Assessing the potential contribution of roads to variation in British bird populations

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May 2020

This thesis is submitted for the degree of Doctor of Philosophy

Preface

Declarations

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration except as declared in the preface and specified in the text. It is not substantially the same as any work that has already been submitted before for any degree or other qualification except as declared in the preface and specified in the text. It does not exceed the 60,000-word limit for the Biology Degree Committee.

Contributions

The original idea of this project was formulated by Paul F. Donald, Andrew Balmford, Stuart E. Newson and Rhys E. Green. Rhys E. Green assisted with the statistical set up of the first two data chapters. Paul F. Donald, Andrew Balmford, Stuart E. Newson and Alison Johnston contributed guidance on the methodologies and foci of all data chapters as well as commenting on manuscript drafts. Alison Johnston also provided extensive statistical and coding support for all data chapters. In addition, Dario Massimino assisted with some of the code writing required for Chapter 2. Finally, Hannah Wauchope taught me the use of the Cambridge High Performance Computing facilities for Chapters 2-4 and, as work experience, Lucy E. Haskell helped with one part of the data preparation for Chapter 2.

Publications

The following publications form the basis of this thesis:

Chapter 2: Cooke, S. C., Balmford, A., Johnston, A., Massimino, D., Newson, S. E. and Donald, P. F. 2019. Road exposure and the detectability of birds in field surveys. *Ibis*, 162(3): 885-901.

Chapter 3: Cooke, S. C., Balmford, A., Johnston, A., Newson, S. E. and Donald, P. F. 2020. Variation in abundances of common bird species associated with roads. *Journal of Applied Ecology*, 57(7): 1271-1282.

Chapter 4: Cooke, S. C., Balmford, A., Donald, P. F, Newson, S. E. and Johnston, A. Roads as a contributor to landscape-scale variation in bird communities. *Nature Communications*, 11: 3125.

In addition, I produced or contributed to the following papers during my PhD:

Izurieta, A., Delgado, B., … , Vissioli, F., Viteri-Mejía, C., Norris-Crespo, L., Cooke, S. C., Veronica Toral-Granda, M. and Sutherland, W.J. 2018. A collaboratively derived environmental research agenda for Galápagos. *Pacific Conservation Biology*, 24:2.

Cooke, S. C., Haskell, L. E., van Rees, C. B. and Fessl, B. 2019. A review of the introduced smooth-billed ani *Crotophaga ani* in Galápagos. *Biological Conservation*, 229: 38-49.

Geldmann, J., … Cooke, S. C., … and Balmford, A. 2020. Insights from two decades of the Student Conference on Conservation Science. *Biological Conservation*, 243: 108478.

Cooke, S. C., Anchundia, D., Caton, E., Haskell, L. E., Jager, H., Kalki, Y., Molla, O., Rodriguez, J., Schramer, T., Walentovitz, A. and Fessl, B. 2020. Endemic species predation by the introduced smooth-billed ani in Galápagos. *Biological Invasions* 22: 2113-2120.

MacLeod, A., Cooke, S. C. and Trillmich, F. 2020. The spatial ecology of invasive feral cats *Felis catus* on San Cristóbal, Galápagos: first insights from GPS collars. *Mammal Research* 65(3): 621-628.

van Rees, C. B., Muñoz, M. A., Cooke, S. C. and Reed, J. M. Morphological differences in the island-endemic Hawaiian subspecies of the common gallinule *Gallinula galeata*. Manuscript accepted.

I have also published articles and blog posts on the above publications and presented my work on multiple platforms, including scientific conferences, public events and radio interviews.

Acknowledgements

I would like to thank the following organisations, institutions and individuals for their support with this work:

- The Natural Environment Research Council for funding this PhD project and the Department of Zoology, University of Cambridge's Postgraduate Hardship Fund, Cambridge Philosophical Society, and King's and Christ's Colleges for hardship support.
- My supervisors Andrew Balmford, Paul Donald, Alison Johnston and Stuart Newson for their ideas, time, enthusiasm and support, both professionally and personally.
- Dario Massimino, Rhys Green, Tom Finch and Calum Maney for their assistance.
- My advisors William Sutherland and Andrea Manica for their support and advice.
- All volunteer BBS fieldworkers for their data collection.
- The editors and reviewers of the three publications forming the basis of this thesis.
- Andrea Manica, Matthias Landgraf, Nicholas Gay, Carrie Vout, Alison Johnston, Hannah Wauchope, Claire Wordley, Emma Garnett, Matthew Hayes, Roza Kokuti, Kiyoko Gotanda, Freya Berry, Emma Caton, Lucy Haskell, Harriet Bartlett, Collin VanBuren, Miriam Shovel, Claudia Vince, Tess Langfield, Sophie Jenns, Roisin Fattorini, Amelia Hood, Ellie Bladon and so many of my other friends and colleagues, for their guidance through my intermission and

phenomenal support through an extremely difficult time in both my PhD and life. Without them, this work may never have been completed.

- King’s College, for welcoming me with open arms and supporting me ever since.
- Past and present members of the Conservation Science Group, for creating such a wonderful and supporting environment to work in.
- My family, for their never-ending support and fantastic proof-reading skills.

Summary

Roads and their traffic are known to affect bird species at both individual and population levels. Collisions with vehicles can cause direct mortality, and noise, light and chemical pollution can have sub-lethal impacts. Additionally, roads can cause habitat degradation, fragmentation and edge effects. However, thus far, the published literature on this topic comprises only relatively small-scale studies and our understanding of the impacts of roads on bird populations at landscape or national scales is limited.

I use bird count and road data from across Great Britain to assess the spatial associations between the density and traffic volumes of roads, and bird populations in the surrounding areas. In Chapter 1, I provide background detail on the impacts of roads on birds and introduce the premise and necessity of my thesis. In Chapter 2, I quantify changes in the detectability of birds in field surveys in relation to road exposure. I find that, while some species are significantly harder to detect in areas of higher road exposure, others are easier. I therefore suggest that, in analyses of bird populations around roads, where possible, variation in detectability with exposure to roads should be accounted for, to avoid under- or over-estimation of road impacts on birds. In Chapter 3, I incorporate my detectability models into a spatial analysis of bird populations and roads across Britain, for 51 common and widespread species. This methodology allows independent assessment of the associations between roads and bird abundance, accounting for the potentially confounding impacts of roads on detectability. I find the abundances of 30 species to vary significantly with exposure to roads, some negatively and others positively. Across the interquartile range of road exposure, the mean decrease in bird abundance (for species with significant negative associations) was -19% and the mean increase (for species with significant positive associations) was +47%.

In Chapter 4, in order to explore interspecific variation in these associations, I analyse a further 24 rarer species, and then test my results for all 75 species in relation to five characteristics. In this analysis I find 58 species to vary significantly in abundance with exposure to roads and the mean changes in bird abundance across the interquartile range of road exposure to increase to -39% and +48%. I also find that, with increasing road exposure, species with higher national populations have relatively higher abundance, while nationally rarer species have relatively lower abundance. Smaller-bodied and migratory species are also more negatively associated with road exposure. The distances over which negative associations between road exposure and bird abundance can be detected reach a mean of 700 m from a road, an area covering over 70% of Britain and 41% of the total area of terrestrial protected sites. I suggest that roads may, like some other forms of human disturbance, create conditions that benefit generally common species at the expense of others, thus having the potential to contribute to large-scale simplification of bird communities. Finally, in Chapter 5, I give an overall discussion of my thesis and highlight the importance of further work to understand in more detail the impacts of roads on birds in Britain and elsewhere, and to mitigate them effectively.

Contents

Chapter 1: Introduction

Background

Bird declines in Britain

Across Great Britain, and indeed the globe, populations of many bird species have declined substantially in the past half-century. In Britain, species' declines have been widespread, with numerous species suffering population reductions of over 50% from 1970 to 2017 (e.g. 58% of farmland species; 24% of woodland species; 19% of wetland species; DEFRA 2019). Although some bird species have increased in abundance, and climate change has enabled a few to expand their ranges, densities of common and widespread breeding species have generally been in decline (**Figure 1**). Between 1967 and 2009, the total number of individual breeding birds in the UK is estimated to have fallen by 44 million, a decline of over 20% (Eaton et al. 2012). These declines have been attributed to changes in agricultural practises and land management, as well as the loss or degradation of habitat, and climate change (Eglington and Pearce-Higgins 2012; Burns et al. 2016; Hayhow et al. 2017; Oliver et al. 2017).

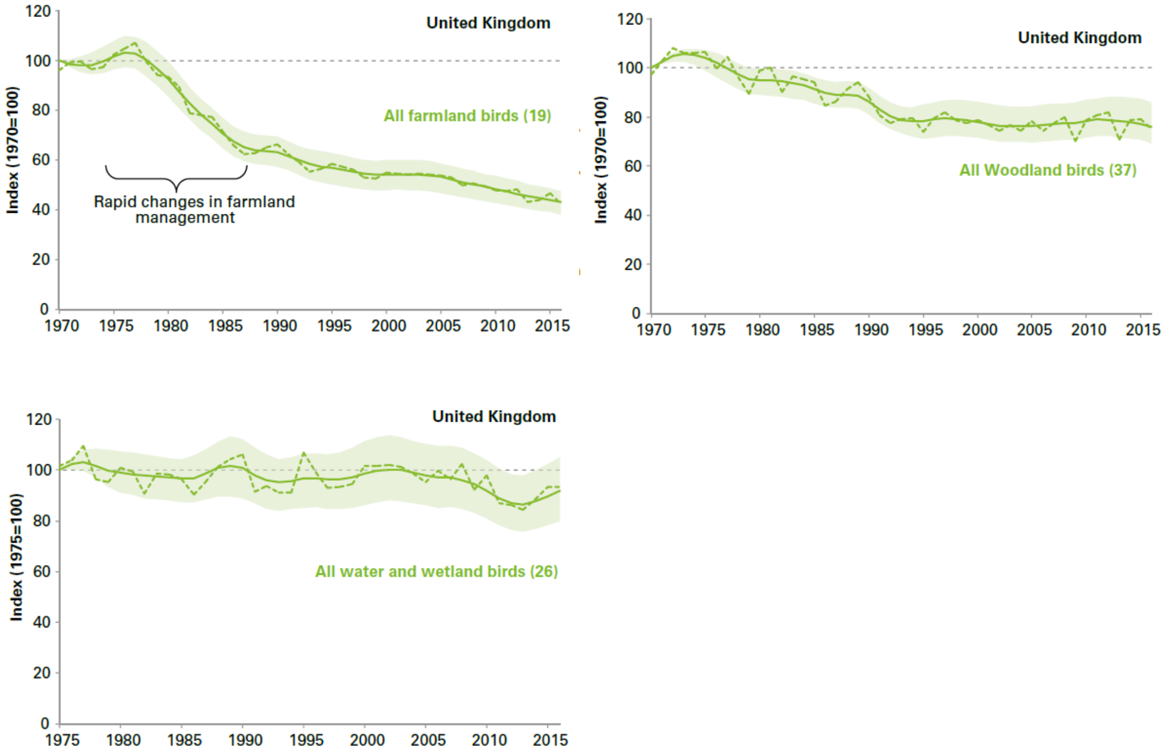


Figure 1. Wild bird indicators for farmland, woodland and wetland birds in the UK, 1975 to 2016. Figures sourced from Hayhow et al. 2017.

Roads as a source of change

However, in the past 50 years, Britain has also experienced large changes in its road network. The total road length across the nation has increased by nearly 25% (DfT 2018) and the traffic volume by over 160% (DfT 2019; **Figure 2**). As yet, the importance of these increases in the context of national bird population changes has not been considered in Britain but, given the correlation of the two (**Figure 3**), and the known impacts of roads on birds from studies elsewhere (summarised below), this appears an important omission.

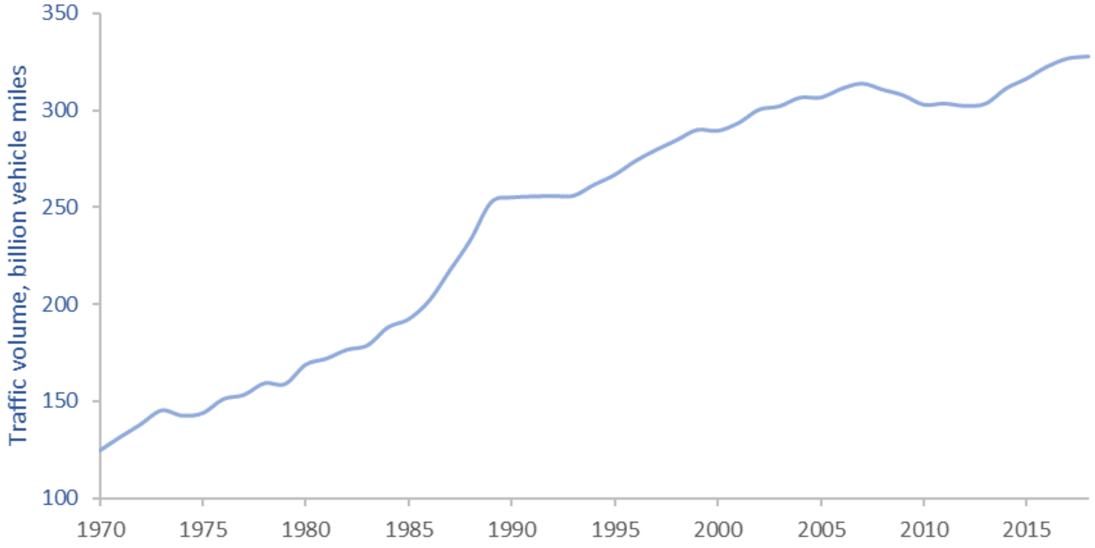


Figure 2. Road traffic in the UK 1970-2018; data sourced from DfT 2019.

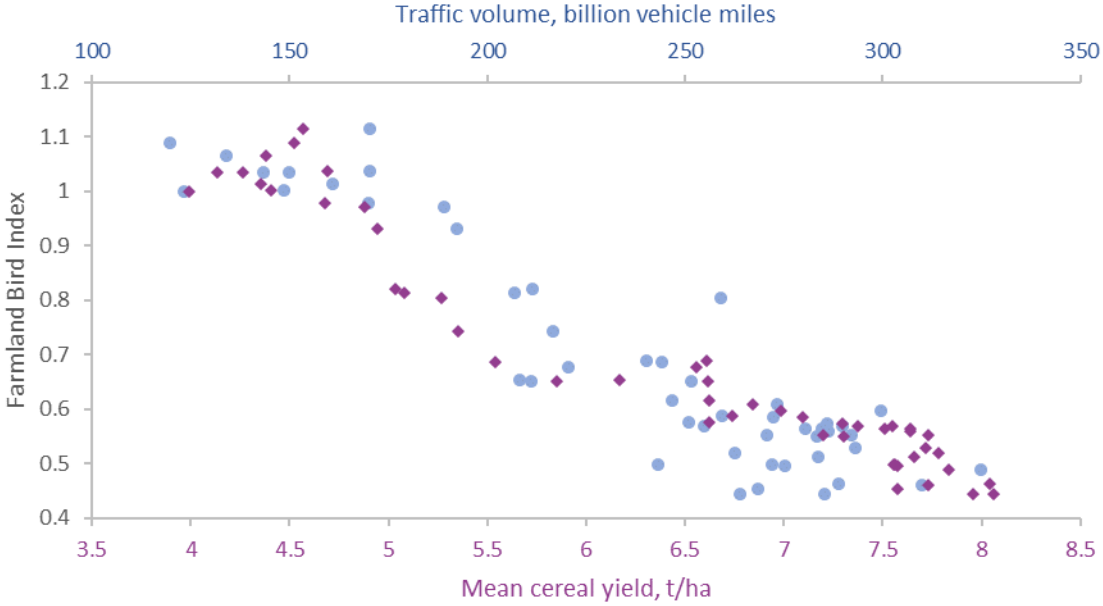
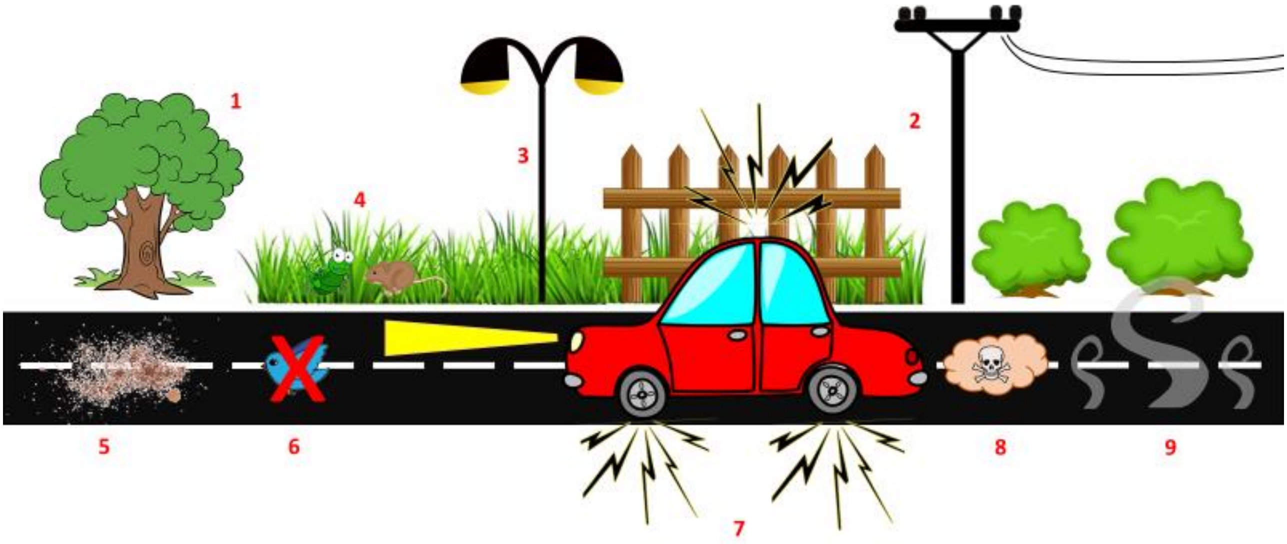


Figure 3. The correlation between the farmland bird index and traffic volume across the UK from 1970 to 2018. As agricultural intensity is frequently cited as a cause of farmland bird declines, I show the same correlation between the farmland bird index and mean cereal yield for comparison. Note that this correlation does not demonstrate causation. Data sourced from DEFRA 2019; DfT 2019; and FAOSTAT 2020.

The potential of roads as drivers of population changes at landscape or national levels has not been well studied outside Britain either (van der Ree et al. 2011). One study in the Netherlands extrapolated measured road impacts on birds to estimate national population reductions of up to 20% (Reijnen & Foppen 2006), but few other studies have attempted such large-scale estimation or measurements. However, the impacts of roads on birds and other wildlife, both at population and individual levels, have been the focus of many smaller-scale studies. Local populations of several species have been shown to be reduced around roads (Fahrig & Rytwinski 2009; Benítez-López et al. 2010; Kociolek et al. 2011), with stronger effects seen around those with heavier traffic volumes (Reijnen et al. 1996; Forman et al. 2002; Bautista et al. 2004; Peris & Pescador 2004). These include many found in Great Britain such as goldcrest *Regulus regulus* (Reijnen et al. 1995; Helldin & Seiler 2003); ring-necked pheasant *Phasianus colchicus* (Reijnen et al. 1995); and willow warbler *Phylloscopus trochilus* (Reijnen & Foppen 1994; Reijnen et al. 1995). These studies have typically focused on areas around a small number of roads and/or have singled out and measured one or two specific mechanisms by which roads might affect birds. In fact, there are a large number of mechanisms by which roads might affect birds (summarised in **Figure 4**), the cumulative impact of which may extend up to (or possibly even over) 1 km from a road itself (Reijnen et al. 1996; Benitez-Lopez et al. 2010; Clarke et al. 2013).



