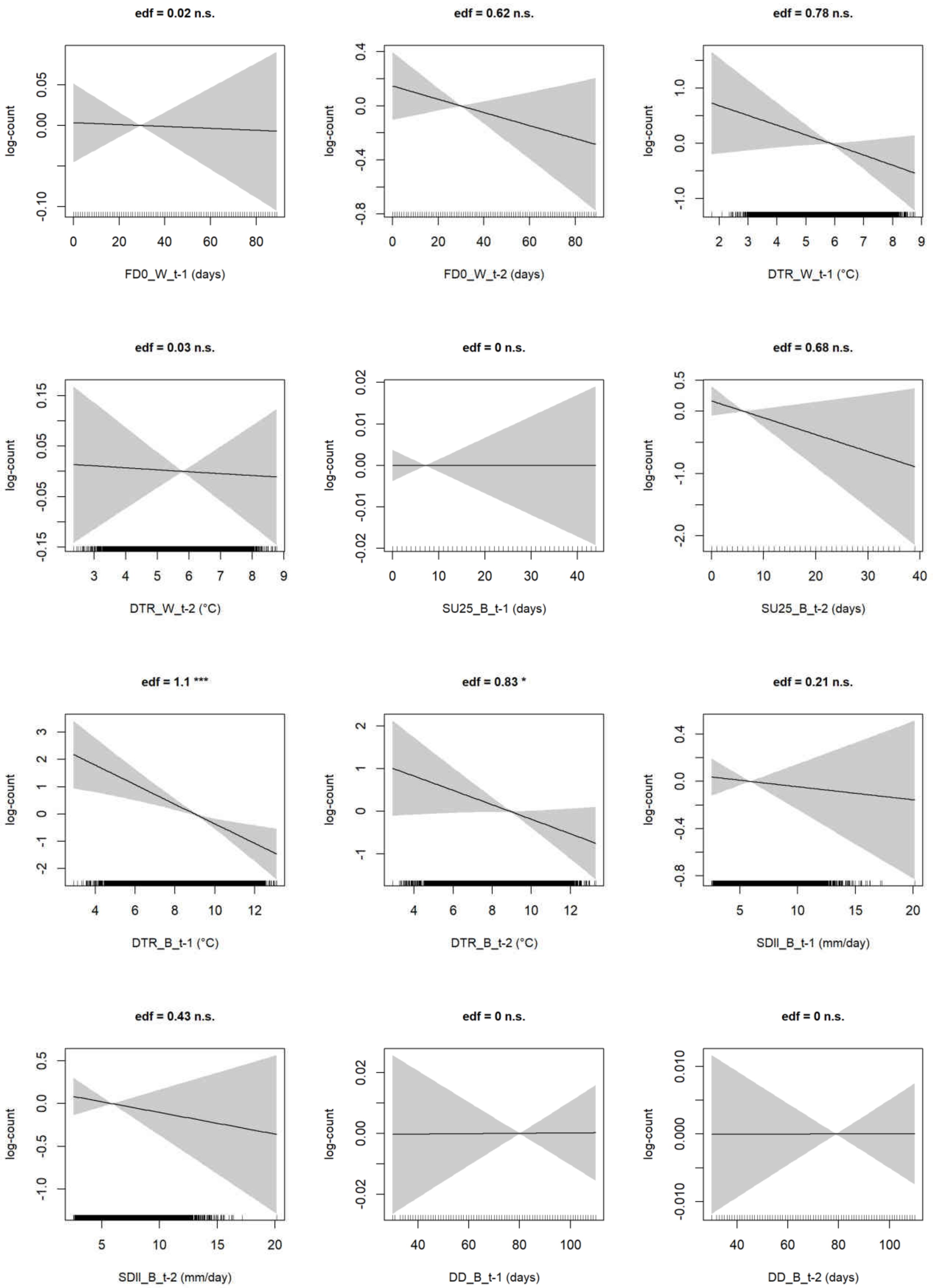
Eurasian Siskin *Spinus spinus*



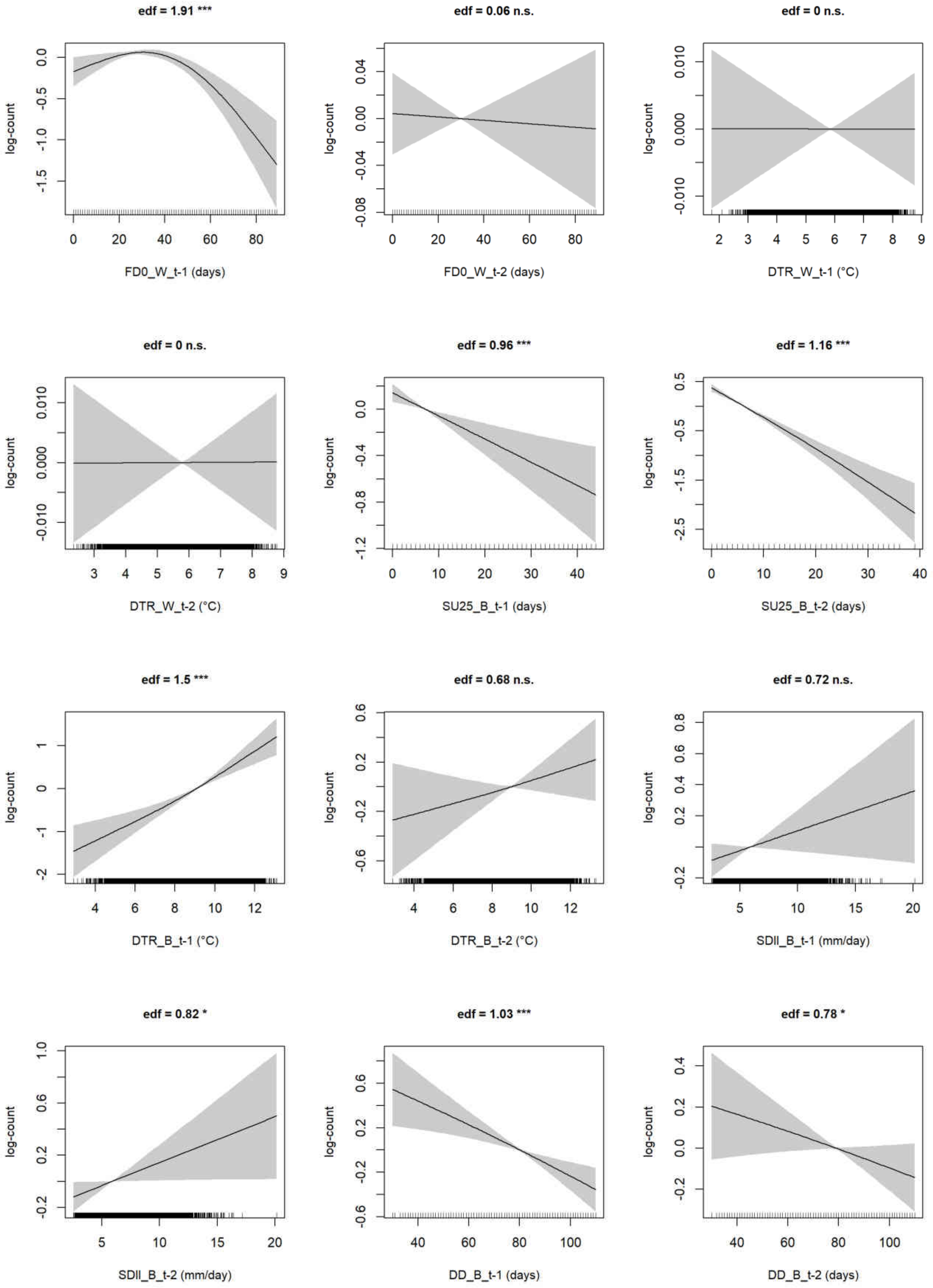
Common Linnet *Linaria cannabina*



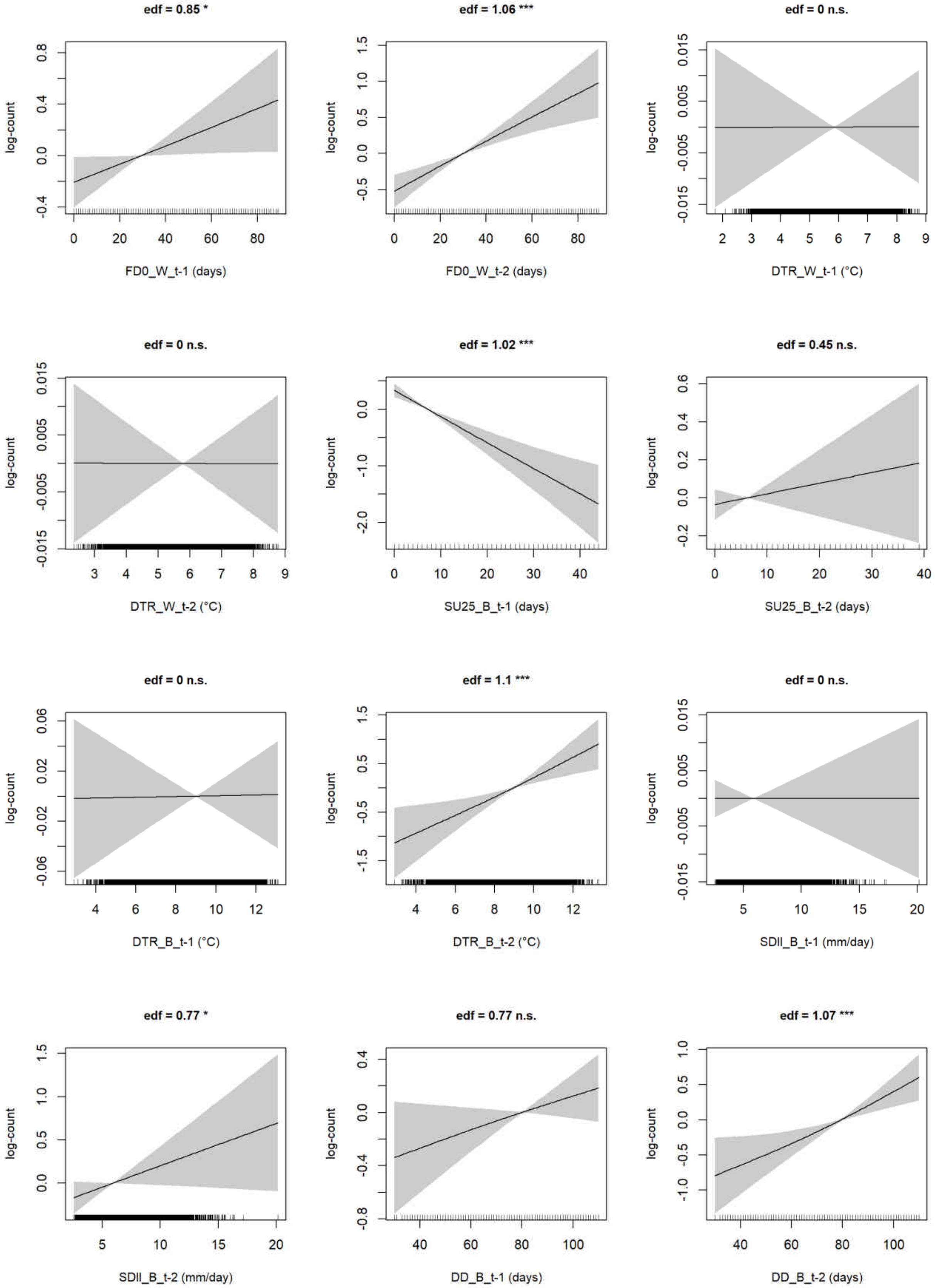
Twite *Linaria flavirostris*



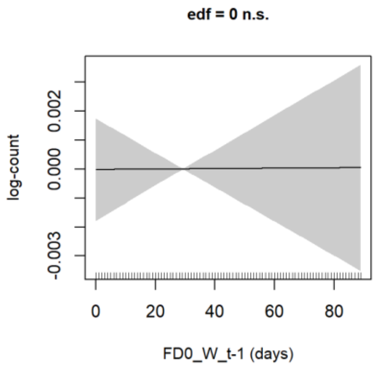
Lesser Redpoll *Acanthis cabaret*

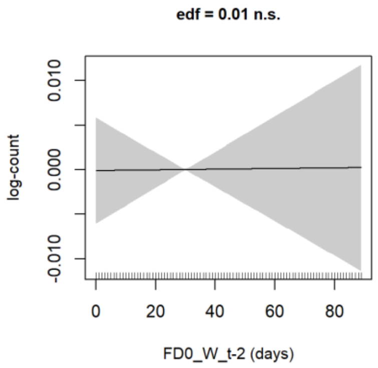


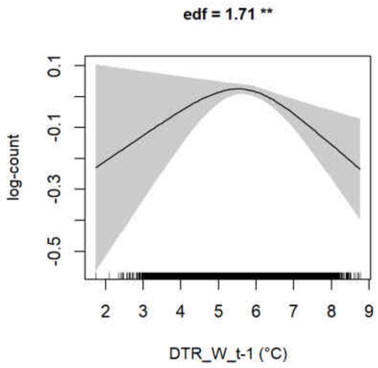
Red Crossbill *Loxia curvirostra*

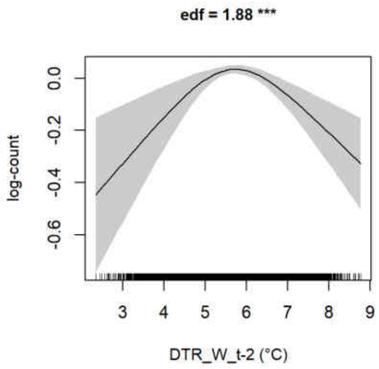


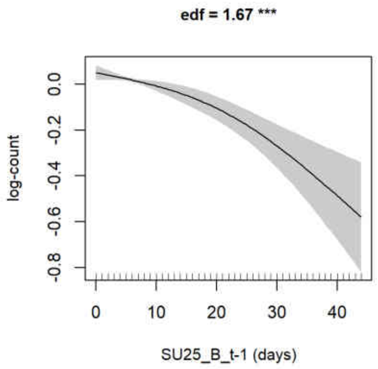
Eurasian Bullfinch *Pyrrhula pyrrhula*

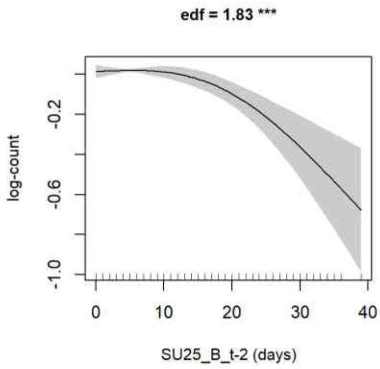


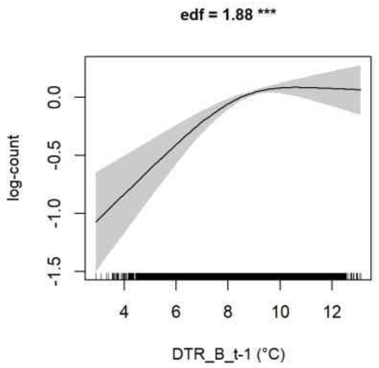


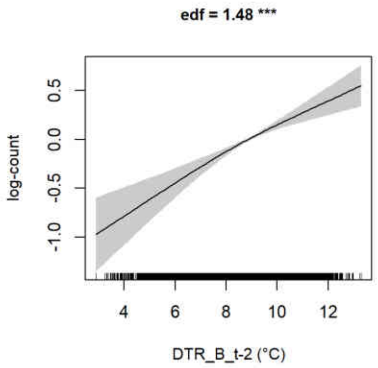


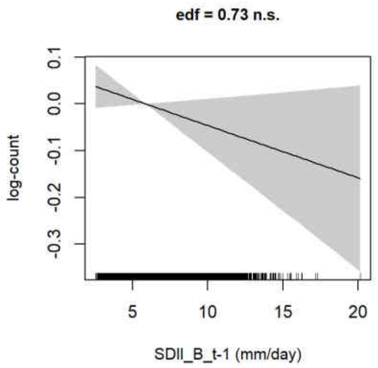


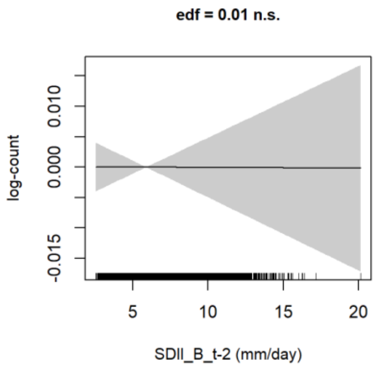


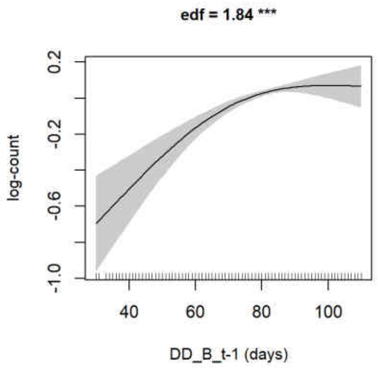


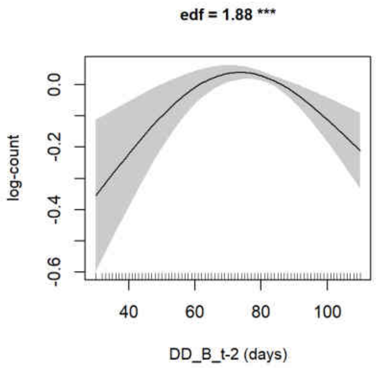




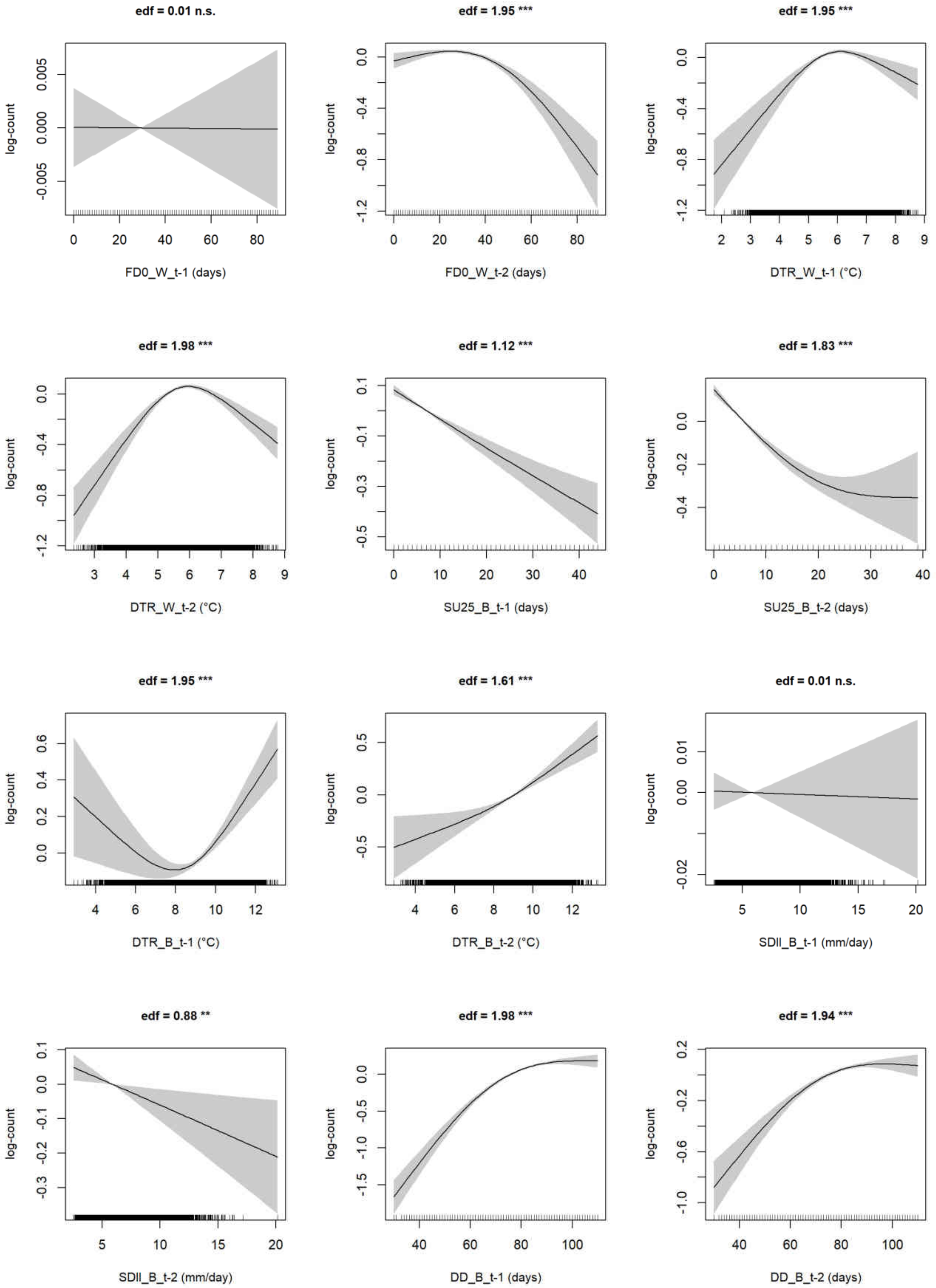




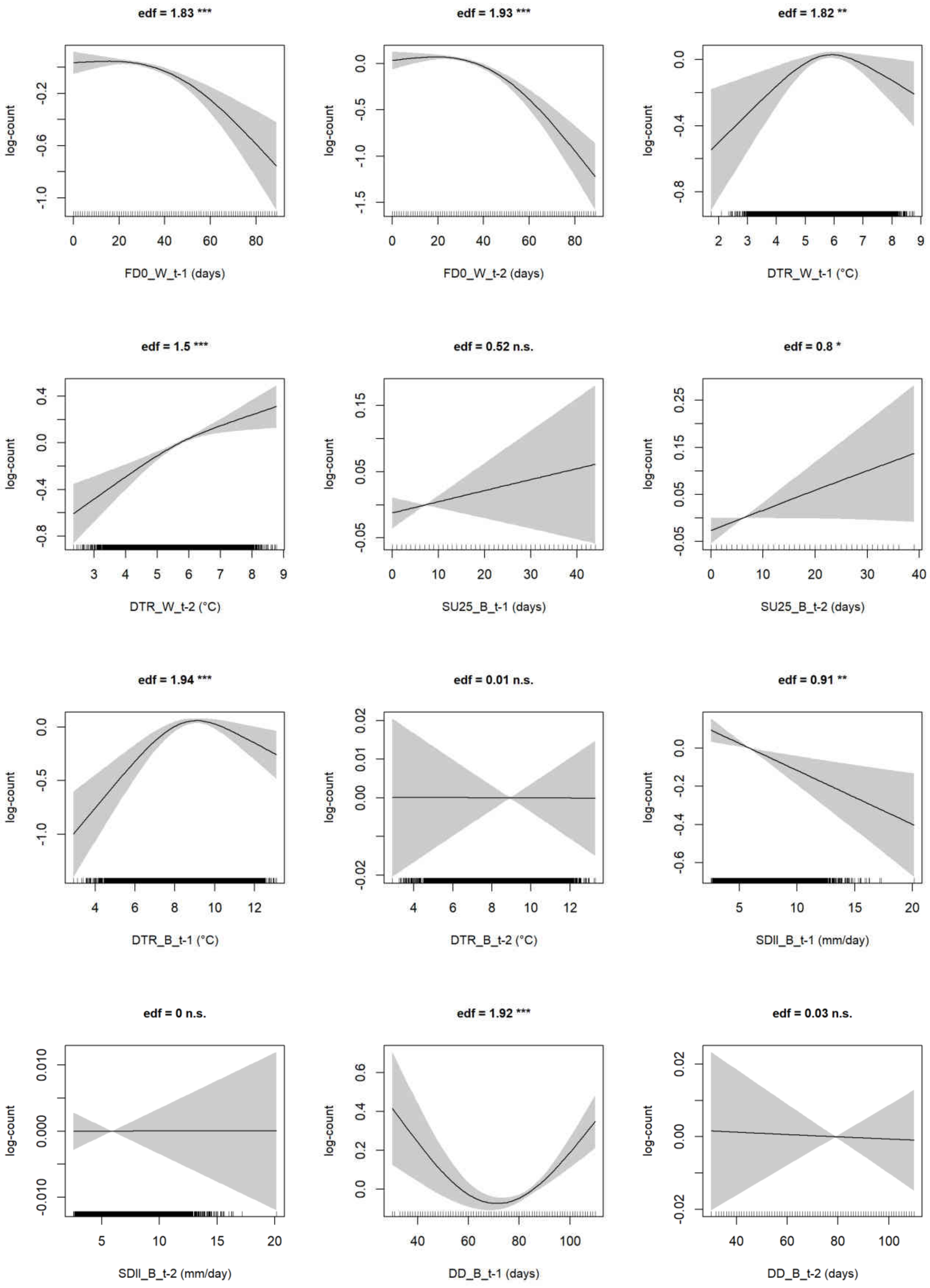




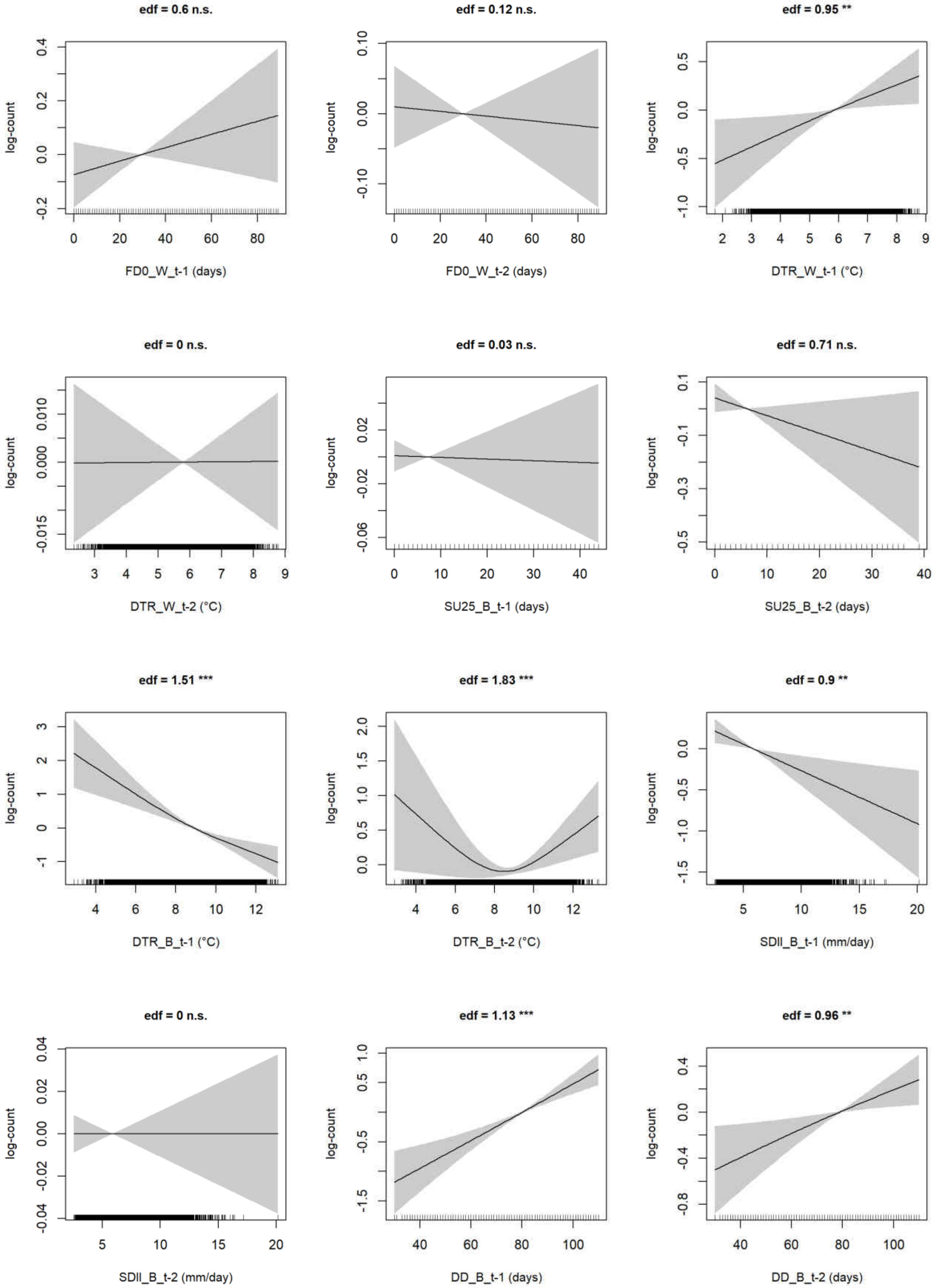
Yellowhammer *Emberiza citronella*



Common Reed Bunting *Emberiza schoeniclus*



Corn Bunting *Emberiza calandra*



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Chapter 6

General conclusions

6.1. Concluding remarks