1. Roadsides often contain a variety of edge habitat
2. Powerlines and fences tend to follow roads, providing perching opportunities
3. Artificial light is produced by headlights and streetlights
4. Small mammals and insects, which can be food sources, often occupy roadside habitat
5. Grit tends to be found on road surfaces
6. Collisions between vehicles and wildlife are common, which causes mortality but also provides food
7. Noise is produced by both vehicle engines and the interaction between tyres and the road surface
8. Combustion-engine vehicles produce a range of emissions
9. Road surfaces are a source of heat

Figure 4. Roads and their vehicles can cause many changes to their surrounding environment, resulting in both positive and negative impacts on wildlife.

Mechanisms by which roads can affect birds

One mechanism frequently singled out as having an important impact on birds, and other wildlife, is noise pollution. Arising from both vehicle engines and the interaction between tyres and the road surface, it is one of the mechanisms that can act over a large distance from a road and varies considerably with traffic intensity, vehicle speed and surrounding habitat (**Figure 5**).

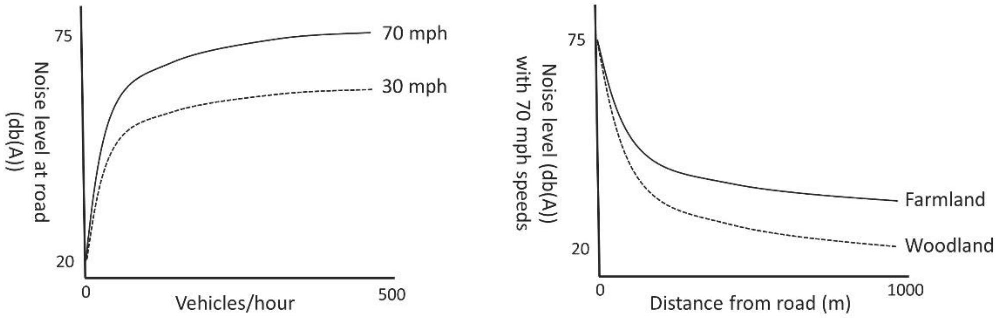


Figure 5. Approximation of road noise level changes with a) traffic intensity and vehicle speed and b) distance from road and surrounding habitat. Background noise level is estimated at 20 db(A).

Noise pollution can affect a bird's ability to detect prey or predators, increasing their time spent being vigilant and thus decreasing time available for foraging (Slabbekoorn & Ripmeester 2008; Ware et al. 2015). It also disrupts communication between birds, by masking their calls, and can affect the efficacy of parent-chick signals (Leonard & Horn 2005; Habib et al. 2007; Templeton et al. 2016). Importantly, the impact of traffic noise on bird populations has been shown to hold even when the structural components of a road are removed – two phantom road studies, using an array of speakers to imitate roads in otherwise roadless areas, have shown the abundance of many bird species to decrease in the presence of road noise (McClure et al. 2013; Senzaki et al. 2020).

Bird-vehicle collisions are also a major cause of mortality along roads (Erritzoe et al. 2003) and, in some species, have the potential to negatively affect local bird abundance around roads (Jack et al. 2015) as well as wider populations (Borda-de-Agua et al. 2014). Artificial light, produced by streetlights and headlights, and air and chemical pollution, produced by engines and tyres, also have the potential to reduce health or breeding success (Day 2003; Mineau & Brownlee 2005; Kociolek et al. 2011) – the former through effects on the timing of circannual events such as breeding (De Molenaar et al. 2006; Dominoni et al. 2013), and the latter through respiratory illnesses and poisoning (Sanderfoot & Holloway 2017). The visual disturbance of roads can stimulate avoidance or anti-predator behaviour in birds, particularly in open landscapes (Forman & Alexander 1998; Day

2003; Vliet et al. 2010; Kociolek et al. 2011), and furthermore, although it is often assumed that birds are unaffected by the fragmentation impacts of roads, studies have shown that many bird species will avoid crossing even an unpaved road, instead responding as if it were a barrier (Rich et al. 1994; Develey & Stouffer 2001; Laurance et al. 2004; Tremblay & Clair 2009).

The impacts of roads can arise not only from the roads themselves and their corresponding infrastructure, but also from variation in the habitat around them. Roadsides tend to contain very heterogeneous edge habitat which, while being unattractive to some species, may be of benefit to others (Meunier et al. 1999; Helldin & Seiler 2003). Particularly in landscapes dominated by open agricultural land, roadside habitat may be important to many species. As well as this, roads can provide food in the form of road-kill (Dean & Milton 2003), as well as grit and heat (Whitford 1985; Erritzoe et al. 2003; Yosef 2009), and perches in the form of powerlines and fences (Knight & Kawashima 1993; Meunier et al. 2000; Morelli et al. 2014). As such, some bird species can exhibit higher densities near to roads, such as house sparrow *Passer domesticus* (Brotons & Herrando 2001; Peris & Pescador 2004); chaffinch *Fringilla coelebs* (Morelli et al. 2015); great tit *Parus major* (Helldin & Seiler 2003; Wiacek et al. 2015); European greenfinch *Chloris chloris* (Helldin & Seiler 2003; Palomino & Carrascal 2007; Morelli et al. 2015); and some corvids and raptors (Meunier et al. 2000; Dean & Milton 2003; Fahrig & Rytwinski 2009; Lambertucci et al. 2009; Yamac & Kirazli 2012). Some species may also benefit from lower competition, due to reductions in populations of others.

However, it is possible that birds attracted to roads may have an increased likelihood of death due to collisions or suffer reduced health and breeding success (Mumme et al. 2000; Liker et al. 2008; Grunst et al. 2020). Disturbance from roads can also affect population structures (Reijnen & Foppen 1994; Bujoczek et al. 2011; McClure et al. 2017). There is, therefore, the potential for roads to act as ecological traps (Foppen & Reijnen 1994; Reijnen & Foppen 1994; Mumme et al. 2000; Schlaepfer et al. 2002). In addition, the attraction to roads by some corvids and raptors may increase the predation risk for others (Pescador & Peris 2007; DeGregorio et al. 2014).

The focus of this study

In Britain, 80% of the land area falls within 1 km of a road (**Figure 6**), with a combination of both major (high speed, high traffic) and minor (varying speeds, lower traffic) roads traversing the island. There are few mitigation measures in place and often an absence of dense, sound-attenuating habitat around roads, therefore it is likely that many birds in Britain avoid large areas around roads due to noise and visual disturbances. In addition, due to the dense network of roads, low driver awareness of collision impacts resulting from a lack of large mammals, and high speed limits on roads outside urban areas, many birds are also likely to be heavily affected by collisions. While the higher traffic levels of major roads may mean greater avoidance by birds due to noise, collision rates may be worse on minor roads due to the intermittence of traffic. However, with urban and agricultural habitat covering large areas of Britain, much of the remaining lowland semi-natural habitat is situated alongside roads. This may mean, therefore, that some British bird populations exhibit higher abundance around roads due to habitat attraction. Overall, interspecific variation in response to roads can be expected, driven by varying habitat needs and sensitivity to disturbance.

In this study, I focus not on one or two road impact mechanisms but the cumulative effect of all, measuring variation in bird populations around roads to improve understanding of the relationships between roads and birds on a large scale. High road density and the existence of good quality, long-term bird data make Britain an ideal site in which to attempt such analysis and the novelty of this study in terms of its scale makes it an important addition to road ecology literature.

Figure 6. Area of Great Britain within 1 km of a paved road (featured in dark red), totalling 80% of the land area

Thesis structure

To assess any associations between roads and bird populations, an understanding of the associations between roads and estimation of those bird populations is necessary, although this has generally not been considered in previous road impact studies. In bird surveys, it is conceivable that traffic noise may lessen the ability of surveyors to detect birds, as has been shown for other noise sources (Pacifici et al. 2008; Ortega & Francis 2012; Koper et al. 2016). Alternatively, bird behaviour may vary around roads, causing them to be easier or harder to detect. In Chapter 2, I assess this possibility, using bird counts from the UK's Breeding Bird Survey (BBS; BTO 2020; **Figure 7**) to quantify changes in the detectability of 51 common and widespread species in relation to a composite measure of the distances and traffic levels of all roads within a 5 km radius, which I term "road exposure".

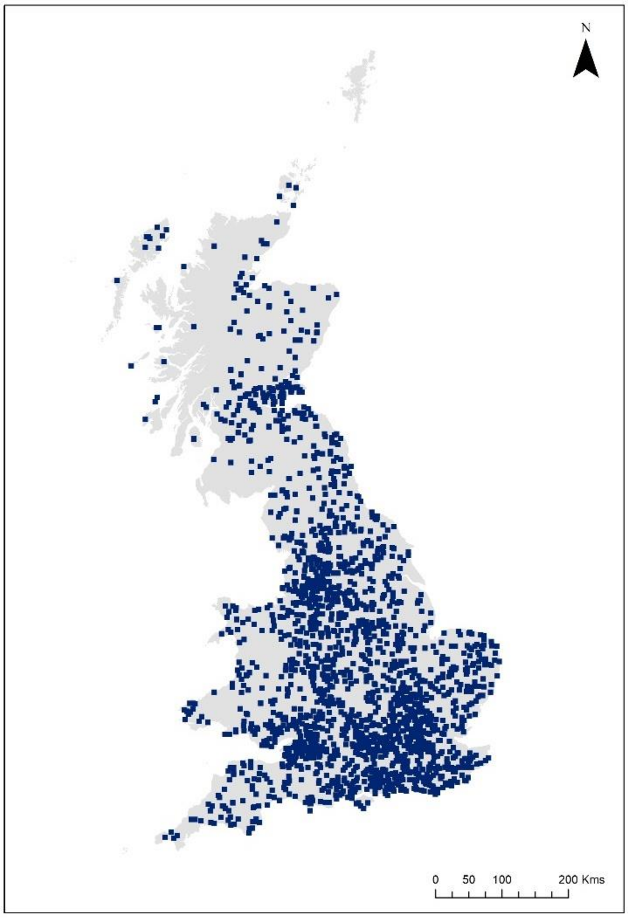


Figure 7. Location of BBS count sites (featured in dark blue) included in this study

In Chapter 3, I use these same raw bird counts to analyse bird abundance in relation to road exposure and several other covariates known, or thought, to affect bird populations, whilst incorporating the detectability models that I produced in Chapter 2. In this way, I am able to quantify the associations between road exposure and bird abundance independently from the impacts of road exposure on bird detectability. I also spatially optimise the distance over which the effect reaches for each species independently, using kernel density estimation. I find that some species exhibit higher abundance with increasing road exposure, while others exhibit reduced abundance. Within this interspecific variation, a hint of a pattern was present, with the more common, urban-dwelling species appearing to be more positively associated with roads than others.

In my final data chapter, Chapter 4, I explore this interspecific variation further using data on a broader selection of species, adding 24 less common species to the analysis. The large sample sizes that were required for creation of the detectability models produced in Chapter 2, meant that I was unable to do the same for species in this analysis, but I confirmed that this would likely affect the effect sizes only marginally, and not alter their direction. I show 77% of species to vary significantly in abundance in relation to road exposure, with negative associations having a mean effect distance of 0.7 km from a road, corresponding to over 70% of the total area of Great Britain and 41% of the total area of terrestrial protected sites. I then analyse the effect sizes for all 75 species in relation to five characteristics: mean body mass; habitat specialisation index; migratory tendency; UK national population size; and long-term national population trend. My results suggest that roads could be a source of broad-scale simplification of avian biodiversity, as has been recognised in other human-disturbed environments.

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Chapter 2: Road exposure and the detectability of birds in field surveys

This chapter was published as Cooke, S. C., Balmford, A., Johnston, A., Massimino, D., Newson, S. E. and Donald, P. F. 2019. Road exposure and the detectability of birds in field surveys. Ibis, 162(3): 885-901.

Summary

Road ecology, the study of the impacts of roads and their traffic on wildlife, including birds, is a rapidly growing field, with research showing impacts on local avian population densities up to several kilometres from a road. However, in most studies, the effects of roads on the detectability of birds by surveyors are not accounted for. This could be a significant source of error in estimates of the impacts of roads on birds and could also affect other studies of bird populations. Using road density, traffic volume and bird count data from across Great Britain, I assess the associations between roads and detectability of a range of bird species. Of 51 species analysed, the detectability of 36 was significantly associated with road exposure, in most cases inversely. Across the range of road exposure recorded for each species, the mean positive change in detectability was 52% and the mean negative change was 36%, with the strongest negative associations found in smaller-bodied species and those for which aural cues are more important in detection. These associations between road exposure and detectability could be caused by a reduction in surveyors' abilities to hear birds or by changes in birds' behaviour, making them harder or easier to detect. I suggest that future studies of the impacts of roads on populations of birds or other taxa, and other studies using survey data from road-exposed areas, should account for the potential impacts of roads on detectability.

Introduction

Population densities of many bird species have been shown to be reduced near roads (e.g., Fahrig & Rytwinski 2009; Benítez-López *et al.* 2010, Kociolek *et al.* 2011). This effect has been detected at distances of up to, and occasionally over, one kilometre from a road (Reijnen *et al.* 1996; Benítez-López *et al.* 2010, Clarke *et al.* 2013). Often, the higher the traffic volume on a road, the greater the population reduction (Reijnen *et al.* 1996; Bautista *et al.* 2004; Peris & Pescador 2004; Reijnen & Foppen 2006). Various mechanisms have been proposed or investigated to explain these phenomena. Noise pollution from vehicles has been shown to reduce local bird populations (Reijnen *et al.* 1995; McClure *et al.* 2013; Ware *et al.* 2015). This may occur via a reduction in breeding success (Halfwerk *et al.* 2011), or in habitat quality. The latter might be caused by disruption to birds' abilities to detect prey or predators (Slabbekoorn & Ripmeester 2008) or to communicate with each other (Lohr *et al.* 2003; Rheindt 2003; Leonard & Horn 2005; Habib *et al.* 2007). Light pollution can affect the navigational abilities of birds (van de Laar 2007) as well as the timing of circannual events such as migration, breeding and physiological changes (De Molenaar *et al.* 2006; Dominoni *et al.* 2013), which could in turn reduce health or breeding success. Other possible mechanisms by which roads could affect bird populations include pollution and poisoning by de-icing agents and other chemicals (Mineau & Brownlee 2005; Kociolek *et al.* 2011); direct mortality from collisions with vehicles (Hernandez 1988; Forman & Alexander 1998; Erritzoe *et al.* 2003); and habitat fragmentation (Rich *et al.* 1994; Develey & Stouffer 2001; Laurance *et al.* 2004; Tremblay & Clair 2009).

Not all bird populations, however, respond negatively to roads. Some species can show higher densities close to roads (e.g. Brotons & Herrando 2001; Peris & Pescador 2004; Palomino & Carrascal 2007), including several corvids (Dean & Milton 2003; Yamac & Kirazli 2012) and raptors (Meunier *et al.* 2000, Fahrig & Rytwinski 2009; Lambertucci *et al.* 2009). This can be due, for example, to foraging opportunities on roads, including that of road-kill (Laursen 1981; Knight & Kawashima 1993; Dean & Milton 2003). In addition, roads can be a source of grit and heat (Whitford 1985; Erritzoe *et al.* 2003; Yosef 2008) and may provide perches in the form of power lines (Knight & Kawashima 1993; Meunier *et al.* 2000, Morelli *et al.* 2014), many of which run alongside roads. Roads can also increase habitat heterogeneity (Meunier *et al.* 1999; Helldin & Seiler 2003) and roadsides can provide good nesting habitat for some species (Laursen 1981). However, individuals of these species may still be detrimentally affected by roads. House sparrows *Passer domesticus*, for example, can be found at higher densities near roads (Brotons & Herrando 2001; Peris & Pescador 2004), yet individuals can suffer reduced body condition (Liker *et al.* 2008) and a high rate of collision with vehicles (Erritzoe *et al.* 2003). It is possible, therefore, that roads act as ecological traps for some species (Reijnen & Foppen 1994 and see Schlaepfer *et al.* 2002 for more information on ecological traps). Furthermore, inflated populations of corvids and raptors around roads may increase the predation risk for other local bird species (Pescador & Peris 2007; DeGregorio *et al.* 2014).

To study the effects of roads on bird populations, bird surveys are often conducted in areas of differing distances from roads, or around roads with different traffic volumes (e.g. Clarke & Kerr 1979; Ferris 1979; Brotons & Herrando 2001; Peris & Pescador 2004; Arevalo & Newhard 2010). A potential source of error in these surveys, not often considered, is that the presence of roads may affect the abilities of surveyors to detect birds. This may cause biased estimates of population densities near roads, leading to road effects being over- or underestimated. There are several mechanisms by which this could occur, which can broadly be considered in two categories – factors acting on the surveyor, and those acting on the birds.

Road noise has a potentially large effect on a surveyor's abilities to hear birds. It may lead them to miss some birds entirely and perhaps to inaccurately estimate the location of others. For some species, such as Cetti's warbler *Cettia cetti* and common nightingale *Luscinia megarhynchos*, which are primarily detected using aural cues (S. E. Newson unpubl. data), road noise could cause especially large errors in estimations of their numbers. Noise from gas and oil infrastructure (Ortega & Francis 2012; Koper *et al.* 2016), as well as background noise (Pacifici *et al.* 2008), has already been shown to affect detectability (i.e. probability of detection) of birds, as has surveyor age (which limits older surveyors' abilities to hear some bird species) (Risely *et al.* 2013; Farmer *et al.* 2014). In contrast, the open space created by roads in forests can increase the detectability of birds, if the traffic volume on them is low (Yip *et al.* 2017).

Factors acting on the birds may work both ways too. Some changes in birds' behaviour could make them more difficult to detect near to roads. For example, some species or individuals might be warier near busy roads, as they are less able to hear approaching predators, and therefore be less visible to surveyors. Alternatively, individual birds near roads could be more habituated to anthropogenic disturbance, less wary of surveyors, and therefore more visible. Species that tend to use road-associated structures such as powerlines and fences (e.g. Knight & Kawashima 1993; Meunier *et al.* 2000, Morelli *et al.* 2014) may also be more visible, as may soaring birds using thermals generated from the heat radiated by roads (Yosef 2009). In addition, some species have been shown to sing more loudly or frequently in the presence of urban noise, including great tits *Parus major* (Slabbekoorn & Peet 2003), common blackbirds *Turdus merula* (Nemeth *et al.* 2013) and common nightingales (Brumm 2004). This adjustment may compensate for the impact of road noise on detectability by surveyors or even make the birds easier to detect.

Despite these possibilities, previous studies have largely overlooked the effects of roads exposure on detectability of birds. Some authors have accounted for the possibility of detectability being affected by road noise (McClure *et al.* 2013) while others have considered it unlikely in their studies (Rheindt 2003; Parris & Schneider 2009), but I am not aware of any empirical test of whether roads affect detectability.

This study therefore aims to assess the potential impact of roads on the detectability of birds in surveys. I use Great Britain as my study area and analyse data from the BTO/RSPB/JNCC Breeding Bird Survey (BBS). These data are collected by volunteer surveyors who are allocated, using a stratified-random protocol (BTO 2018), a 1-km grid reference square, within which they walk along two 1-km transect routes (**Figure 1**). As they walk, the surveyors count every bird they see or hear, recording the estimated distance each bird is situated from the transect (Harris *et al.* 2018). As it is unlikely that every bird along the transect will be detected, these counts are often adjusted for detectability using distance sampling in order to estimate abundance (e.g. Newson *et al.* 2008; Harris *et al.* 2018). This involves pooling the raw counts from all transect sections and estimating detectability of each species using the variation in the number of birds detected at different distances from the transect. The shape of this distribution is unaffected by the absolute number of birds (**Figure 2**). As factors such as habitat and survey date can affect the relationship between distance and detectability, they are usually incorporated into the distance sampling model as covariates (e.g. Marques & Buckland 2003; Johnston *et al.* 2014). Mean values of detectability are then estimated for each recorded combination of covariates and bird abundance is estimated accordingly (Buckland *et al.* 2004).

Via mechanisms described above, I predict that nearby roads could reduce the accuracy of both the numbers of birds detected and their estimated distances from transects in field surveys. When distance sampling is used, this could affect the shape of the distance function, leading to biased estimates of detectability and therefore also estimated bird abundance. I test this prediction by fitting distance sampling models to BBS count data for 63 common species, with site road exposure (calculated using both road density and traffic volume around each transect section) and measures of habitat and survey date incorporated. As BBS transect sections follow a variety of access routes and, mostly, do not follow roads (64% of the transect sections in this analysis did not follow any type of road along any part of them), I am able to analyse associations between roads and detectability independent of those between roads and bird abundance.

Some of the inter-specific variation in associations between road exposure and detectability may be attributable to certain species traits. For example, smaller species may be more vulnerable to predation and more likely to change their behaviour around roads if predators are at higher densities yet more difficult to detect due to road noise. Secondly, variation in species' song frequencies and amplitudes, typically correlated with body size (Ryan & Brenowitz 1985; Wiley 1991), may also affect the impacts of road noise on detectability by humans. Thirdly, detection by observers of species for which aural cues are important in surveys may be harder in areas exposed to road noise. I therefore incorporate measures of two traits - body mass and the importance of aural versus visual cues in detection of each species – in my data analysis.

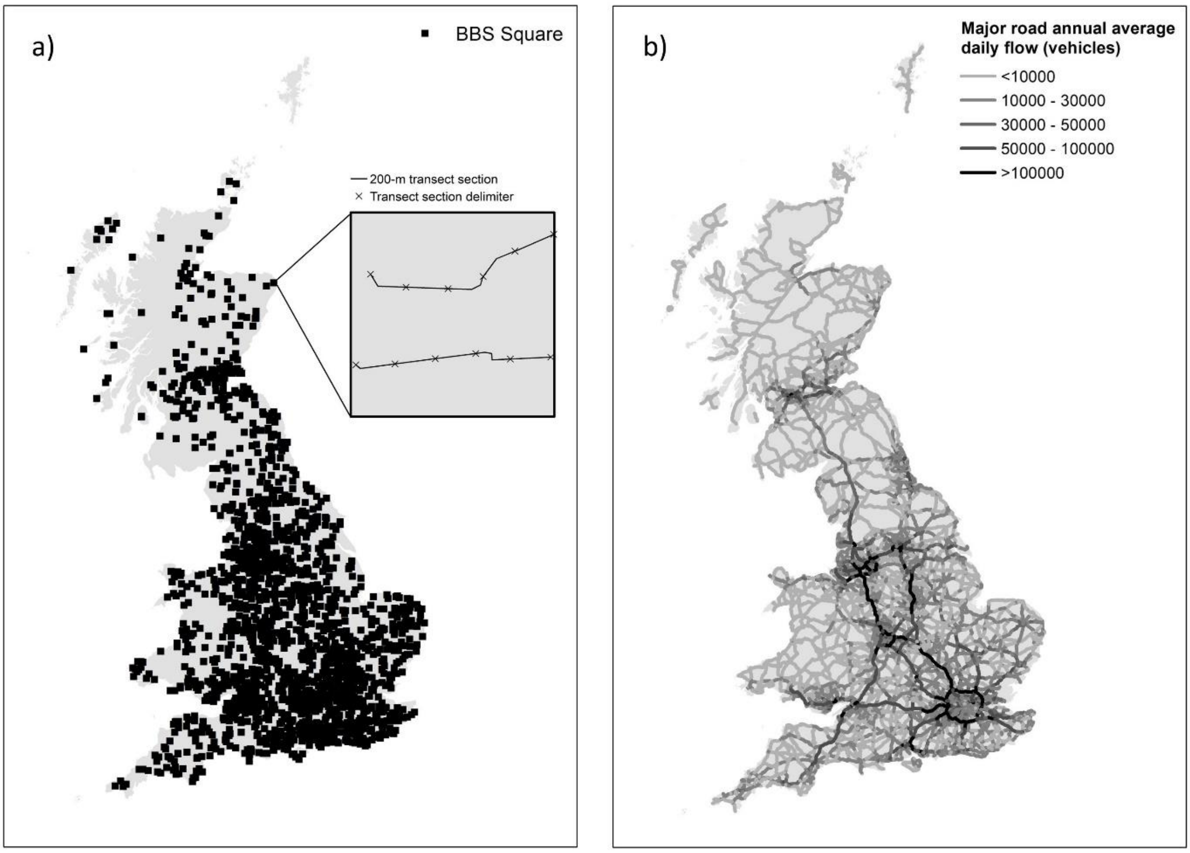
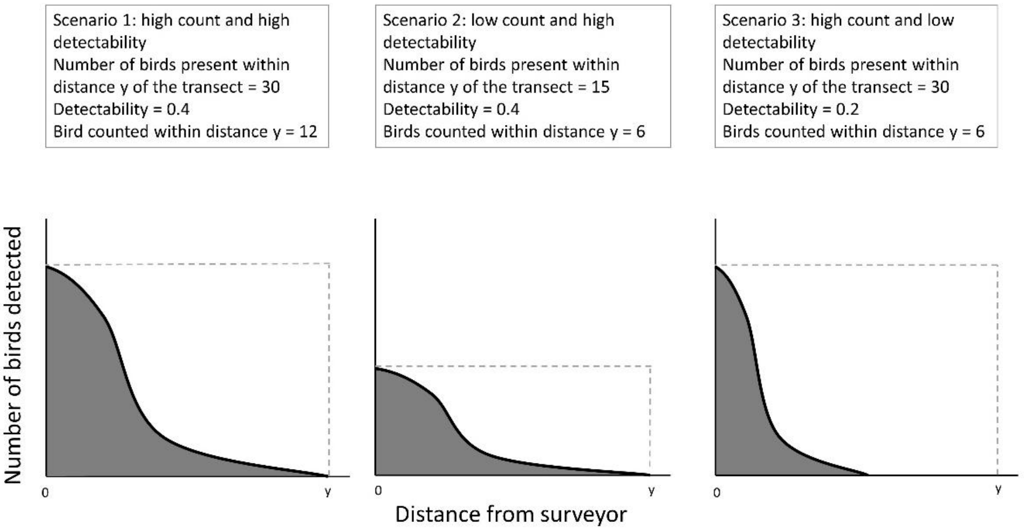


Figure 1. a) Locations of BBS squares used in this study with an inset example of the layout of a BBS square, crossed by two 1-km transects, and **b)** a map of major roads in Britain with their traffic volumes.



Scenario 1: high count and high detectability
Number of birds present within distance y of the transect = 30
Detectability = 0.4
Bird counted within distance y = 12

Scenario 2: low count and high detectability
Number of birds present within distance y of the transect = 15
Detectability = 0.4
Birds counted within distance y = 6

Scenario 3: high count and low detectability
Number of birds present within distance y of the transect = 30
Detectability = 0.2
Birds counted within distance y = 6

Figure 2. Graphical representation of bird count versus detectability. Distance sampling assumes that detectability = 1 along the transect line (where the distance from the surveyor = 0) and declines with increasing distance. The actual bird abundance is represented by the area enclosed within the dashed lines. Within this, the shaded area represents birds counted, the unshaded area represents birds missed. Detectability is calculated using the ratio of birds counted to birds missed at every distance between zero and

y. Abundance can then be estimated from the raw counts accordingly. By analysing changes in the ratios of birds counted to birds missed and using transects which predominantly do not follow along roads, I am able to quantify the associations between road exposure and detectability, independent of those between roads and bird abundance.

Methods

To analyse associations between road exposure and detectability in bird surveys, I fitted distance sampling models to raw bird count data, using estimates of both minor and major road exposure as covariates along with habitat and an approximation of survey date. I used ArcMap 10.3.1/10.5.1 (ESRI 2015; 2017) and R 3.4.4 (R Core Team 2018) for all data preparation and analyses.

Data collection and preparation

Bird counts

I obtained bird counts and habitat data from the UK Breeding Bird Survey (BBS) from BBS squares surveyed every year from 2012-2014 inclusive. Full methods for the BBS are available at BTO (2018). In brief, data are collected in two early morning visits each year (early visit: beginning of April to mid-May; late visit: mid-May to end-June). During these visits, surveyors walk two 1-km transects, each consisting of five approximately 200-m transect sections, across a 1-km grid reference square (**Figure 1**). I extracted counts for species for which the total count across the three years > 1,000, resulting in a final dataset of raw counts of 63 bird species (**Table B1**) from 19,909 200-m transect sections in 2,034 BBS squares spread widely across Britain (**Figure 1**). Full methods for count data preparation are given in **Appendix A**.

Road exposure

I obtained shapefiles for all road classes in Great Britain - motorways, A-roads, B-roads, classified unnumbered (known informally as C-roads) and unclassified roads (known informally as D-roads), as recorded in 2013. As these did not cover the Isles of Scilly, I excluded these islands from the study, but retained all other island groups. Classification of each road type is as follows. Motorways are built for fast travel over long distances. They have several lanes, can only be joined or exited at slip roads and only allow certain types of traffic. A-roads are not restricted in the same way but are also intended for fast travel and provide large-scale transport links. B-roads have varying speeds and are intended to connect different areas and to link A-roads to smaller roads. Classified unnumbered and unclassified roads are smaller roads that facilitate connection within the road network and support local traffic (DfT 2012). In 2013, Great Britain had 3,641 km of motorways, 46,749 km of A-roads, 30,217 km of B-roads and 314,853 km of classified unnumbered and unclassified roads (DfT 2017). I combined all motorways and A-roads into one shapefile, and all B-roads, classified unnumbered and unclassified roads into another. These are referred to as major and minor roads respectively.

I obtained traffic data in the form of estimated annual average daily flow (AADF) from the Department for Transport (DfT 2016). AADF is the mean number of motorised vehicles passing traffic count points in the road network each day and is estimated through a combination of manual and automated traffic counts. The mean for sampled major and minor roads in 2013 was 17,400 and 1,300 vehicles respectively (DfT 2015). Whilst AADF estimates are available for all major roads, only data for a very limited sample of minor roads are collected, so I incorporated traffic volume for major roads only. Where major road traffic data were missing, I used interpolation to estimate the AADF. I then combined the major road shapefile with the traffic data and identified and corrected any errors resulting from misalignment of the two. Further detail of this process is given in **Appendix A**. The result was a digital map of Great Britain with every major road and its traffic volume (**Figure 1**).

To estimate a measure of exposure of each 200-m BBS transect section to both major and minor roads, I used kernel density estimation (KDE). I considered major and minor roads separately, due to the lack of traffic data for the latter, and because their effects on birds might differ (e.g. Reijnen & Foppen 2006; Silva *et al.* 2012). For major roads, exposure was calculated using the locations of major roads within a 5-km radius of the midpoint of each transect section, weighted by their traffic volumes. For minor roads, the locations of roads within a 5-km radius were used without any weighting (due to the lack of traffic data available). As some road impacts are likely to act across areas surrounding roads (e.g. bird behavioural changes due to noise), but others only on or over the road surface itself (e.g. increased visibility of birds due to perches along roads) I assumed a negative exponential relationship between distance from a road and the exposure of a site to that road, with exposure being highest on the road itself. There was one estimable parameter in the negative exponential, k, which here specified the spatial scale of the relationship between road exposure and distance from the road. To optimise k for each species and road type, I ran multiple iterations of the distance sampling model (described below), using different values of k. For each species, and road type, I chose two initial values – identified in preliminary analyses as being above and below the plausible values, which I used to estimate road exposure at the midpoint of every 200-m BBS transect section. I then narrowed these ranges using a bisection, or interval-halving, method (which repeatedly bisects a range of values being tested and selects the best subrange) until k converged on an optimum value (‘k_{major}’ for major roads and ‘k_{minor}’ for minor roads). Full KDE methods are given in **Appendix A**.

Data analysis

Fitting the distance sampling models

To quantify the associations between road exposure and detectability, I fitted distance sampling models (using the R package "mrds" (Laake *et al.* 2017)) to the count data for each species, using raw count at each 200-m transect section as the response, and the following as covariates: habitat (defined as one of nine broad classes); survey visit (early or late); major road exposure; and minor road exposure. I used a half-normal detection function with no adjustment, considered appropriate as the bird count data were from only two distance bands.

Within this, detectability was estimated as:

$$g(d;\sigma) = \exp(-(d^2/2\sigma^2))$$

where:

g = detectability at distance d and for standard deviation σ

$\sigma = \exp(\beta_0 + \sum \beta_c \zeta_c))$

β_0 = intercept

β_c = coefficient

ζ_c = covariate value

A mean value of detectability (i.e. the probability of a bird within 100 m of the transect line being detected) for each species at each recorded combination of the covariates was then calculated, allowing the association with each covariate to be estimated.

From the model results, I extracted the estimated effect sizes (E), (i.e. the coefficients), and standard errors (SE) of major and minor road exposure and assessed their significance. To account for the possibility of significance through chance, as multiple species were tested, I applied Bonferroni correction, dividing the chosen critical alpha level (0.05) by the number of species that achieved model convergence (n = 51). I then calculated confidence limits using the t-value from the Student's t-distribution that corresponded to the adjusted alpha as: *upper confidence limit = E + SE*t-value; lower confidence limits = E – SE*t-value*. I accepted significance if these limits did not span zero.

For species that showed significant associations between detectability and major or minor road exposure, I calculated the relative effect size to allow comparison between species. I achieved this by dividing the effect size by the $\log_{10}$-transformed value of k_{major} or k_{minor} used for that species. This value combines the magnitude of the effect (coefficient) with the spatial area (determined by k_{major} or k_{minor}) over which the effect occurs.

To estimate the magnitude of the associations in real terms, for each species that showed a significant association between major or minor road exposure and detectability, I calculated (with the same values of k_{major} or k_{minor} used in the model) the minimum and maximum major and minor road exposure values present across all counts of that species. I then used the model for that species to predict detectability at the two major road exposure values, holding minor road exposure at zero, and vice versa. I did this for all combinations of habitat and survey visit recorded for that species. From these, I calculated the mean detectability at minimum and maximum major road exposure and the difference between them, and the same for minor road exposure.

Analysing road exposure and detectability associations with respect to species traits

To further understand interspecific patterns in the associations between road exposure and detectability, I compared the results with species-specific values for two traits in Generalized Estimating Equations (GEEs), using the R package “Zelig” (Choirat *et al*. 2018). I ran separate equations for each trait due to a high level of correlation between them (Pearson’s $r = 0.68$). The first was the mean body mass of each species, as recorded in Robinson (2005), and the second was the relative importance of visual versus aural cues in the detection of each species. I calculated this as the proportion of individual birds first detected by sight as opposed to their song or call. I used only data from 2014 for this, as this was the first year in which surveyors were asked to record mode of detection (S. E. Newson unpubl. data). By incorporating taxonomic family into the GEEs, I was able to account for any non-independence between species, resulting from phylogenetic relatedness. I performed these analyses using species that showed significant negative associations between minor roads and detectability only, as the sample sizes for the other results were much smaller.

Results

Road exposure

The models successfully converged for 51 of 63 species. Convergence most likely failed for the other 12 species as either the sample size was too small or there were not enough counts at either high or low levels of minor or major road exposure. Of the 51 successfully modelled species, 28 showed a significant negative association between minor road exposure and detectability, while seven showed a positive association (**Figure 3**). Three showed a negative association between major road exposure and detectability and three a positive association (**Figure 3**). The detectability of 15 species had no significant association with either minor or major road exposure. Full results for all species tested are given in **Tables B1-B3**.

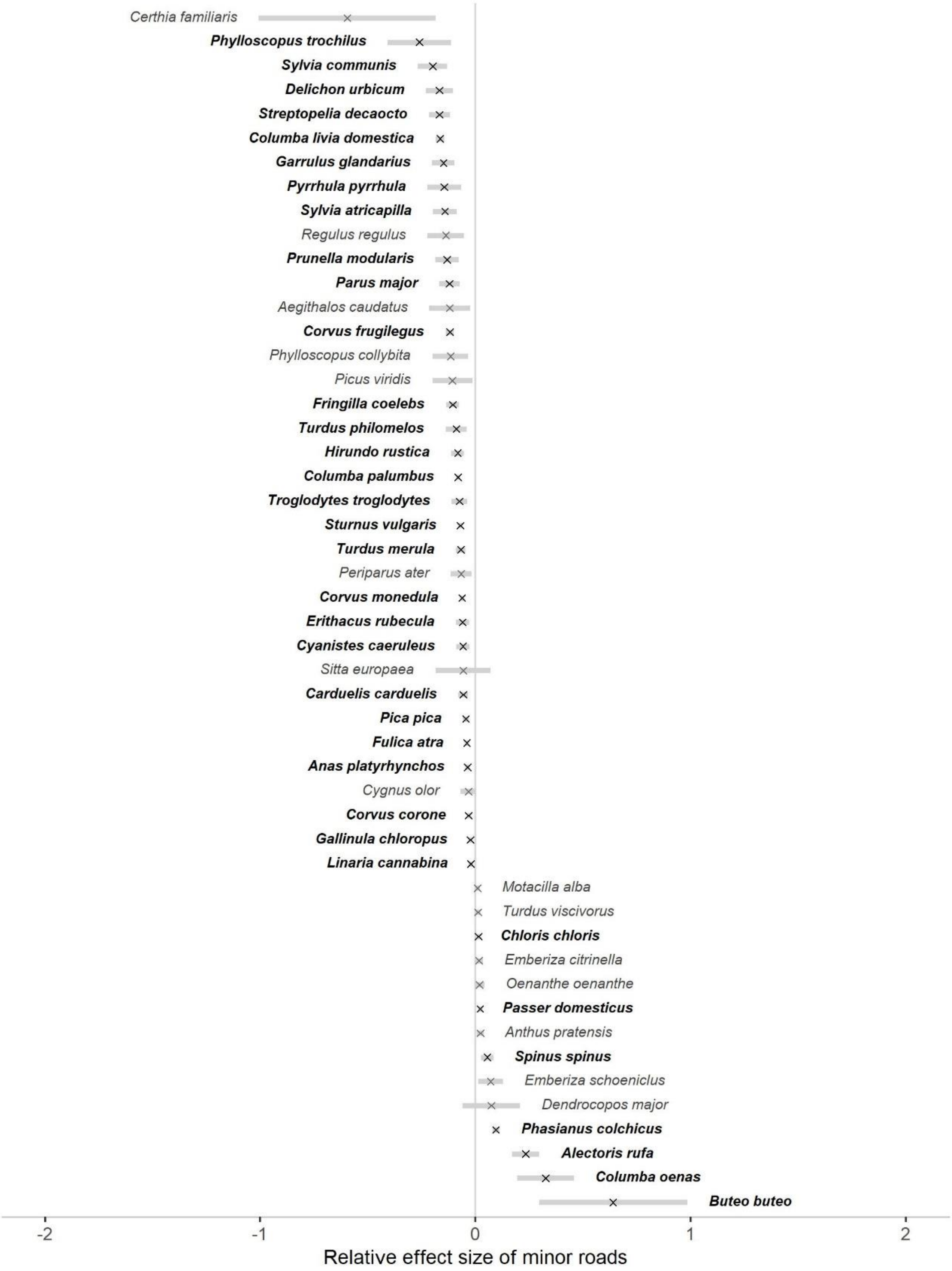

Certhia familiaris
Phylloscopus trochilus
Sylvia communis
Delichon urbicum
Streptopelia decaocto
Columba livia domestica
Garrulus glandarius
Pyrrhula pyrrhula
Sylvia atricapilla
Regulus regulus
Prunella modularis
Parus major
Aegithalos caudatus
Corvus frugilegus
Phylloscopus collybita
Picus viridis
Fringilla coelebs
Turdus philomelos
Hirundo rustica
Columba palumbus
Troglodytes troglodytes
Sturnus vulgaris
Turdus merula
Periparus ater
Corvus monedula
Erithacus rubecula
Cyanistes caeruleus
Sitta europaea
Carduelis carduelis
Pica pica
Fulica atra
Anas platyrhynchos
Cygnus olor
Corvus corone
Gallinula chloropus
Linaria cannabina
Motacilla alba
Turdus viscivorus
Chloris chloris
Emberiza citrinella
Oenanthe oenanthe
Passer domesticus
Anthus pratensis
Spinus spinus
Emberiza schoeniclus
Dendrocopos major
Phasianus colchicus
Alectoris rufa
Columba oenas
Buteo buteo
-2
-1
0
1
2
Relative effect size of minor roads

Figure 3. Association between detectability and minor and major road exposure for each species. For ease of comparison, the effect size for each species has been divided by the $\log_{10}$ of its optimum identified value of k_{minor} or k_{major} to show the relative effect size. This combines the magnitude of the effect with the spatial area over which the effect occurs. Species with significant effects (calculated with Bonferroni correction) are highlighted in black bold and 95% confidence intervals are displayed by the grey bars. Note that the effect sizes of minor roads are not directly comparable to those of major roads due to the inclusion of traffic data in the latter.