An extensive knowledge about population responses to ongoing environmental and climatic changes is a primary goal to enhance environmental policies and promote the conservation of biodiversity. This thesis focused on some important aspects of avian ecology from both a methodological and applicative point of view, providing novel and valuable findings not only for bird studies but also in a broad ecological perspective.

One of the most direct ecological responses of wild populations to environmental changes is the variation of the population size over time (i.e. the population trend). Population trends are used as one of the most important tools for assessing the conservation status in wild populations and defining conservation priorities (IUCN, 2012). Thus, improving their estimates represent a primary goal in conservation biology. The first work explained in *Chapter 2* consisted in a methodological study that investigated the effects of the environmental bias, overdispersion and zero inflation on the estimation process of population trends. The study proposed a multi-step modelling approach to address these three issues, and provided evidence of their effects on trends as results of their inclusion or exclusion from the modelling. Findings highlighted that the environmental bias, which may affect many existing surveys because of a variation in the sampling effort over space and time, was the most important factor that causes differences in trend estimates across models. Additionally, overdispersion and zero inflation can influence, also significantly, the estimates, and modelling frameworks should consider their evaluation in the statistical approach. Such last findings were furtherly enforced when the modelling framework proposed in *Chapter 2* was applied for the assessment of long-term population trends for 76 common breeding birds at regional scale (*Chapter 3*). Indeed, results showed the zero-inflated GAMs were the best performing models for predicting annual population indices for 55 species, encouraging a wider use of zero-inflated models in population trend analysis. In *Chapter 3*, the evaluation of long-term trends (1992–2019) in Lombardy (northern Italy) for common breeding birds revealed a good conservation status for roughly three-quarters of the species, with 34 and 24 avian species showing increasing or non-significant variations of the population size, respectively. On the other hand, findings stressed 24% of the species under study underwent population declines that exceeded 50% for 12 species and 80% for six of them, with decreasing tendencies that do not seem to halt. This emphasises the urgency to deal with environmental policies to implement conservation strategies, which cannot disregard the identification of the specific factors at the basis of the observed