For species that showed a significant association between minor road exposure and detectability, I calculated the change in detectability as minor road exposure increased from the lowest to highest values recorded across the counts of that species. On average, an individual of a species whose detectability was negatively associated with minor road exposure was 34% less likely to be detected at maximum minor road exposure. An individual of a species whose detectability was positively associated with minor road exposure was, on average, 66% more likely to be detected at maximum minor road exposure (**Figure 4; Table B2**). I also calculated the changes in detectability across the range of major road exposure recorded for each species that showed a significant association with major road exposure. On average, at the maximum major road exposure, an individual of a species whose detectability was negatively associated with major road exposure was 50% less likely to be detected, and an individual of a species whose detectability was positively associated with major road exposure was 88% more likely to be detected (**Figure 4; Table B3**).

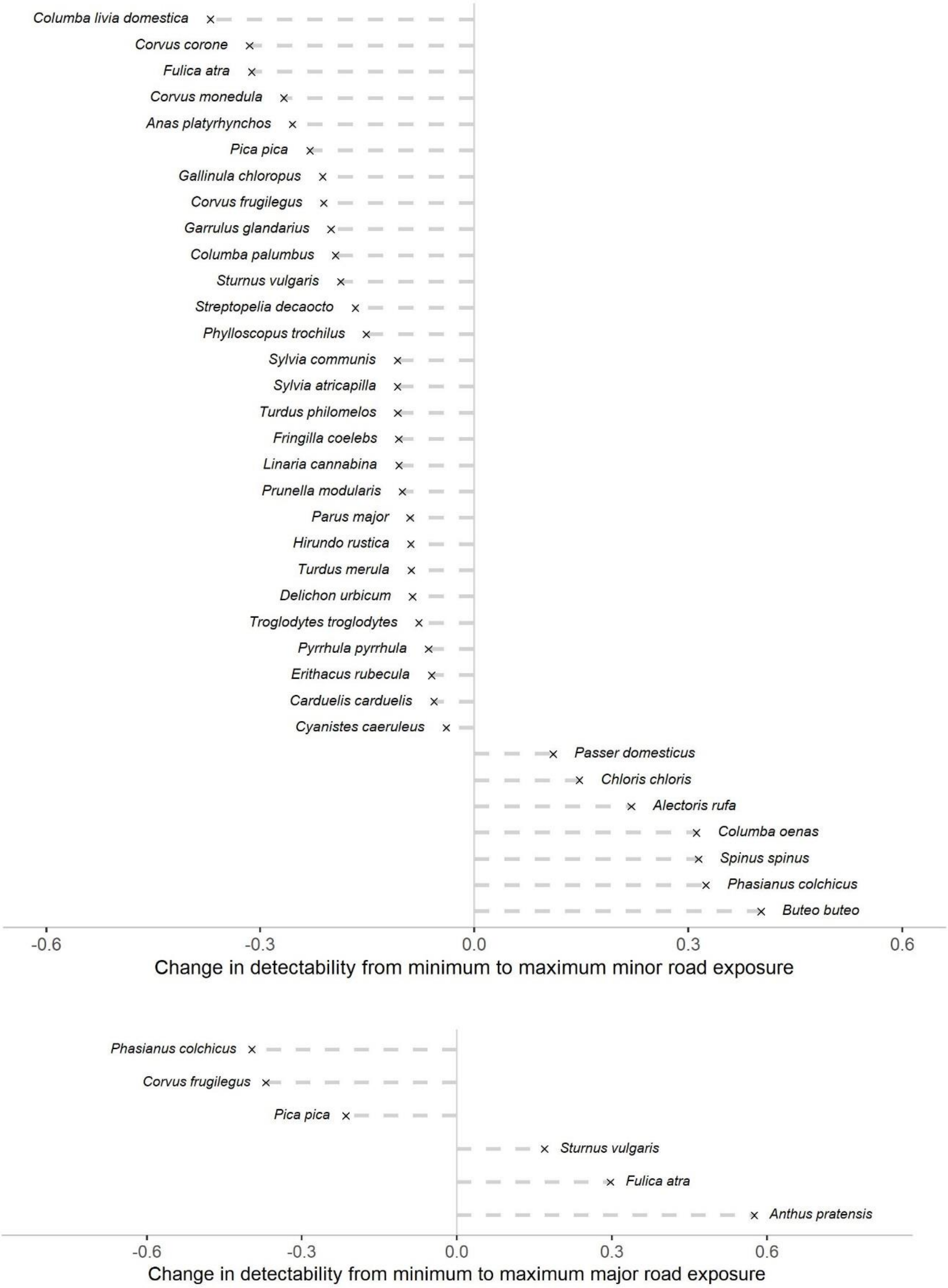


Figure 4. Change in detectability between the minimum and maximum minor road exposure values, and minimum and maximum major road exposure values, recorded for each species. Only species for which associations between minor or major road exposure and detectability were found to be significant are featured here.

The range of distances up to which the associations between minor road exposure and detectability were present for different species (defined as exposure being calculated as > 0.01 (**Figure 5; Appendix A**)) was 70 m to 2.1 km (k_{minor} values of 70.3 and 2.2 respectively). The equivalent distances for major road exposure were 110 m and 1.8 km (k_{major} values of 42.3 and 2.5 respectively).

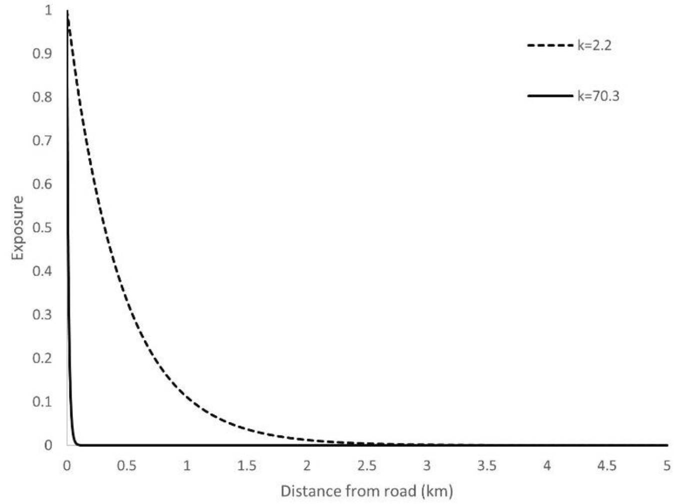


Figure 5. Relationship between distance from road and road exposure with k values of 2.2 and 70.3.

Survey visit and habitat

Survey visit was significantly associated with detectability in 15 of the 51 species tested and 26 species showed significant differences in detectability across different habitat types. The full results for these two covariates are given in **Table B4**.

Species traits

I examined whether species with certain characteristics had different magnitudes of negative associations between minor road exposure and detectability. I found road exposure to be more negatively associated with the detectability of smaller birds and those more likely to be detected aurally (body mass: $P = 0.004$; detection type: $P = 0.002$; **Figure 6**). The mean body mass and the proportion of birds detected visually for each species are given **Table B5**.

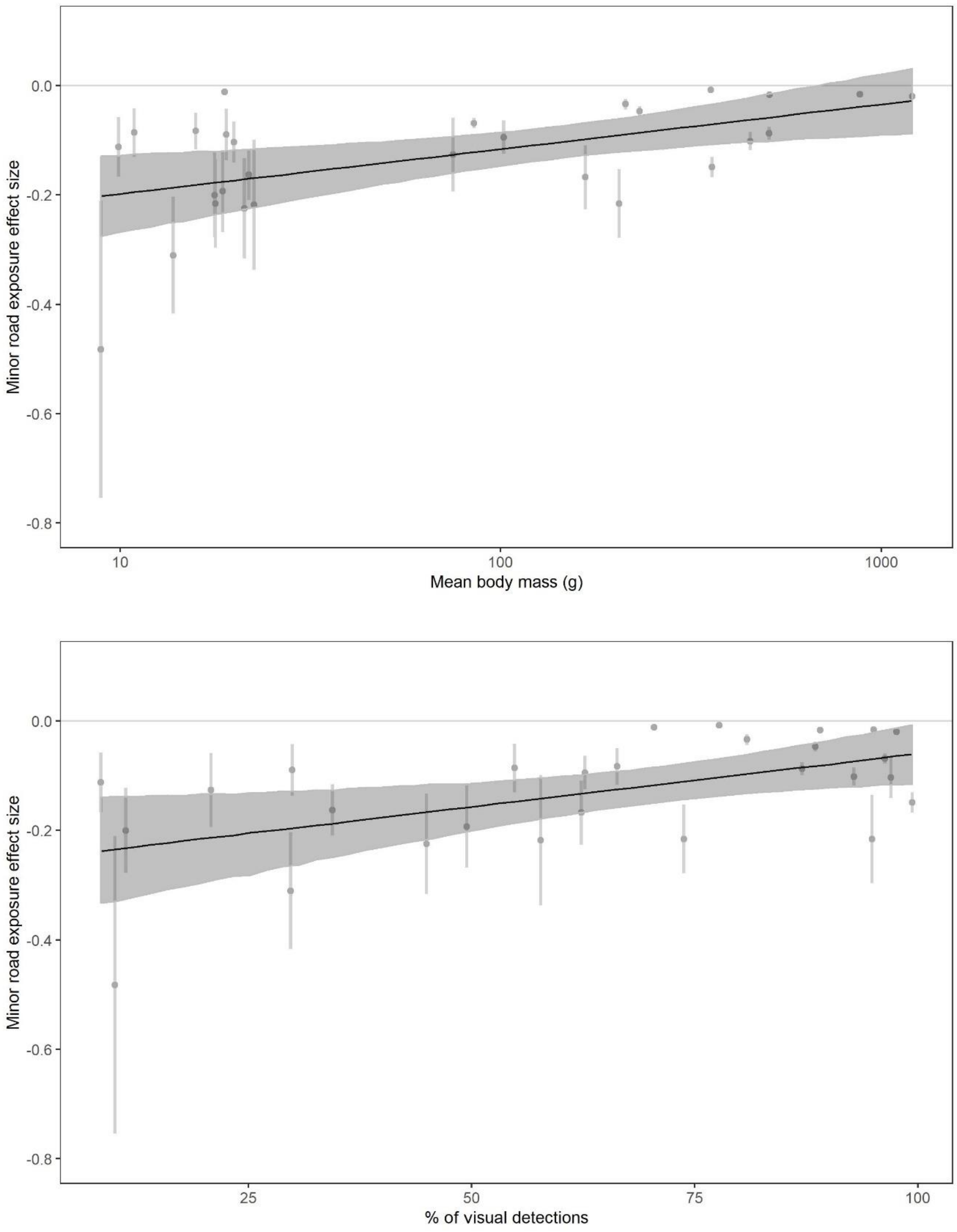


Figure 6. The relationships between effect size and both $\log_{10}$-transformed mean body mass and percentage of visual detections for species that showed a negative effect of minor road exposure on detectability. Black lines represent the relationships between those effect sizes and each trait. 95% prediction intervals around each trait relationships (calculated using the simulation function “sim” in the R package “Zelig”) are shown by the shaded grey bars. Grey dots indicate effect size estimates for each species, while the confidence intervals around each effect size estimate are shown by grey lines.

Discussion

Of 51 species, 36 (71%) showed significant associations between either major or minor road exposure and detectability, the majority of which were negative. For each species, I identified the range of road exposure values recorded at the transect sections the species was detected from, and estimated detection across these ranges. Considering both road types, the mean decrease in detectability across the range of road exposure recorded for each species was 36% and the mean increase was 72%. While the former could lead to overestimation of negative impacts of roads on birds, the latter could cause underestimation.

Considering minor roads, 35 of 51 (69%) species showed a significant association between exposure and detectability, 28 (80%) of which were negative. For species with significant results, relative effect sizes were usually similar within higher taxa, particularly Paridae, Turdidae, Sylvidae, and Phylloscopidae, Rallidae, Hirundinidae and Corvidae, all groups that showed negative associations between minor road exposure and detectability. These negative associations could be, for example, because of road noise reducing the ability of surveyors to detect birds (as seen with gas and oil infrastructure noise (Ortega & Francis 2012; Koper *et al.* 2016)), or due to birds being warier near roads due to collision risk or their reduced ability to detect predators aurally, or a combination. Some bird species have been shown previously to have increased fright or flight and stress responses in the presence of anthropogenic noise (Ortega 2012) and others may change their behaviour to avoid vehicle collisions (Coffin 2007).

Hypotheses for some of the positive associations between minor road exposure and detectability can also be made – for example ring-necked pheasants *Phasianus colchicus* and red-legged partridges *Alectoris rufa* often walk along rural roads to collect grit and are perhaps more visible there than when in fields or woodland where they may be concealed by emergent vegetation. However, I believe the positive result for Eurasian siskin *Spinus spinus* may be a Type I error as its sample size was one of the smallest. In addition, if minor road exposure for all species is calculated using a constant value of $k_{minor} = 1$, Eurasian siskin has the lowest percentage of counts in the upper quartile of the exposure values recorded across all species, implying that there are very few data to support the detected association. Excluding Eurasian siskin, the mean increase in detectability with minor road exposure fell to 55%.

Only 6 of 51 (12%) species showed significant associations between major road exposure and detectability, half of which were negative. It is likely that my analysis underestimated the associations with major road exposure due to there being a limited number of counts in areas of high major road exposure (while 9344 squares were within 100 m of a minor road, only 1813 were within 100 m of a major road). Due to the stratified-random selection process of BBS squares (BTO 2018), surveyors have some choice over where they survey, and it is likely that they avoid surveying next to busy major roads. Of the six significant results for major roads, I consider the result for meadow pipit *Anthus pratensis* to be unreliable. Like Eurasian siskin with minor roads, it had a very low proportion of counts in the upper quartile of major road exposure values recorded across all species (when exposure was calculated using $k_{major} = 1$ for all species). Excluding meadow pipit brought the mean increase in detectability with major roads down to 42%. With both Eurasian siskin and meadow pipit removed, mean increase in detectability for both road types fell to 52%.

I found associations between detectability and road exposure to be present up to 2.1 km from a road. In general, where the association was stronger, the distance over which the association was present was small (i.e. the identified optimum value of k_{minor} or k_{major} was high). This could be explained by changes in the dominant mechanisms by which road exposure affects detectability across different spatial scales, or it could simply be that effects acting over smaller distances are only detectable when of greater magnitude.

For species that showed a significant negative association between minor road exposure and detectability, effect sizes were greater in those with smaller body masses and in species more likely to be detected aurally. However, as these two traits are correlated quite highly, it is difficult to determine which is the most important factor. Smaller species may be more vulnerable to predation and therefore more likely to adopt cautious behaviours around roads due to their reduced ability to hear predators. This could make them more difficult to detect than larger species. Alternatively, or additionally, differences in typical song frequencies and amplitudes of larger versus smaller species (Ryan & Brenowitz 1985; Wiley 1991) may lead to differences in the effect sizes of minor roads on detectability. Regarding the result for detection type, road noise is a likely mechanism behind the stronger negative associations between road exposure and detectability in species for which aural cues are more important in detection.

This study was limited by the need for large sample sizes and wide data spread in order to fit the distance sampling models. I was therefore only able to consider detectability of common bird species. In addition, due to the limited number of BBS squares near to major roads, my power of analysis for major roads was much less strong than for minor roads. I was also unable to incorporate interaction terms to test, for example, the impacts of different habitats on the association between road exposure and detectability. In addition, I was unable to analyse separately detections that were first recorded aurally and those first recorded visually, as mode of detection was only recorded in 2014. It may be that the two detection types are affected differently within some species, which I was unable to test. Nevertheless, my results demonstrate the potential importance of accounting for the associations between roads and detectability of birds, and perhaps other taxa, in field surveys. Previous studies may have incorrectly estimated the impacts of roads on bird populations if they did not account for road effects on surveyors' abilities to detect birds. Some studies of road impacts on birds have been carried out using methods which may be less affected by detectability influences, such as mist-netting (e.g. Reijnen *et al.* 1995; McClure *et al.* 2017), or by undertaking surveys during pauses in artificially-created road noise (e.g. McClure *et al.* 2013). Road noise has also been shown to affect the health of individual birds and breeding success (e.g. Halfwerk *et al.* 2011; Crino *et al.* 2013). My finding of significant associations between road exposure and detectability does not, therefore, imply that current general thinking on the effects of roads on birds is incorrect, but rather that, in many studies, effect sizes could have been substantially over- or underestimated.

Given that many countries have very high densities of roads (e.g. 80% of Great Britain falls within one kilometre of a road (S. C. Cooke, unpubl. data)), effects of roads on detectability may also affect other studies involving bird population estimates. Although BBS squares are found in low density around major roads, they are spatially biased towards areas of high minor road density (S. C. Cooke, unpubl. data). This may increase the likelihood that population trends calculated from them are biased by the impacts of roads on detectability.

I therefore suggest that future studies involving bird surveys, and possibly those of other taxa, in areas exposed to roads recognise, and correct for, the potential impacts of road exposure on detectability. As high-resolution traffic data are not readily available everywhere, and I found major road exposure weighted by traffic intensity at my analysed BBS transect sections to be strongly correlated with unweighted major road exposure (Pearson's r of 0.80, calculated using $k_{major} = 1$), the latter could be used as an approximation. Either way, I recommend the method of KDE to produce road exposure values as opposed to, for example, simply measuring the distance to the nearest road or recording noise levels at survey sites. I showed detectability of some species that are primarily detected using visual cues to be affected by road exposure, as well as those for which aural cues are more important. This indicates that behavioural changes, which could be caused purely by the presence of a road, may be a mechanism of these impacts as well as noise. KDE can capture variation in road exposure better than other methods, as it includes all roads in the surrounding area, and may account for a wider range of impact mechanisms on detectability of birds and other taxa.

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Chapter 3: Variation in abundances of common bird species associated with roads

This chapter was published as Cooke, S. C., Balmford, A., Johnston, A., Newson, S. E. and Donald, P. F. 2020. Variation in abundances of common bird species associated with roads. Journal of Applied Ecology, 57(7): 1271-1282.

Summary

The global road network, currently over 45 million lane-km in length, is expected to reach 70 million lane-km by 2050, while the number of vehicles utilising it is expected to double. Roads have been shown to affect a range of wildlife, including birds, but most studies have been relatively small scale. I use data from across Great Britain to analyse the associations between roads and the spatial distributions of bird populations. I model counts of 51 common and widespread species from the U.K. Breeding Bird Survey in relation to road exposure, which I calculated for each count site using the density, distance and traffic volume of all roads within a 5 km radius. In these models, I incorporate other factors known to affect bird populations, including agricultural intensity, human population, habitat and climate. Importantly, I also account for differences in detectability of birds near to roads.

The abundances of 30 species were strongly significantly related to exposure to either major or minor roads. Species were generally in higher abundances with increasing exposure to minor roads (20/28). In contrast, most significant associations between major road exposure and bird abundance were negative (7/8). For species with significant effects of road exposure, I assessed how estimated abundance changed across the central 50% of road exposure experienced for each species. The mean decrease in abundance was 19% and the mean increase was 47%. These changes in bird abundance were up to half as large as those associated with increasing agricultural intensity, a factor often cited as a major cause of bird population changes.

My research shows many species to vary in abundance with increasing road exposure. This suggests that roads may modify bird populations on a national scale and that their potential as drivers of biodiversity change should not be overlooked. My work highlights the need for appropriate mitigation of roads, particularly in areas important for avian biodiversity. This could include efforts to reduce impacts of road noise and/or collisions, such as reduced speed limits or quieter road surfaces in sensitive areas.

Introduction

The global road network is estimated to be over 45 million lane-km in length (Dulac 2013) and, in many places, is still expanding. Twenty-five million lane-km are expected to be added to the paved road network by 2050 (Dulac 2013), and the number of vehicles is estimated to reach up to 2.8 billion (WEC 2011; Meyer et al. 2012), more than double the 2015 figure (OICA 2015). Much of this expansion is expected in emerging economies, such as China and India (van der Ree et al. 2015; Dulac 2013), which still have areas with comparatively low road density. Many nations with longer histories of industrialisation are already so saturated with roads that areas still distant from them are few and often exist as small patches (Ibisch et al. 2016; Science for Environmental Policy 2017). Great Britain alone contains nearly 400,000 km of paved roads (DfT 2018), enough to encircle the globe ten times.

The impacts of roads on wildlife have been the subject of much research and there is a wealth of published studies demonstrating animal populations to be reduced near roads (e.g. Fahrig & Rytwinski 2009; Benítez-López et al. 2010). The road-effect zone - the area over which the ecological effects of roads extend (Forman & Deblinger 2000) - can be up to several kilometres wide (Reijnen et al. 1996; Benítez-López et al. 2010; Clarke et al. 2013), encompassing large portions of many countries. For example, > 80% of Great Britain falls within 1 km of a paved road (Cooke, S. C., unpubl. data.). In addition, areas with lower road densities are typically those less hospitable to humans, such as upland regions, which are also often areas of naturally lower species richness (Rahbek 1995).

Birds are relatively well represented in road ecology literature. Many studies have shown bird populations to be reduced around roads (e.g. Fahrig & Rytwinski 2009; Benítez-López et al. 2010; Kociolek et al. 2011), with stronger effects seen near those with heavier traffic volume (e.g. Reijnen et al. 1996; Bautista et al. 2004; Peris & Pescador 2004; Reijnen & Foppen 2006). These reductions can be severe: roads in the Netherlands, for example, have been estimated to cause reductions in national bird populations of 2-20% (Reijnen & Foppen 2006). There are several processes by which these effects may occur, including the following. Traffic noise is widely regarded as an important mechanism underlying changes in bird populations around roads (Reijnen et al. 1995; Rheindt 2003) and has been shown to cause abundance declines even when other potential mechanisms are removed (McClure et al. 2013; Ware et al. 2015). Noise can disrupt the ability of birds to communicate (Lohr et al. 2003; Rheindt 2003; Habib et al. 2006; Leonard & Horn 2012) and to detect prey or predators (Slabbekoorn & Ripmeester 2008). This may reduce breeding success (Halfwerk et al. 2011) and body condition (Ware et al. 2015) or cause avoidance of the area by individuals (McClure et al. 2013). Birds also suffer direct mortality through collisions (Hernandez 1988; Forman & Alexander 1998; Erritzoe et al. 2003) and this may reduce abundance near roads (Jack et al. 2015).

Light pollution, known to affect the timing of circannual events such as breeding and physiological changes (De Molenaar et al. 2006; Dominoni et al. 2013), may also affect populations around roads (De Molenaar et al. 2000; Day 2003; Kociolek et al. 2011). Other processes by which roads may negatively affect birds include chemical pollution (Mineau & Brownlee 2005; Kociolek et al. 2011), which may reduce breeding success (Fry 1995) and bird health (Llacuna et al. 1993); and habitat fragmentation, due to avoidance of edge habitat around roads, or reluctance to cross the road itself (Rich et al. 1994; Develey & Stouffer 2001; Laurance et al. 2004; Tremblay & St. Clair 2009).

While many bird populations may be reduced around roads, others can show the opposite effect, for example house sparrows *Passer domesticus* (Brotons & Herrando 2001; Peris & Pescador 2004), and some raptors and corvids (Meunier et al. 2000; Dean & Milton 2003; Fahrig & Rytwinski 2009; Lambertucci et al. 2009; Yamac & Kirazli 2012). For some species, roads provide food (in the form of road-kill) (Laursen 1981; Knight & Kawashima 1993; Dean & Milton 2003), grit and heat (Whitford 1985; Erritzoe et al. 2003; Yosef 2009). Powerlines, many of which run alongside roads, can also provide perches (Knight & Kawashima 1993; Meunier et al. 2000; Morelli et al. 2014). In addition, roads can increase habitat heterogeneity, due to creation of varied edge habitat along roadsides (Meunier et al. 1999; Helldin & Seiler 2003), and the co-location of roads with hedges, ditches and other microhabitat features means that roadsides can offer good foraging or nesting habitats (Laursen 1981). However, it is possible that birds attracted to roads suffer ill-effects regardless, by direct mortality or via sub-lethal impacts on health and breeding success. House sparrows, for example, suffer high levels of collisions with vehicles (Erritzoe et al. 2003) and reduced body condition closer to roads (Liker et al. 2008). Barn owls *Tyto alba* are also frequently involved in collisions, and it has been suggested that this can affect population numbers (Massemin & Zorn 1998; Borda-de-Água et al. 2014). There is potential, therefore, for roads to act as ecological traps for some species (Reijnen & Foppen 1994; Schlaepfer et al. 2002).

To date, however, most research on the impacts of roads on birds has been relatively small scale. To investigate how bird abundance may vary in relation to roads on a broader scale, I analyse bird populations across Great Britain with respect to road exposure, which I calculate as a function of road density and traffic volume. Many bird populations in Great Britain have declined substantially in the past half-century (DEFRA 2018), declines that have been linked to factors including: changes in agricultural practises and land management; habitat loss and degradation; and climate change (Eglington & Pearce-Higgins 2012; Burns et al. 2016; Hayhow et al. 2017; Oliver et al. 2017). However, as traffic volume since 1970 has increased by > 160% (DfT 2019), roads may also have contributed to these declines. In considering this in my analyses, I also account for the impacts of roads on detectability (Cooke et al. 2019), a factor important, yet often overlooked, in studies of this nature.

Methods

My analytical framework involved modelling spatially explicit bird count data in relation to the proximity and traffic volume of nearby roads. I also incorporated other predictors known, or thought likely, to influence bird counts, including the impacts of roads on detectability (Cooke et al. 2019). I used all areas and island groups of England, Scotland and Wales, except for the Isles of Scilly which I excluded due to limited traffic data. I used ArcMap 10.3.1/10.5.1 (ESRI 2015; 2017) and R 3.4.4 (R Core Team 2018) for all data preparation and analyses.

Data collation and preparation

Bird counts

I obtained bird count data from an extensive survey - the UK Breeding Bird Survey (BBS) – in which two 1-km transects, each divided into five 200-m transect sections, spanning a 1-km square, are surveyed by experienced volunteers (**Figure 1**). Unlike the North American BBS (USGS 2019), these transects mostly do not run alongside roads (64% of the transect sections used in this analysis did not follow a paved road along any part of them). For my analyses, I extracted counts from BBS squares that had been surveyed each year from 2012-2014 inclusive. These transects are surveyed in two visits each year, early and late in the breeding season. I chose to use counts from the early visit for resident species and the late visit for migrant species as these tend to contain the highest counts for each. I also extracted the dominant habitat type for each transect section.

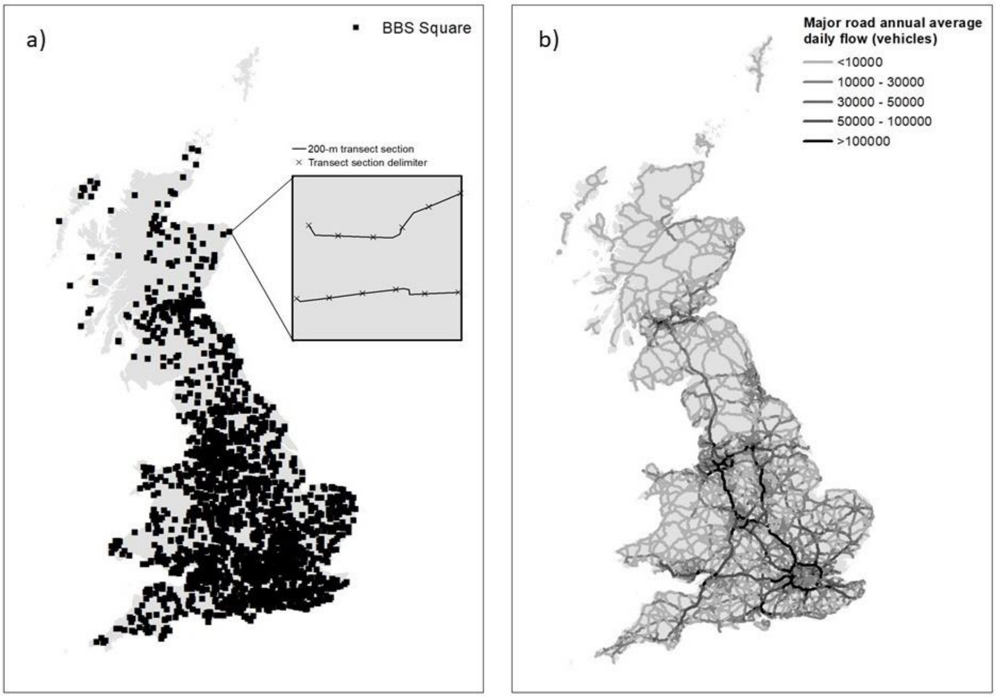


Figure 1. a) Locations of BBS squares used in this study with an inset example of the layout of a BBS square, crossed by two 1-km transects, and **b)** a map of major roads in Britain with their traffic volumes. First published in Cooke et al. (2019).

Detectability is important to consider when analysing bird survey results as it is unlikely that all birds around a transect will be recorded (e.g. Harris et al. 2018; Newson et al. 2008). Additionally, roads may impact both bird abundance and detectability, and these two effects are confounded in raw bird counts. I therefore explicitly estimated detectability of birds in relation to roads, in order to account for this effect when analysing the counts. For 51 widespread and common species, I pooled all counts from two distance bands (0-25 m and 25-100 m) over the three years and used the R package "mrds" (Laake et al. 2017) to produce distance sampling models that estimated detectability in relation to roads as well as habitat. For more information on creation of these models see Cooke et al. (2019). If any road type (major or minor – see 'road exposure' section below for definitions) was not significantly associated with variation in detectability of a species, I reproduced that species' distance sampling model excluding the covariate relating to that road type (a summary of the covariates included the distance sampling model for each species is provided in **Table C1**).

For each species, I then calculated the mean bird count in each 200-m transect section, summing across distance bands and averaging across years, to use as the response variable in my analyses. My final dataset contained counts from 19,709 200-m transect sections in 2,033 BBS squares. I then used my distance sampling models to produce species- and transect-specific estimates of detectability. I produced these estimates to use as offsets in my analyses, so that I could account for inaccuracies in the bird counts due to variation in detection. By incorporating detectability estimates rather than using the detectability models to correct the raw bird counts, I allowed estimation of undetected birds in sites where the count was zero. For more detail on the survey methodology and my calculation of mean bird counts see **Appendix A**.

Road exposure

For the midpoint of each 200-m BBS transect section, I estimated the exposure of that point to roads - hereafter road exposure. This was calculated from the density, distance and traffic volume of roads within a 5 km radius, using the following methods. I obtained shapefiles of all road classes used in Great Britain - motorways, A-roads, B-roads, classified unnumbered (informally known as C-roads) and unclassified roads (informally known as D-roads), as recorded in 2013. I combined all motorways and A-roads into one major road shapefile, and all B-roads, classified unnumbered and unclassified roads into a minor road shapefile.

I then obtained major road traffic flow data for 2012-2014 from the Department for Transport’s (DfT) Traffic Counts website (DfT 2016). These were in the form of estimated annual average daily flow (AADF), calculated as the mean number of motorised vehicles passing specific points (traffic count points) in the road network per day. These estimates are obtained through both manual and automated traffic counts. In 2013, the estimated mean daily traffic flow for sampled major and minor roads, as reported by the DfT, was 17,400 and 1,300 vehicles respectively (DfT 2015). I was not, however, able to incorporate traffic flow data for minor roads as the DfT collects only a limited sample of data for these. I then calculated the mean AADF across the three years and combined these data with the major road shapefile (**Figure 1; Appendix A**).

I used kernel density estimation (KDE) to estimate the exposure of the midpoint of each 200-m BBS transect section to both major and minor roads within a 5-km radius. I considered major and minor roads separately because of the lack of traffic data for the latter, and because their effects on birds may differ (e.g. Reijnen & Foppen 2006; Silva et al. 2012). Within the KDE, to estimate major road exposure, I used both the locations of all roads (by placing points every 100 m along every road and calculating their distance from the transect section midpoint) within the radius and their traffic volumes. To estimate minor road exposure, I used only the former. As some road impacts are likely to act on birds in areas around roads (e.g. noise disturbance and habitat effects), but others only on or over the road surface itself (e.g. collisions and perching opportunities), I assumed a negative exponential relationship between distance from a road and the exposure of a site to that road, with road exposure being highest on the road itself and declining with distance. There is one estimable parameter in the negative exponential, k, which here determined the spatial scale of this relationship i.e. the distance over which any relationship between roads and bird abundance acts. For each species, and road type, I chose two values of k – identified in preliminary analyses as being above and below the range of plausible values, which I used to estimate road exposure at the midpoint of every 200-m BBS transect section. I then ran multiple iterations of a Generalized Additive Mixed Model (GAMM; described below), narrowing these ranges using a bisection, or interval-halving, method. This repeatedly bisected the range of k values being tested, selecting the best subrange each time. This led k to converge on an optimum value (‘k_{major}’ for major roads and ‘k_{minor}’ for minor roads). If no optimum value for k_{major} or k_{major} could be identified for a species, the corresponding road covariate – major or minor road exposure – was excluded from the analyses for that species. Full KDE methods are given in **Appendix A**.

Other covariates

To account for other factors that I expected to affect bird abundance, I incorporated human population density, temperature and rainfall data for the midpoint of each transect section as covariates, as well as the following estimations for 5-km buffers around each midpoint: tree cover density, proportion of arable land (as a proxy for yield) and largest field area. Only two pairs of covariates had a Pearson's $r > 0.5$: temperature and precipitation ($r = -0.67$); proportion of arable land and largest field area ($r = 0.68$). I also checked the correlation between human population density and both major and minor road exposure across all species, which returned a mean Pearson's r of 0.22 and 0.54 respectively. For information on calculation of these data see **Appendix A**.

Data analysis

I analysed the associations between both major and minor road exposure and abundance of each bird species using a Poisson family GAMM, with the R package "mgcv" (Wood 2017). I ran models for each species separately, using mean bird count for each 200-m transect section as the response variable and the following as covariates: dominant habitat (as recorded in the BBS); major road exposure; minor road exposure; human population density; temperature; rainfall; tree cover density; proportion of arable land; and largest field area. From initial inspection of the associations between proportion of arable land and bird count, I fitted proportion of arable land quadratically rather than linearly for five bird species (**Table C1**). I incorporated estimated detectability at each transect section as an offset and BBS square as a random effect (to account for the non-independence of counts among each square's ten 200-m transect sections). I included a spatial smooth to account for large-scale variation in bird abundance not associated with the other covariates. The spatial smooth included Easting and Northing as a joint tensor product smooth with a maximum of 50 degrees of freedom (selected with preliminary analyses).

I assessed the significance of the results of each species by extracting the estimated effects (E), (i.e. the coefficients), and standard errors (SE) of major and minor road exposure. As I tested multiple species, I applied Bonferroni correction, dividing my chosen critical alpha level (0.05) by the number of species tested (n = 51). I then used the *t*-value from the Student's *t*-distribution that corresponded with this new alpha to calculate confidence limits as: *upper confidence limit = E + SE*t-value*; *lower confidence limits = E – SE*t-value*. I accepted significance if these limits did not span zero.

Where major or minor road exposure was significantly associated with bird abundance, I calculated the relative effect size to allow easier comparison between species. I did this by dividing the coefficient by the $\log_{10}$-transformed value of k_{major} or k_{minor} used for that species. This value combines the magnitude of the effect (coefficient) with the spatial area (determined by k_{major} or k_{minor}) over which the effect occurs.

To estimate the magnitude of associations between roads and bird abundance in real terms, I predicted, using the model for each species, bird abundance across the ranges of major and minor road exposure values recorded at transects from which that species was observed. I did this separately for the two road exposure types, holding the value for the other at zero and all other continuous covariates at the mean values of the counts of that species. For the two categorical covariates, I used the BBS square with the smallest absolute coefficient and the habitat with the largest number of counts.

In order to compare the scales of these changes with those associated with the proportion of arable land - which was not distance-optimised as the road exposure covariates were - I reran my models using a coarser measure of road exposure. This was simply the number of points placed every 100 m along the roads within a 5 km buffer. I then estimated and compared the changes in estimated bird abundance across the interquartile ranges (from the lower (0.25) to upper (0.75) quartiles) of all three covariates.

Results

Of the 51 species tested, 30 showed significant associations between either major or minor road exposure and abundance. In general, abundance was lower with increasing major road exposure and higher with increasing minor road exposure. The association directions between each species and both road types are given in **Table 1**. Considering both road types together, the mean decrease in estimated abundance across the interquartile range of road exposure was 19% and mean increase 47%.

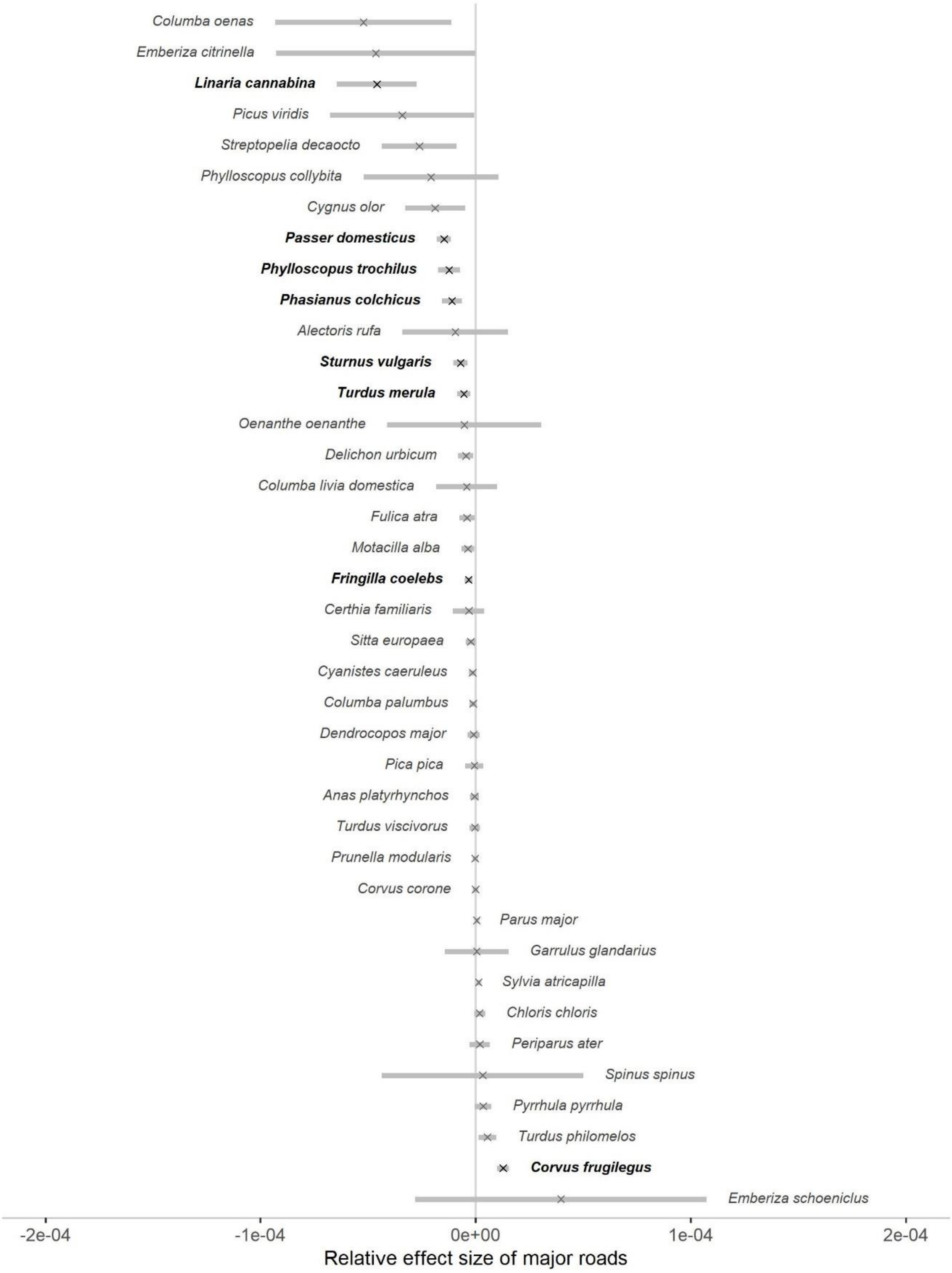
Table 1. Associations shown by all species between bird abundance and major and minor road exposure

		MAJOR ROAD EXPOSURE		
		Significant positive association	**No significant association**	**Significant negative association**
MINOR ROAD EXPOSURE	**Significant positive association**	*Corvus frugilegus*	*Cyanistes caeruleus* *Streptopelia decaocto* *Prunella modularis* *Columba livia domestica* *Carduelis carduelis* *Chloris chloris* *Parus major* *Delichon urbicum* *Corvus monedula* *Erithacus rubecula* *Hirundo rustica* *Turdus philomelos* *Columba palumbus* *Troglodytes troglodytes* *Emberiza citrinella*	*Turdus merula* *Fringilla coelebs* *Passer domesticus* *Sturnus vulgaris*

	No significant association		21 species (see **Table C1**)	*Linaria cannabina* *Phylloscopus trochilus*
	Significant negative association		*Buteo buteo* *Sylvia atricapilla* *Fulica atra* *Regulus regulus* *Anas platyrhynchos* *Anthus pratensis* *Emberiza schoeniclus*	*Phasianus colchicus*

The abundance of eight species differed significantly with major road exposure (**Figure 2**). All except rook *Corvus frugilegus* showed reduced abundance with increased major road exposure. From the 0.25 to 0.75 quartile of major road exposure values calculated for each species with a significant negative association, the mean decrease in estimated bird abundance was 2%, with a maximum decrease of 11%. The increase in abundance shown by rooks was also 2% (**Figure 3**). These estimated effects are likely underestimated due to insufficient data spread (see Discussion).