responses. In this context, a trait-based approach could highlight the existence of shared ecological pressures across groups of species with similar life-history or ecological traits. Thus, in the second part of the research described in *Chapter 3*, the inclusion of traits' information in population trend modelling allowed identifying which avian functional groups need greater attention. Migrants, farmland birds, ground-nesters, species feeding on invertebrates and plants, species with high fecundity and long incubation period were the most threatened guilds in the study area, confirming already known patterns across other European countries and highlighting new evidence as well. Sensitivity of species traits could help to shed light on ecological processes acting on populations, emphasise where conservation efforts should be conveyed to plan future research aimed at quantifying the effects of specific drivers and finding adequate solutions to prevent further biodiversity loss. Findings from *Chapter 3* also remark the importance to carry on studies at local spatial scale, because species responses at regional level may be different compared to responses at broader scales.

Environmental changes could push a species to undergo new conditions that have never or little been faced before. The ability of a species to adapt to, tolerate or be favoured by such conditions may significantly influence the lasting of a species in a specific geographic area. Ecological niche modelling is an efficient tool for better understanding ecological dynamics. However, the use of niche modelling to assess how the niche may evolve within a population (or sub-populations) of the same species over time is poorly explored in ecology. Moreover, a totally overlooked aspect is the potential relationship between niche changes and both population trends and species traits. In *Chapter 4,* I described a case study of a multi-species niche analysis for 71 common breeding birds in Lombardy (northern Italy), exploring changes occurred in the realised Grinnellian niche over 26 years and their relationship with both population trends (obtained from results in *Chapter* 3) and species traits. Findings supported evidence of niche divergence for 10% of the species, 56% showed niche conservatism, while 34% highlighting less consistent responses. This highlights as niche conservatism is not a ubiquitous condition, and some species are actually changing their niches. Such changes could be the result of high or low environmental plasticity, but may involve microevolutionary processes under rapid and directional environmental changes. Findings from this chapter also stressed a general tendency to adjust the niche centroids towards warmer thermal conditions. It could result from distinct processes due to several drivers acting in a different way across species: i) passive niche centroid shift as consequence of absence or delay in niche tracking; ii) shift towards different habitats because of changes in habitat suitability; iii) colonisation of sub-optimal environments due to density-dependent effects. Moreover, linking different types of population responses (e.g. population trends and niche changes) could highlight interesting relationships. Indeed, results showed a positive correlation between niche expansion and increasing populations, and a signal that species retaining their niche over time could be more prone to undergo population declines. It provides evidence that species with greater environmental plasticity or tolerance respond to environmental changes better than other species. Moreover, moderate evidence for a non-random association between niche changes and species traits, especially for body size, clutch size, number of broods per year, landscape type, and migration strategy was found. The study highlighted the importance of enhancing the knowledge about the relationship between niche changes and population trends, as well as the relevance of working at the level of both functional groups and single species.