Regarding exposure to minor roads, eight species showed significantly lower abundance with higher minor road exposure, while 20 species had significantly higher abundance (**Figure 2**). Note that the relative effect sizes of major and minor roads are not directly comparable as the inclusion of traffic data in the former means the two road exposure types are on very different scales. For species with significant negative associations the mean decrease in estimated bird abundance from the 0.25 to 0.75 quartile of minor road exposure values was 34%, with a maximum decrease of 57%. For species with significant positive associations the mean increase was 49%, with a maximum increase of 120% (**Figure 3**). **Figure C1** provides a graphical depiction of the predicted changes in abundance across the full ranges of road exposure values recorded. The results for all other model covariates are given in **Table C2**.


Columba oenas
Emberiza citrinella
Linaria cannabina
Picus viridis
Streptopelia decaocto
Phylloscopus collybita
Cygnus olor
Passer domesticus
Phylloscopus trochilus
Phasianus colchicus
Alectoris rufa
Sturnus vulgaris
Turdus merula
Oenanthe oenanthe
Delichon urbicum
Columba livia domestica
Fulica atra
Motacilla alba
Fringilla coelebs
Certhia familiaris
Sitta europaea
Cyanistes caeruleus
Columba palumbus
Dendrocopos major
Pica pica
Anas platyrhynchos
Turdus viscivorus
Prunella modularis
Corvus corone
Parus major
Garrulus glandarius
Sylvia atricapilla
Chloris chloris
Periparus ater
Spinus spinus
Pyrrhula pyrrhula
Turdus philomelos
Corvus frugilegus
Emberiza schoeniclus
-2e-04
-1e-04
0e+00
1e-04
2e-04
Relative effect size of major roads

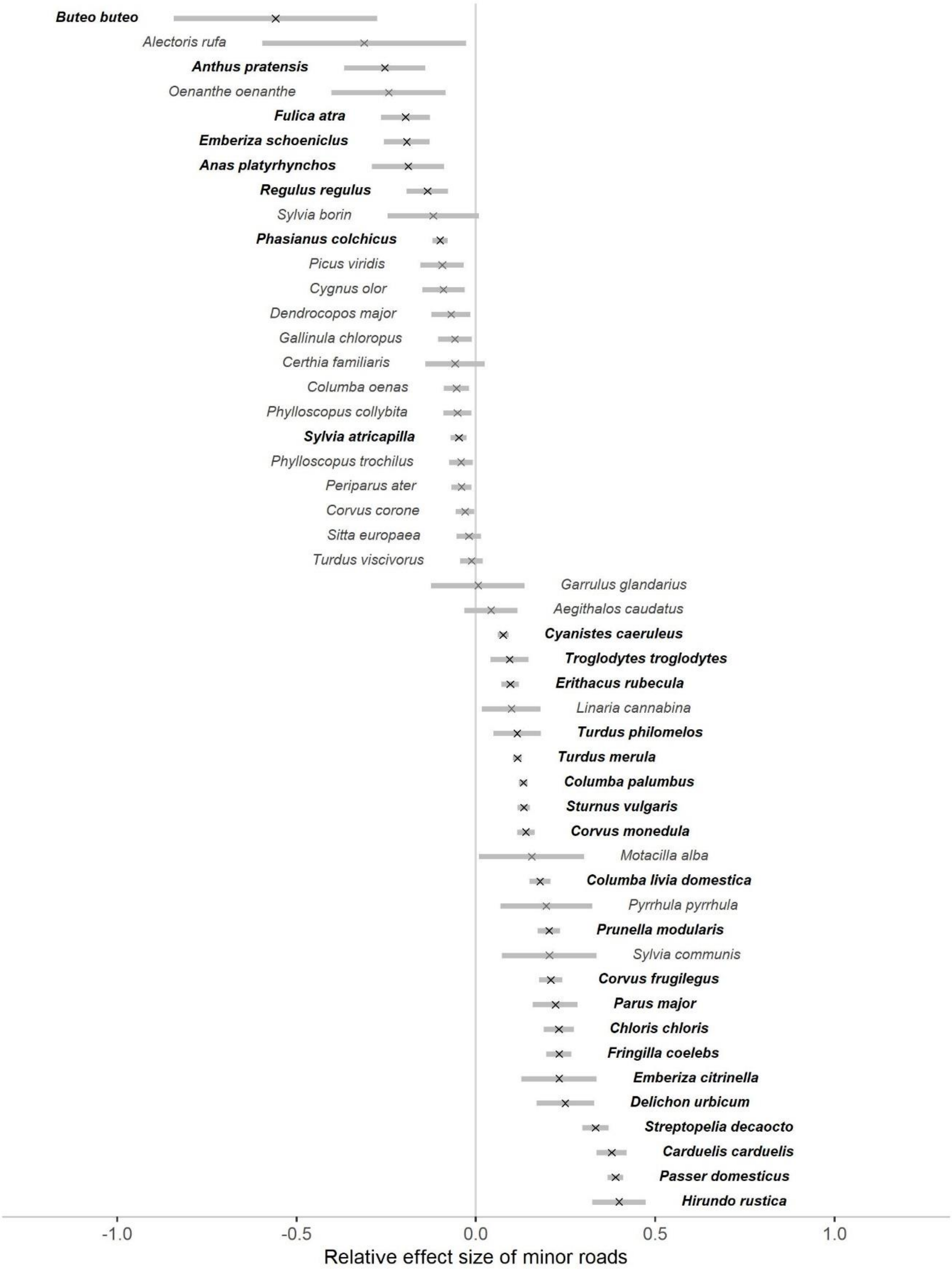


Figure 2. Associations between bird abundance and exposure of count sites to major roads and minor roads. For ease of comparison, the effect size for each species has been divided by the $\log_{10}$-transformed optimised parameter defining the spatial scale of the association: k_{major} for major roads or k_{minor} for minor roads. This combines the magnitude of the effect with the spatial area over which the effect occurs. Species with significant effects (calculated with Bonferroni correction) are highlighted in black bold. 95% confidence are displayed by the grey bars. Note that the effect sizes of minor roads are not directly comparable to those of major roads due to the inclusion of traffic data in the latter, and also that not all species could be tested with

both major and minor road exposure as it was not always possible to identify optimum values of k_{major} or k_{minor} (see **Appendix A** for further details). One species, *Sylvia borin*, is excluded from the major road graph due to particularly wide confidence limits.

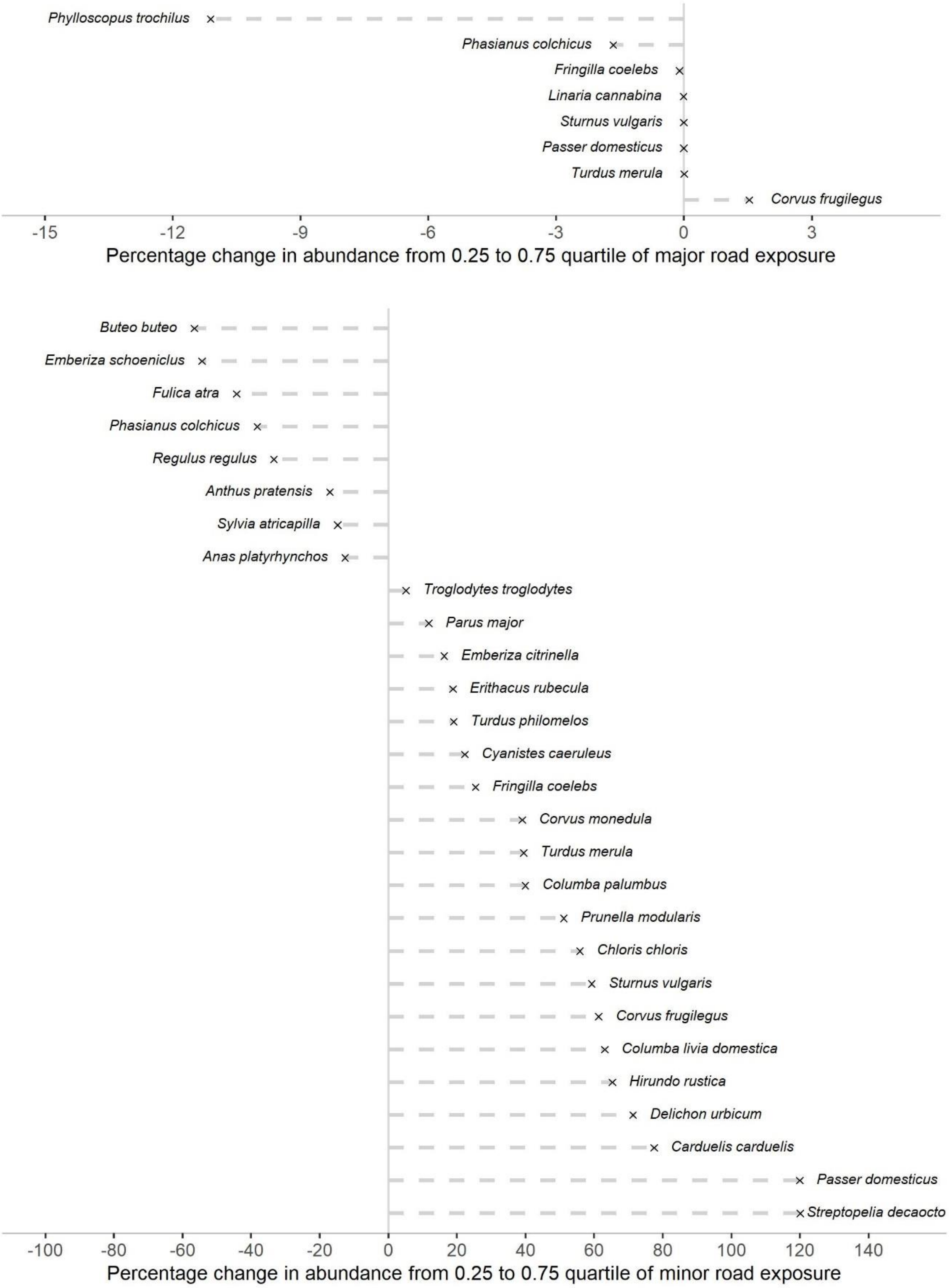


Figure 3. Predicted percentage changes in bird abundance with changing road exposure values. For both major and minor road exposure, I calculated the estimated change in bird abundance across the interquartile range of that covariate (quartiles 0.25 to 0.75), while holding all other covariates constant. Only species with

significant associations between bird abundance and major/minor road exposure are included here. It is likely that my estimates for major roads are underestimated due to insufficient sample sizes and data spread.

The distances from a major road up to which an effect was detectable (defined as major road exposure, unweighted by traffic, > 0.01; see **Appendix A** for further detail) ranged from approximately 200 m to 1.1 km, with a mean of 340 m (corresponding to k_{major} values of 23.5, 4.4 and 13.4 respectively). The distances up to which an association between minor road exposure and abundance could be detected (defined as minor road exposure > 0.01) ranged from 100 m to 2.2 km, with a mean of 370 m (corresponding to k_{minor} values of 33.75, 2.125 and 12.33 respectively).

I also compared the estimated abundance changes with increasing road exposure, to those with increasing proportion of arable land (for species linearly associated to proportion of arable land; n = 46). I did this using measures of road exposure which were not distance-optimised, to be comparable to the arable land covariate. Of the 46 species, 10 showed a significant association between proportion of arable land and bird abundance, seven of which were positive. For these species, across the interquartile range of the proportion of arable land, the mean decrease in estimated abundance (for those showing significant negative associations) was 59% and the mean increase (for those showing significant positive associations) was 52%. For the non-distance-optimised measures of minor road exposure, the mean significant increase in abundance across the interquartile range was 23%, and mean significant decrease was 25%. Only one positive association and one negative association between major road exposure and abundance were significant and these corresponded to changes of 14% and -11%. Both the absolute mean change in abundance (of all significant and non-significant results) associated with major road exposure (mean = 0.12) and that associated with minor road exposure (mean = 0.16) were significantly different from the absolute mean change in abundance associated with the proportion of arable land (mean = 0.32) (Welch's two-sample t-tests: major roads t = -4.79, *P* < 0.001; minor roads t = -3.9, *P* < 0.001; **Figure 4)**.

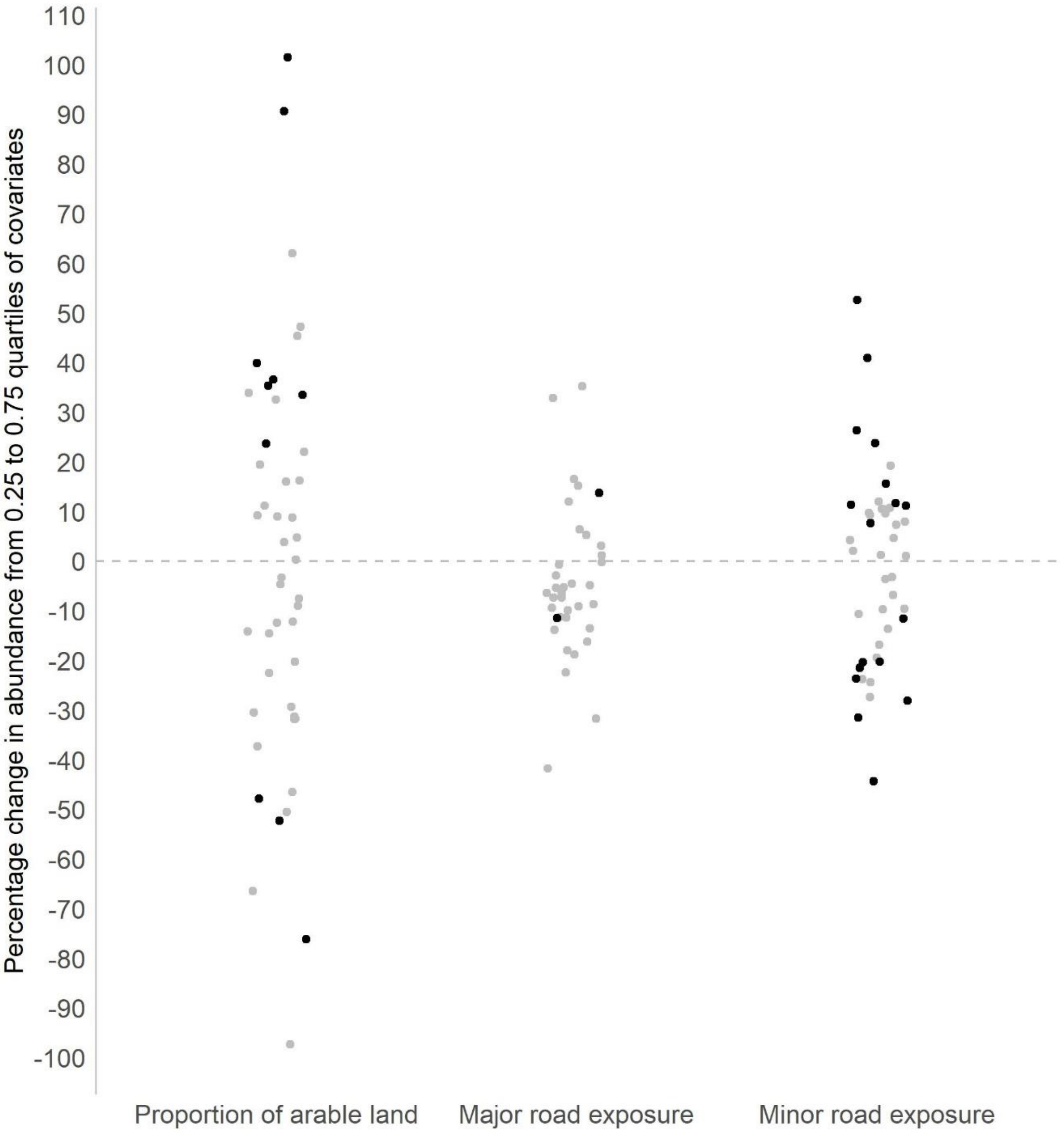


Figure 4. A comparison of estimated percentage changes in bird abundance across the interquartile ranges of proportion of arable land and road exposure covariates. In order to more accurately compare these covariates, major and minor road exposure here were included without distance optimisation, to make them comparable to the proportion of arable land. Each point represents a single species, non-significant associations are represented by grey symbols and significant associations by black symbols. Only species for which I fitted proportion of arable land as a linear effect are included here.

Discussion

Over half (30/51) of the species I assessed showed significant positive or negative associations between road exposure and bird abundance. While 7 of 8 of the species' associations with major road exposure were negative, 20 of 28 of the associations with minor road exposure were positive. Across the interquartile ranges of road exposure calculated for each species, the mean reduction in estimated abundance (for species with negative associations) was 19% and the mean increase (for species with positive associations) was 47%. These scales of population changes are not unlike those found in other studies (e.g. Reijnen et al. 1996 – population reductions of 12-56% within 100 m of a road). They were also up to half as large as those associated with the proportion of arable land (my proxy for yield), an important correlate of changes in bird populations (e.g. Burns et al. 2016). I found mean effect distances of 340 m for major roads and 370 m for minor roads, which are also within the range of those found in previous studies (e.g. Reijnen et al. 1995: 40-1500 m; Reijnen et al. 1996: 20-1700 m; Palomino & Carrascal 2007: mean effect distance of 300 m; Mammides et al. 2016: road effect strongest when 500 m buffer used).

Most species showed either lower or higher abundance with increasing minor road exposure and lower abundance, or no change, with increasing major road exposure. Of those that showed no or little association with either major or minor road exposure, some may reflect reality, but others may be due to insufficient sample sizes or data spread, particularly in the case of major roads. Although it is possible that birds are better able to adapt to major roads due to their constant traffic levels, as opposed to the more intermittent levels typically found on minor roads, I believe my results for major roads to be largely underestimated, both in significance and effect sizes. This is most likely because there were a limited number of BBS squares close to major roads (while 47% of transect sections were within 100 m of a minor road, only 9% were within 100 m of a major road).

Eight of the study species exhibited lower abundance with increasing minor road exposure, and seven with increasing major road exposure. These reductions could be due to an increased death rate and/or reduced breeding success around roads, or avoidance of road areas by birds, which could, in turn, be increasing competition in other areas. Some of these results are in line with those of previous studies, for example, negative associations between populations and road density, road noise or traffic level have been found in common linnet *Linaria cannabina* (Peris & Pescador 2004), common reed bunting *Emberiza schoeniclus* (Helldin & Seiler 2003), Eurasian coot *Fulica atra* (Reijnen et al. 1996), goldcrest *Regulus regulus* (Reijnen et al. 1995; Helldin & Seiler 2003), meadow pipit *Anthus pratensis* (Reijnen et al. 1995; Helldin & Seiler 2003), ring-necked pheasant *Phasianus colchicus* (Reijnen et al. 1995) and willow warbler *Phylloscopus trochilus* (Reijnen & Foppen 1994; Reijnen et al. 1995). Unlike us, Bautista et al. (2004) found common buzzard *Buteo buteo* to be in greater abundance closer to a road than further away, though they declined on days with increased traffic volume. However, this study focused on only one road and spanned winter, when roadsides can be more important for this species (Meunier et al. 2000).

While I found that only rooks were more prevalent with increasing major road exposure, twenty species had higher abundance with increasing minor road exposure. Many of these species have been shown previously to be positively correlated with road density and/or traffic levels, for example, barn swallow *Hirundo rustica* (Palomino & Carrascal 2007), chaffinch *Fringilla coelebs* (Morelli et al. 2015), European goldfinch *Carduelis carduelis* (Morelli et al. 2015), European greenfinch *Chloris chloris* (Helldin & Seiler 2003; Palomino & Carrascal 2007; Morelli et al. 2015), great tit *Parus major* (Helldin & Seiler 2003; Wiacek et al. 2015), house sparrow (e.g. Brotons & Herrando 2001; Peris and Pescador 2004; Palomino & Carrascal 2007), rock dove/feral pigeon *Columba livia* (Palomino & Carrascal 2007) and yellowhammer *Emberiza citronella* (Helldin & Seiler 2003). Others have been previously found to be negatively associated with roads or high traffic levels, for example common woodpigeon (Reijnen et al. 1995) and Eurasian wren (Morelli et al. 2015), but this may reflect the inclusion of roads with higher traffic levels in these studies.

In my study, most of the species whose abundance increased with road exposure are commonly found in urban habitats and thus are presumably able to tolerate some level of anthropogenic disturbance, including that of roads. Increases in abundance with road exposure could be explained by attraction to the road itself, for purposes of food or grit, or to the roadside habitat. In Great Britain, semi-natural habitats are limited, and road verges, which often contain areas of trees, shrubs, wildflowers and hedgerows, may be important areas for many species that are able to tolerate road exposure. Roads are also associated with edge habitat, which may explain some of the increased abundance, such as that of yellowhammer. However, it is difficult to ascertain the direction of causality here: roads are often built along pre-existing field or property boundaries, which may include ditches or hedges; however, these features might also be installed alongside roads as a consequence of their construction. Finally, powerlines and fences often run along roads and can provide perches (Meunier et al. 2000). This may be the reason behind the increased abundance of swallows and house martins I found. While I am unable to say how much either the positive or negative variation I found in bird abundance is associated with variation in roadside habitat, as opposed to the road itself, previous studies that have controlled for habitat have found significant negative effects of road traffic, in several of the same species I did (Reijnen et al. 1995; 1996).

Four of the species tested exhibited positive associations with minor road exposure and negative associations with major road exposure, suggesting that there may be a threshold of traffic volume beyond which the benefits of being near roads are outweighed by the costs. As well as higher traffic volume, vehicles on major roads usually move at faster speeds, meaning the risk of collision is likely to be higher, as well as noise, light and chemical pollution. Differences in the effects of lower- versus higher-traffic roads on bird densities have been reported in several papers previously (e.g. Bautista et al. 2004; Brotons & Herrando 2001; Reijnen & Foppen 2006; Peris & Pescador 2004; Reijnen et al. 1996) and my results also suggest that this distinction is important in studies of road impacts.

Without further study of the status, health and breeding success of individual birds inhabiting road areas in the study site, it is not possible to understand the broader implications of my findings. It may be that the associations I found are due to avoidance or attraction to roads by certain bird species, which does not impact their wider populations. However, previous studies do suggest that density reductions around roads can result in overall population reductions (e.g. Reijnen & Foppen 1994;1995). Roads may act as ecological traps for some species (Reijnen & Foppen 1994; 2006), if they are attracted to them for the seemingly good habitat but then suffer health impacts, reduced breeding success or collision mortality as a result. There may also be differences in the responses of birds to noise depending on their status and age, leading to changes in population structure around roads (McClure et al. 2017; Reijnen & Foppen 1994).

In this study I was able only to consider common and widespread species, due to the high sample sizes that were required to produce the models of the impacts of road exposure on detectability in Cooke et al. (2019). It is possible that many rarer species have lower abundance with both major and minor road exposure and therefore my findings here should not be taken to be representative of British birds as a whole. However, even with this limitation, my findings suggest that roads may modify local bird community structures, on a scale potentially comparable to that of agricultural activities. Given that my analysis spans the whole of Great Britain, these effects appear to be operating at a large scale. This has implications for our overall understanding of the impacts of infrastructure on biodiversity, for the design of appropriate mitigation for road development, and for protected areas and conservation projects near to roads, which may be prevented from reaching their full potentials as a result.

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Chapter 4: Roads as a contributor to landscape-scale variation in bird communities

This chapter was accepted as Cooke, S. C., Balmford, A., Donald, P. F., Newson, S. E. and Johnston, A. 2020. Roads as a contributor to landscape-scale variation in bird communities. Nature Communications, 11: 3125.

Summary

Roads and their traffic can affect wildlife over a kilometre away and in regions with dense road networks may influence a high proportion of the ecological landscape. However, we have limited understanding of road impacts on animal populations at large spatial scales. In the most extensive study to date, I assess how the local abundance of 75 bird species varies with road exposure at 20,000 sites across Great Britain. 77% of species showed significant variation in numbers with increasing road exposure and 63% retained significance with the use of a conservative Bonferroni correction. Of these, 53% exhibited reduced abundance and 47% increased abundance, though further analysis indicated that abundance reductions were more common around roads with high traffic levels. For species exhibiting reduced abundance, the distance at which the effect became negligible averaged 700 m from a road, an area that covers over 70% of Great Britain and includes 41% of its total area of terrestrial protected sites. Species with larger national populations generally had higher relative abundance with increasing road exposure, whereas the opposite was true for rarer species. Smaller-bodied and migratory species were also more negatively associated with road exposure than larger-bodied and resident species. By creating environmental conditions that benefit generally common species at the expense of others, road networks may echo other anthropogenic disturbances in bringing about large-scale simplification of avian communities.

Introduction

The ever-expanding environmental footprint of humans is affecting global wildlife populations via a wide range of mechanisms, many of which we are only beginning to understand. Extinctions and population declines are widespread (Ceballos et al. 2015; Monroe et al. 2019), but not evenly spread across taxa. It has been argued that differences in species' abilities to tolerate anthropogenic disturbance are leading to simplification of species assemblages in human-disturbed environments (McKinney & Lockwood 1999; Clergeau et al. 2006; Davey et al. 2012; Le Viol et al. 2012; Sullivan et al. 2016; Newbold et al. 2018).

Known human drivers of population change are numerous and include habitat loss (Keil et al. 2015), human-wildlife conflict (Woodroffe et al. 2005), overharvesting (Diaz et al. 2019) and climate change

(Bellard et al. 2012). In recent years, another environmental issue has become a subject of increasing attention – the extensive and expanding global road network. Forty-five million lane-kms of paved roads traverse the Earth's land surface (Dulac 2013) serving around 1.3 billion vehicles (OICA 2015), figures that are expected to increase to 70 million lane-km (Dulac 2013) and 2.8 billion vehicles (WEC 2011; Meyer et al. 2012) by 2050. Yet efforts to mitigate potential road impacts on wildlife are minimal or non-existent in most countries.

Roads are a source of noise, wildlife-vehicle collisions, chemical pollution and visual disturbance, including artificial light (Forman & Alexander 1998; Erritzoe et al. 2003; Fahrig & Rytwinski 2009; Benítez-López et al. 2010). Their construction leads to fragmentation effects and changes in local habitat, and often exposes surrounding areas to further development and other human activities (Laurance et al. 2004; Laurance et al. 2014). Roads have been shown to affect local populations of a range of taxa, and their impacts can extend far from the roads themselves. Studies have measured effect distances of several hundred metres, with some reporting distances of over a kilometre (Benítez-López et al. 2010; Reijnen et al. 1996; Clarke et al. 2013). Birds show similar patterns to other groups, exhibiting behavioural changes, physiological responses and population changes around roads (Peris & Pescador 2004; Reijnen & Foppen 2006; Parris & Schneider 2009; Crino et al. 2011; Kociolek et al. 2011; Ware et al. 2015). Many of the studies behind these findings, however, are relatively small-scale and our understanding of the larger-scale relationships between roads and animal populations is limited[31]. In addition, while predictors of species' involvements in vehicle collisions have been studied previously (Santos et al. 2016; González-Suárez et al. 2018), in general, predictors of road impacts on wildlife populations are poorly understood.

Great Britain has one of the densest road networks in the world, with over 80% of land falling within 1 km of a road. I use data from the extensive UK Breeding Bird Survey (BBS) to analyse populations of 75 British bird species in relation to the paved road network, and to assess predictors of these patterns. As potential predictors, I choose three species-level characteristics – mean body mass; migratory tendency; and an index of habitat specialisation – and two population-level characteristics – national population size; and long-term national population trend.

Communication in smaller-bodied species may be more affected by road noise, due to their typically quieter and higher-frequency songs (Ryan & Brenowitz 1985; Parris & Schneider 2009; Rheindt 2003), and body mass may affect likelihood of involvement in collisions (Santos et al. 2016; González-Suárez et al. 2018). Habitat generalists may be more able to adapt to disturbance by roads than specialists (Devictor et al. 2008) and therefore be more likely to utilise roadside habitat, and previous work has shown migratory populations to be reduced around roads more than resident species, possibly due to a more limited ability to adapt to noise (Mammides et al. 2016; Laurance 2015). Species with reduced abundances around roads may also have smaller national population sizes, either because roads have contributed directly to their declines or because their national scarcity is caused by their inability to tolerate disturbance, which may also manifest itself in an avoidance of roads.

By assessing populations of a range of species across the whole of Great Britain, this study provides insights into patterns of bird distribution in relation to roads on an unprecedented scale. I also consider predictors of these patterns, finding evidence to suggest roads may contribute to broad-scale simplification of avian communities. My findings provide much-needed information for potential road mitigation and conservation around roads.

Results

Associations between road exposure and bird abundance

I calculated the road exposure of almost 20,000 BBS transect sections using the locations of all paved roads (as mapped in 2013) within a 5-km radius of the midpoint of each transect section. Within these calculations I estimated the spatial scale of the relationship between distance to road and road exposure (determined by a parameter '*k*') for each species separately. I calculated species-specific mean annual bird counts, across 2012-2014 inclusive, for each transect section. I then modelled the mean annual counts of 75 species in relation to road exposure, using Poisson Generalized Additive Mixed Models (GAMMs), whilst also accounting for other potential predictors of bird abundance.

My results show the abundance of 77% (n = 58/75) of species tested to be significantly associated with road exposure (determined using a critical alpha level of 0.05). To account for the increased likelihood of Type I errors arising due to the testing of multiple species I applied Bonferroni correction, after which 63% (n = 47/75) of associations retained statistical significance. Increased road exposure was associated with reduced abundance in 25 species and greater bird abundance in 22 species (**Figure 1; Table D1; Figure D1**), and the maximum distances over which these negative and positive effects could be detected averaged 700 m and 500 m respectively. The results for all other model covariates are given in **Table D2**.

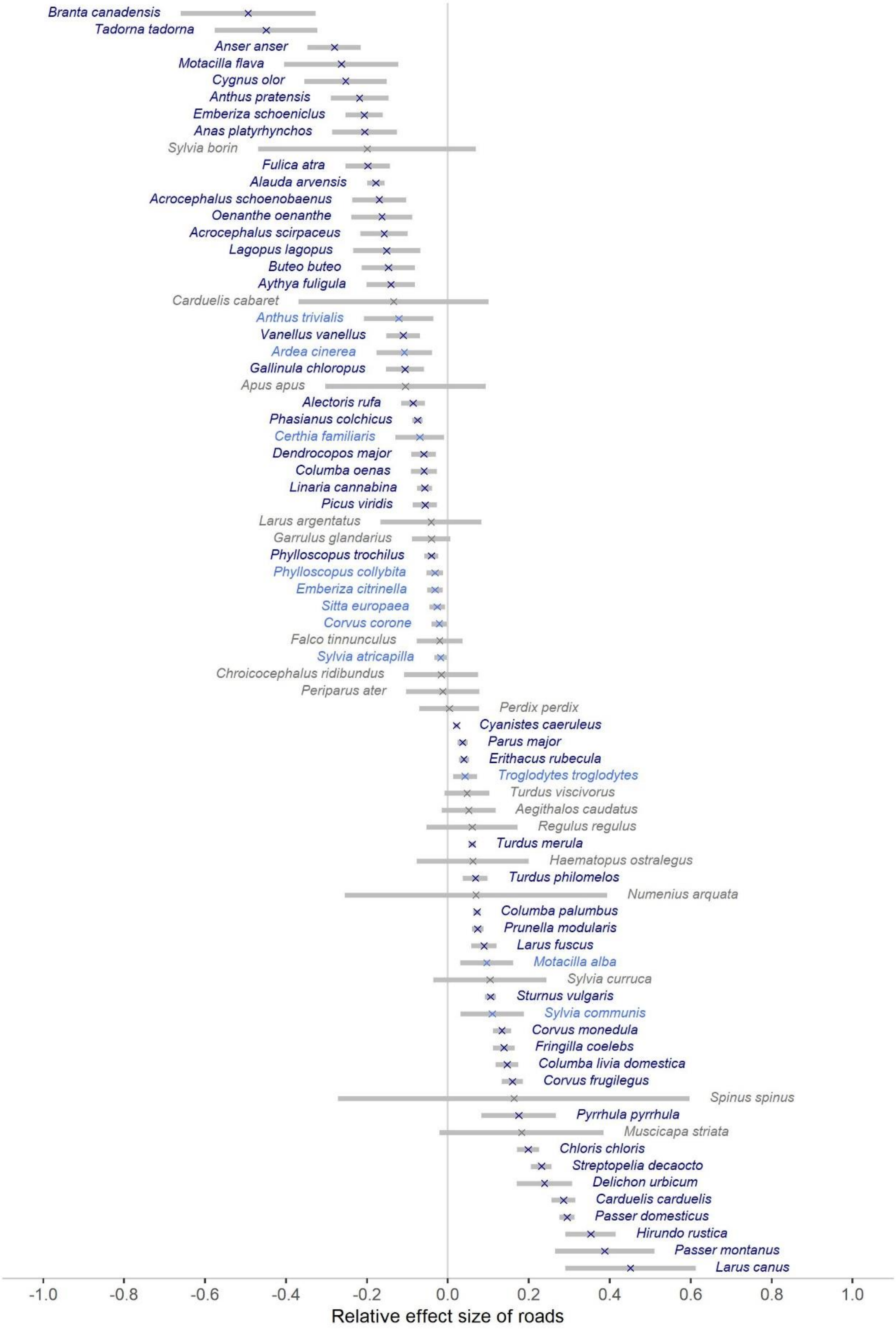

Figure 1. Relative effect size of associations between road exposure and bird abundance. For each species, the relative effect size was calculated as a composite of the magnitude of the effect size of road exposure and the spatial scale over which the effect could be detected (the latter being determined by the parameter '*k*'). Species with significant associations, determined using a critical alpha level of 0.05, are labelled in blue, with

those whose significant associations were retained after Bonferroni correction in dark blue. 95% confidence intervals are displayed by the grey bars.

To estimate the real-world magnitude of the associations between road exposure and bird abundance, I used my models to predict changes in abundance across the ranges of road exposure values recorded for each species. For species with strongly significant associations between abundance and road exposure (i.e. those significant after Bonferroni correction), the mean change in abundance from the 0.25 to 0.75 quartiles of road exposure was -40% for species showing negative associations, and +48% for species showing positive associations (**Figure 2**).

Figure 2. Abundance changes across the interquartile ranges of road exposure recorded for each species. Only species for which associations between road exposure and abundance were found to be significant after Bonferroni correction are featured here. Relative effect size of roads (as shown in **Figure 1**) is represented by point size. Percentage change in abundance across the interquartile range of road exposure and relative effect size are not strongly correlated as the former is affected both by the absolute numbers of birds and the range of road exposure present across counts of each species.

Two species considered in detail

To explain my results in more detail, I use the examples of Eurasian bullfinch *Pyrrhula pyrrhula* and meadow pipit *Anthus pratensis*, species with significant positive and negative associations with road exposure respectively. Eurasian bullfinch had a road exposure effect size of 0.21. This is the effect size where road exposure = 1, i.e. directly beside a single road (higher values of road exposure result from the cumulative effect of multiple roads). I would therefore expect Eurasian bullfinch abundance to be 23% (exp(0.21)) higher next to a road than in an area where road exposure = 0. This effect size declines with distance, becoming negligible at 290 m from a road (determined by the parameter '*k*' and defined as the distance at which road exposure reaches < 0.01; **Figure 3**). Conversely, meadow pipit had a road exposure effect size of -0.24, so I predict its abundance to decrease by 21% (1-exp(-0.24)) next to a road, compared to a location with no road exposure. The maximum effect distance for meadow pipit was 350 m. These values translate to Eurasian bullfinch experiencing a 28% increase in abundance, and meadow pipit a 31% decrease in abundance, over their interquartile ranges of road exposure (**Figure 4**; **Figure D1**).

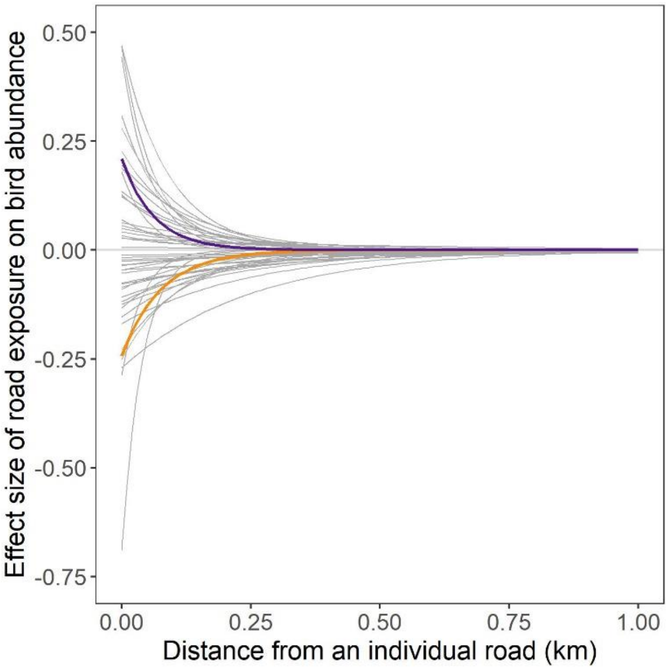

Figure 3. Effect curves for each species with distance from an individual road. The intercept is determined by the coefficient and the rate of decline is determined by the parameter '*k*', which defines the spatial scale of the relationship between distance from road and road exposure for each species. Only species with strongly

significant associations (determined with Bonferroni correction) between road exposure and bird abundance are featured here. The effect curves for Eurasian bullfinch and meadow pipit are highlighted in purple and orange respectively.