Lastly, the thesis contributed to make advances in studies about the consequences of climate change in the field of ecology and conservation biology by investigating the effects of the increasing phenomenon of extreme climatic events. Climate change has been recognised as one of the major threats for biodiversity and species conservation. The exacerbation and the increase of extreme climatic events poses new global challenges for nature conservation, stressing the importance to assess their impacts on long-term responses of populations over large spatial scale (Bailey & van de Pol, 2016). In *Chapter 5*, in a study carried out in collaboration with the British Trust for Ornithology, I assessed the effects of extreme climatic events on relative abundance for 100 resident bird species over large spatial and temporal scales using the UK Breeding Bird Survey, spanning over 25 years. Findings highlighted widespread and significant effects of extreme climatic events, with both common one-year and two-year lagged effects. Winter severity, hot temperatures and intensity of rainfall during the breeding season showed broad negative effects, while the diurnal temperature range during both winter and breeding season and drought in the breeding season showed more diversified effects across species, with a prevalence of positive effects. Moreover, the study also identified several species that were more susceptible to detect effects of extreme weathers and the direction of the responses, suggesting the use of such species for future studies in this research field. Long-term data revealed to be extremely important for assessing responses of populations in a changing environment and are essential to achieve a comprehensive perspective of ecological processes that can affect biocenosis and ecosystems.

6.2. Future perspectives

This research contributed to enhance the knowledge around the long-term effects of environmental and climatic changes on avian populations, with important implications in the field of conservation and applied ecology. Methodologies and findings, beyond to be significant for bird studies, have a broad ecological perspective and may be valuable for future research on other taxonomical groups, as well. Future research directions that approach to the topics addressed in this thesis should be aimed at investigating some still open research questions that were already presented throughout the chapters and that were here summarised below.

Firstly, we need to implement modelling approaches for the estimation of population trends. Specifically, the environmental bias should be considered not only when data derive from distinct structured surveys, but also in many long-term surveys when it could be caused by variations of the sampling effort over time. Furthermore, the increasing amount of semi-structured and non-standardised data that are now available, mainly due to citizen science projects or opportunistic collections uploaded on web-platforms (e.g. eBird, https://ebird.org/; EuroBirdPOrtal, https://www.eurobirdportal.org/; GBIF, https://www.gbif.org/) represents an extraordinary source of information but that press to develop statistical approaches to be able to handle the potential biases. In addition to biases, zero-inflated models merit greater consideration in population trend modelling, and the implementation of algorithms and software that are able to provide further statistical specifications about such models is a goal to be achieved. Moreover, our results suggested that count distributions for species with flocking foraging and/or colonial breeding behaviours could be characterised by both overdispersion and zero inflation. It may implies that a non-random association between species behaviours and structure of count data distribution may exist. Further research should extensively verify such pattern in order to provide some guidelines to be applied to large-scale and long-term trend assessment for a well-founded a priori selection of the count distribution and modelling choice that would allow saving computational time.

Secondly, linking niche changes to population trend analysis represent a crucial step for a better knowledge of population dynamics. Given the neglect of the topic in ecological studies, future research should explore such linkage with a particular focus on cause-effect relationships between population trends and niche dynamics, which would allow untangling which processes cause the observed responses. We also need to implement niche modelling by including all the components of the realised niche of a species: biotic factors (i.e. bionomic variables describing the Eltonian niche), abiotic factors (scenopoetic variables describing the Grinnellian niche, as done in this research), and dispersal capacities (BAM diagram, Biotic-Abiotic-Movement, Soberón & Peterson, 2005; Soberón, 2007). Furthermore, assessing niche changes throughout the full annual cycle (i.e. breeding, migration, wintering) would provide a more comprehensive point of view to understand if responses could vary along different life phases that are likely to be influenced by different factors that could lead to diversified responses also with contrasting inter-seasonal patterns.

Thirdly, considering the great impact of climate change on biodiversity and the increasing evidence of the biological and ecological effects of extreme climatic events, further studies should aim at investigating both direct and indirect mechanisms through which they can affect wild populations. Furthermore, we need to focus on synergistic effects resulting from interaction between climate and other anthropogenic pressures (e.g. land-use changes) because the resulting effects could vary if these drivers are considered individually and untangling the relative contributions will be crucial.

Lastly, analyses upon multiple species provide a more exhaustive perspective of population responses, and their application will continue to be important in the future. Future studies in these research fields should encompass a trait-based approach more extensively. Testing the consistence of the effects of species traits along spatial and temporal gradients represent a key issue, because traits' information can highlight shared patterns across functional and ecological groups of species, thus providing the foundations to test specific hypotheses about the causes of the observed responses and identifying the best strategies for nature conservation.

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Peer-reviewed articles

Articles produced as output from this thesis:

1. **Tirozzi, P.**, Massimino, D., & Bani, L. (*submitted manuscript*). Extreme climatic events have widespread effects on UK breeding bird populations.
2. **Tirozzi, P.**, Orioli, V., Dondina, O., & Bani, L. (2022). New evidence on the linkage of population trends and species traits to long-term niche changes. *Birds*, *3*(1), 149–171. DOI: 10.3390/birds3010011.
3. **Tirozzi, P.**, Orioli, V., Dondina, O., Kataoka, L., & Bani, L. (2022). Population trends from count data: handling environmental bias, overdispersion and excess of zeroes. *Ecological Informatics*, *69*, 101629. DOI: 10.1016/j.ecoinf.2022.101629.
4. **Tirozzi, P.**, Orioli, V., Dondina, O., Kataoka, L., & Bani, L. (2021). Species traits drive long-term population trends of common breeding birds in northern Italy. *Animals*, *11*(12), 3426. DOI: 10.3390/ani11123426.

Other articles produced during the three years of Ph.D. research:

1. Fehlinger, L., Misteli, B., Morant, D., Juvigny-Khenafou, N., Cunillera-Montcusí, D., Chaguaceda, F., …, **Tirozzi, P.**, …, & Rimcheska, B. (2022). The ecological role of permanent ponds in Europe: A review of dietary linkages to terrestrial ecosystems via emerging insects. *Inland Waters*, DOI: 10.1080/20442041.2022.2111180.
2. Dondina, O., Orioli, V., **Tirozzi, P.**, & Bani, L. (2022). Long-term dynamic of nestedness in bird assemblages inhabiting fragmented landscapes. *Landscape Ecology, 37,* 1543–1558. DOI: 10.1007/s10980-022-01419-7
3. Balestrieri, A., Mosini, A., Fonda, F., Piana, M., **Tirozzi, P.**, Ruiz-González, A., Capelli, E., Vergara, M., Chueca, L.J., Chiatante, G., & Movalli, C. (2021). Spatial ecology of the stone marten in an Alpine area: combining camera-trapping and genetic surveys. *Mammal Research, 66*, 267–279. DOI: 10.1007/s13364-021-00564-9.
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5. Stefani, F., Schiavon, A., **Tirozzi, P.**, Gomarasca, S., & Marziali, L. (2020). Functional response of fish communities in a multistressed freshwater world. *Science of The Total Environment*, *740,* 139902. DOI: 10.1016/j.scitotenv.2020.139902.

Conferences and congresses

Contributions from this thesis as presenting author:

1. **Tirozzi, P.**, Orioli, V., Dondina, O., & Bani, L. (2022). New Evidence on the Linkage of Population Trends and Species Traits to Long-Term Niche Changes. Contributed talk: *6th European Congress of Conservation Biology*, 22-26 *August 2022, Prague, Czech Republic*.
2. **Tirozzi, P.**, Orioli, V., Dondina, O., Kataoka, L., & Bani, L. (2022). Species traits drive long-term trends of common breeding birds in northern Italy. Contributed talk: *28th International Ornithological Congress, 15-19 August 2022, online.*
3. **Tirozzi, P.**, Orioli, V., Dondina, O., Kataoka, L., & Bani, L. (2022). Species traits drive long-term trends of common breeding birds in northern Italy. Poster: *22nd Conference of the European Bird Census Council – Beyond the Atlas: challenges and opportunities, Lucerne, Switzerland, 4-9 April 2022*.
4. **Tirozzi, P.**, Orioli, V., Dondina, O., Kataoka, L., & Bani, L. (2021). Population trends from count data: handling environmental bias, overdispersion and excess of zeroes. Contributed talk: *BOUsci21 – Developments in monitoring science, British Ornithologists' Union, 24-25 November 2021*.

Other contributions:

1. Rimcheska, B., Fehlinger, L., Misteli, B., Balibrea, A., Kolář, V., Souto, M., …, **Tirozzi, P.**, …, & Labat, F. (2022). Odonata fauna across European ponds – a case study from the EUROPONDS project. In Vinko, D., & Bedjanic, M. (Eds.), *Book of abstracts: ECOO 2022, 6th European Congress on Odonatology, 27-30 June 2022, Kamnik, Slovenia, Book of Abstracts*. Slovene Dragonfly Society – Slovensko odonatološko društvo: Ljubljana, p. viii + 100.
2. Fehlinger, L., Rimcheska, B., Fekete, J., Bozóki, T., Misteli, B., Balibrea, A., …, **Tirozzi, P.**, …, & Várbíró, G. (2022). A comparative study of larval Odonata data within permanent ponds across

Hungary. In Vinko, D., & Bedjanic, M. (Eds.), *Book of abstract: ECOO 2022, 6th European Congress on Odonatology, 27-30 June 2022, Kamnik, Slovenia, Book of Abstract*. Slovene Dragonfly Society – Slovensko odonatološko društvo: Ljubljana, p. viii + 100.

3. Fehlinger, L., Rimcheska, B., Mondav, R., Nash, L., Drohan, E., Misteli, B., …, **Tirozzi, P.**, …, & Zawadzka, M. (2021). Preliminary results of EUROPONDS: early researchers shedding light on overlooked water bodies. In *Abstract book: SEFS 12, Symposium for European Freshwater Sciences, 25-30 July 2021, virtual conference.*
4. Fehlinger, L., Rimcheska, B., Tomás-Martín, M., Soto-García, P., Mondav, R., Nash, L., …, **Tirozzi, P.**, …, & Maniezhilan, E. (2021). Ecological assessment of a renaturalised pond in the quarries of Alpedrete (Spain). In *Abstract book: SEFS 12, Symposium for European Freshwater Sciences, 25-30 July 2021, virtual conference*.
5. Rimcheska, B., Fehlinger, L., Misteli, B., Chaguacheda, F., Cunillera-Montcusi, D., Juvigny-Khenafou, N., …, **Tirozzi, P.**, …, & Zawadzka, M. (2021). Overseen ecosystem services of ponds and their insects – their role for supporting terrestrial consumers and biodiversity "EUROPONDS". In *Balkan Bio: 5th Balkan Scientific Conference on Biology – Book of Abstracts, 15-16 April 2021*. Plovdiv University Press: Plovdiv, Bulgaria. eISBN: 978-619-202-644-8.
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Period abroad

During the third year of the Ph.D. course, I spent six months (December 2021 - May 2022) as visiting student at the British Trust for Ornithology, Thetford, Norfolk, UK, under the scientific supervision of Dr. Dario Massimino.

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