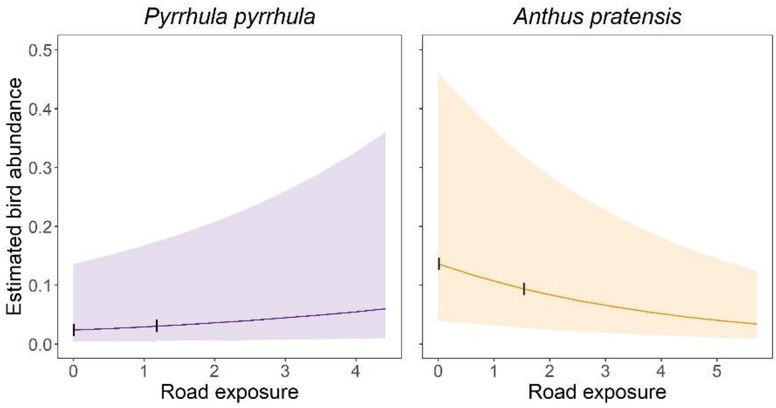

Figure 4. Estimated abundance of two species across the full range of road exposure recorded for each. Bird abundance refers to the number of birds within 100 m of a 200-m BBS transect section. The 0.25 and 0.75 quartiles of road exposure for each species are indicated by the vertical lines and 95% prediction intervals by the shaded areas. These graphs are available for all species in **Figure D1**.

Separate analyses of major and minor roads

Previous studies have suggested differences in the potential impacts of higher and lower traffic level roads (Reijnen & Foppen 2006; Silva et al. 2012; Cooke et al. 2020). To investigate this I analysed a subset of 29 species with high sample sizes and significant associations with road exposure (without Bonferroni correction) in relation to major roads (motorways and A-roads; mean daily traffic volume in 2013 of 17,400 vehicles; DfT 2015) and minor roads (B-, C- and D-roads; mean daily traffic volume in 2013 of 1,300 vehicles; DfT 2015) separately. Of these, 16 had significant associations with both major and minor roads (**Figure 5**). From my results I can see that the original associations with roads are heavily driven by minor roads, which is as expected given their considerably higher prevalence (87.3% of total road length; DfT 2017). Most species (13/16) were negatively associated with major roads and, of these, seven were positively associated with minor roads. Clear exceptions were the two corvid species, rook *Corvus frugilegus* and Eurasian jackdaw *Corvus monedula,* both of which were positively associated with minor roads, and even more so with major roads. The full results for this analysis are presented in **Table E1** and effect curves for all three road categories are compared for each species in **Figure E2**.

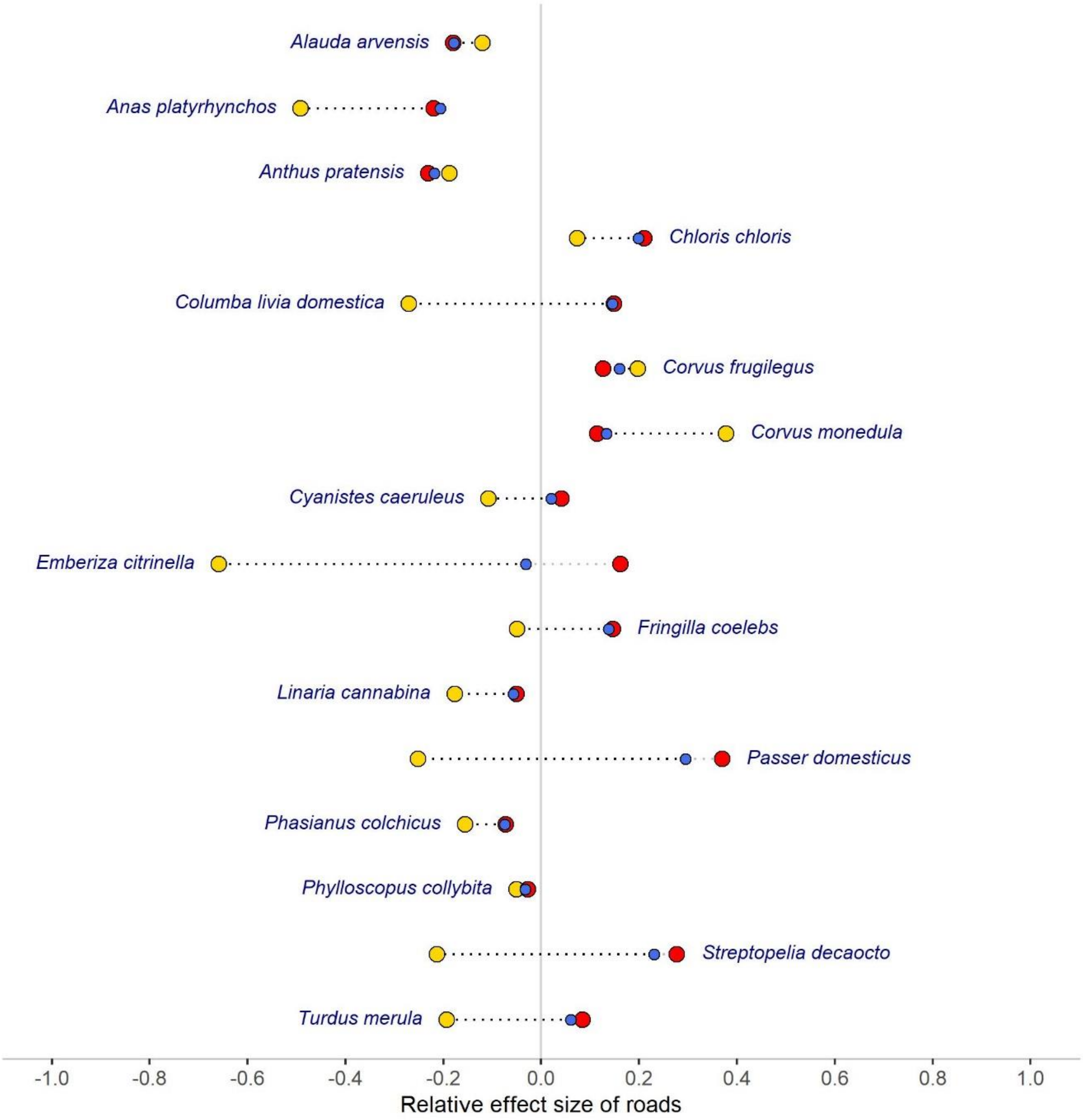

Figure 5. Relative effect size of associations between bird abundance and exposure to different road types. As in **Figure 1**, the relative effect size was calculated as a composite of the magnitude of the effect size of road exposure and the spatial scale over which the effect could be detected. Associations with major roads are shown in yellow, minor roads in red, and both road types together in blue. Only species with significant associations for all three road categories, determined using a critical alpha level of 0.05 without Bonferroni correction, are featured here.

Species characteristics and associations with road exposure

To assess predictors of the associations I found between road exposure and bird abundance, I analysed the relative effect sizes (of all roads together) in relation to five species characteristics: mean body mass; migratory tendency; an index of habitat specialisation; national population size; and long-term national population trend, using a Generalized Estimating Equation. Within this, I accounted for non-independence resulting from similarity within phylogenetic families. I also weighted each species by 1/variance of the effect size of road exposure, to increase the influence of species with more precise association estimates between bird abundance and road exposure.

I found that species with smaller national population sizes generally decreased in abundance with increasing road exposure, whereas the opposite was true for more common species (**Table 1; Figure 6**). I also found migrants and smaller-bodied species to be more negatively associated with road exposure than resident and larger-bodied species. No variables included in the models had variance inflation factors (VIF) greater than 2.0, indicating that multicollinearity among the predictors was low and unlikely to affect the results. I found no significant links between the relative effect size of road exposure and habitat specialisation or long-term national population trend.

Table 1. Relationships between species characteristics and associations with road exposure. Significant relationships are highlighted in bold.

Characteristic	Effect size	Standard error	*P*-value
Mean body mass	**0.027**	**0.009**	**0.004**
Migratory tendency	**-0.042**	**0.012**	**< 0.001**
Habitat specialisation	0.08	0.10	0.43
National population size	**0.092**	**0.018**	**< 0.001**
Long-term national population trend	0.012	0.061	0.84

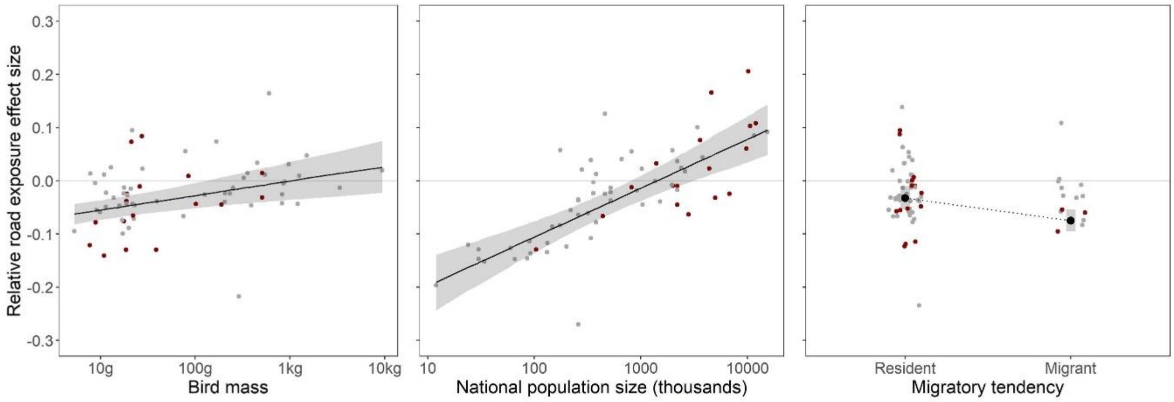

Figure 6. Relationships between species characteristics and associations with road exposure. Black lines/points represent the relationships between relative effect size and each species characteristic, from a model in which all five characteristics were included. 95% prediction intervals around each relationship are shown by the shaded grey bars. The grey and red points represent the sum of the predicted effect size and the model residual for each species - those in red are in the top 25% of model weight and thus had the strongest influence on the model.

Discussion

Our study provides insights into broad-scale associations between paved road exposure and local bird abundance, and considers interspecific variation in these associations in relation to species characteristics. Of the 75 species I tested, 63% showed strongly significant variation in abundance with increasing road exposure, with 53% of these exhibiting reduced abundance. When major and minor roads were analysed separately, of the species with significant associations with major roads, 81% were negative. Finally, I found the effect sizes of road exposure to be more negative for rarer, smaller-bodied and migrant species.

Several smaller-scale studies have shown bird abundance to increase or decrease with proximity to roads (Reijnen et al. 1995; Peris & Pescador 2004; Palomino & Carrascal 2007; Cooke et al. 2020) with similar scales of change and mean effect distances to those found here (Reijnen et al. 1995; 1996; Palomino & Carrascal 2007). Reductions in abundance may be attributed to direct mortality from collisions (Erritzoe et al. 2003), or avoidance of areas around roads due to noise (Halfwerk et al. 2011; McClure et al. 2013) or visual disturbance (Forman & Alexander 1998; Kociolek et al. 2011; Day 2003; Vliet 2010), which decrease the perceived habitat quality. This can lead not only to population reductions but also to changes in population structures (Reijnen & Foppen 1994; McClure et al. 2017). Increases in abundance could be explained by attraction to the road surface for food, grit or heat (Whitford 1985; Erritzoe et al. 2003; Yosef 2009), or to roadside habitat (Laursen 1981; Meunier et al. 1999) and associated structures such as powerlines and fences (Meunier et al. 2000).

The influence of roadside habitat is particularly difficult to quantify here as, although I incorporated habitat in my models, it was not captured at high enough resolution to account for subtle changes in roadside areas. Roads can create a variety of edge habitat (Meunier et al. 1999; Helldin & Seiler 2003), which may be of benefit to some species but be avoided by others. Britain has very few areas of lowland semi-natural habitat and so road verges, which often contain hedgerows and trees, may be important for some species. In addition, many roads may have been built alongside existing edge habitat, in which some birds were perhaps already at reduced or increased abundance. However, some previous studies have controlled for habitat and still found negative effects of road traffic, including on several species in this analysis (Reijnen et al. 1995; 1996). Most likely, my results arise from a combination of road and habitat effects, both varying in importance around different road types. I found several species to differ in their associations with major and minor roads, with varying effect distances, which suggests that different mechanisms may be of greater or lesser importance around each. In particular, my finding of several species being associated positively with minor roads and negatively with major roads suggests that high-levels of traffic may outweigh habitat benefits, even for those species that are able to tolerate lower-level disturbance.

Our finding of a significant positive relationship between national abundance and road exposure effect size could imply that rarer birds are more inclined to avoid roads. It is possible that roadside habitat is unattractive to rarer species, as their reduced national abundance is, in part, due to their reduced ability to thrive under human disturbance in general. This reduction in competition in areas of higher road exposure could then result in an increase in abundance of species that are more able to tolerate human disturbance and are therefore more common nationally. Smaller-bodied species and migrants may also be found in lower abundances around roads due to increased sensitivity to road-related disturbances such as noise.

As I did not find a significant link between abundance around roads and long-term national population trend, the broader outcome of this lower abundance of some species around roads is difficult to interpret. It could be that road areas act as a sink for these species, or that they are simply avoided by them, but that abundance in areas with lower road exposure has increased enough to stabilise the national population. However, it is important to note that my measures of long-term population trends only began in 1970. Although traffic volume in Great Britain has increased greatly in that time, the total road length has increased by less than 25% (DfT 2015). Therefore, by the beginning of this period, sensitive species may have already adjusted to the presence of the road network.

Shifts in species assemblages in areas of high human disturbance have been identified in both urban (Clergeau et al. 2006; Newbold et al. 2018) and agricultural (Finch et al. 2019) environments, and in response to climate change (Davey et al. 2012; Newbold et al. 2018). Rather than declines of so-called 'loser' species happening in isolation, simultaneous replacement of those species by expanding 'winner' species occurs (McKinney & Lockwood 1999; Le Viol et al. 2012; Sullivan et al. 2016; McGill et al. 2015). These processes, it is suggested, are leading to homogenisation, or simplification, of biodiversity in large areas. My results indicate that roads may create environments that benefit already common species at the expense of others. In this way, they may contribute to this simplification effect, maintaining total bird numbers but reducing species richness and diversity. Given the extent of the global road network, it is likely that my findings are not unique to Britain and so studies to test this pattern in other countries would be beneficial. Replicability of this study is dependent on wide-scale and high-resolution bird and road data but, with increasing citizen science projects worldwide, there may already be many areas in which this is possible. Furthermore, if changes in both road and bird densities were analysed over time, and areas monitored before and after road development, this could give a stronger idea of the level of causality between the two, and an ability to predict the impact of further construction of transport infrastructure.

Compression of already vulnerable species into shrinking pockets of low road density may increase future declines and extinctions in countries with high road densities. My results showed that, for species that declined in abundance with increasing road exposure, this effect extended to a mean of 700 m from a road. Almost three-quarters (72%) of Great Britain's land surface falls within 700 m of a road, leaving limited areas with road exposure low enough not to be associated with abundance changes. In addition, disturbance by roads may be a limiting factor for the success of conservation projects situated near to roads. In Great Britain, 41% of the total area of terrestrial protected sites lies within 700 m of a road. Further work to identify cost-effective methods of mitigation is urgently required, and a particular focus on noise reduction would likely be beneficial (Reijnen et al. 1997). Global traffic and road construction are predicted to continue increasing on a large scale and so mitigation of road impacts on wildlife must be a priority for governments and land managers. As road-related disturbance such as noise pollution is thought to be harmful also to humans (Maheswaran & Elliott 2003; Krzyżanowski et al. 2005; Ndrepepa & Twardella 2011), mitigation for wildlife could be approached in tandem with that for people.

Methods

Overview

I modelled count data from the UK Breeding Bird Survey (BBS) for 75 species in relation to the proximity of nearby roads, whilst also accounting for other potential predictors of bird abundance. In a second step, I then analysed these results with respect to a range of species-specific characteristics to identify predictors of associations between road exposure and bird abundance. I used ArcMap 10.5.1 (ESRI 2017) and R 3.4.4 (R Core Team 2018) for all data preparation and analyses.

Data collation and preparation

I obtained bird count data from the UK BBS, a nationwide survey in which experienced volunteers walk two 1-km transects across a 1-km square, each transect being divided into 200-m sections. These transects mostly do not follow roads (64% of the transect sections used in this analysis did not follow a paved road along any part of them). I extracted counts from squares that had been surveyed every year from 2012-2014 inclusive. I then calculated the mean bird count for each 200-m transect section across that period, removing any species with a total mean annual count < 100. I also extracted the dominant habitat type recorded for each transect section. My final dataset contained counts from 19,709 transect sections in 2,033 squares. Preparation of these data is detailed in **Appendix A**.

I obtained shapefiles for all road classes (major roads: motorways and A-roads; minor roads: B-, C- and D-roads) in Great Britain, as recorded in 2013. I then used kernel density estimation to calculate a measure of road exposure for the midpoint of every 200-m transect section, using the locations of all roads within a 5-km radius. I optimised the spatial scale of the relationship between distance from road and road exposure, represented by the parameter *k*, for each species individually. Further detail on the preparation of the road data can be found in **Appendix A**.

To account for factors other than road exposure that I expected to affect bird abundance, I calculated human population density, temperature and rainfall values for the midpoint of each transect section. I also calculated the following for 5-km buffers around each midpoint: tree cover density, proportion of arable land (as a proxy for yield) and largest field area (as a proxy of agricultural intensity). For information on data sources and calculation of these data see **Appendix A**.

Data analysis

Our goal was to understand how bird abundance varies in relation to roads and to identify the characteristics of species that best predict these associations. I therefore modelled counts of each species, as recorded on BBS transects, as a function of road exposure and other factors that I also expected to affect bird abundance (habitat (as recorded in the BBS); proportion of arable land; largest field area; human population density; temperature; rainfall; and tree cover density). I ran Poisson GAMMs for each species separately, using the R package "mgcv" (Wood 2017). I fitted each variable with a linear effect on the response but, from initial inspection of the relationships between proportion of arable land and bird count, I fitted proportion of arable land quadratically for 11 species (**Table D1**). I incorporated BBS square as a random effect (to account for the non-independence of counts at each square's transect sections) and I included a spatial smooth to account for large-scale variation in bird abundance not associated with the other covariates. The spatial smooth included Easting and Northing as a joint tensor product smooth with a maximum of 50 degrees of freedom (selected with preliminary analyses).

I performed an additional analysis of species that showed significant associations with road exposure (without Bonferroni correction), incorporating major road exposure and minor road exposure in separate models. As there are fewer major roads, and fewer BBS squares near to major roads (93% and 47% of transect sections were within 1000 m and 100 m of a minor road respectively, and 44% and 9% were within 1000 m and 100 m of a major road respectively), for this analysis I selected species with total mean annual counts > 1000, in a minimum of 100 BBS squares, and only used squares within 5 km of a major road.

Cooke et al. (2019) demonstrated the importance of accounting for differences in detectability of birds when analysing the impacts of roads, but this is only possible with large sample sizes and a broad spread of data in relation to road exposure. As here I was interested in interspecific variation in patterns and hence required a large number of species, I could not account for detectability, but confirmed through sensitivity testing on 48 more commonly-recorded species that this was only likely to modify the size of significant effects slightly and not change their direction (**Appendix E**).

To assess significance, I calculated confidence limits for each species as the effect size ± standard error multiplied by the appropriate t-value from the Student's t-distribution, using a critical alpha level of 0.05. I then applied Bonferroni correction, dividing my critical alpha level by the number of species tested (n = 75) and recalculating the confidence limits. In both cases, I declared significance if the confidence limits did not span zero. To allow easier comparison of results between species, I calculated the relative effect size for each, dividing the effect size by the $\log_{10}$-transformed value of k used for that species (k is inversely proportional to the distance over which the effect occurred), thus combining the magnitude of the effect with the spatial area over which the effect occurred. I then used my models to predict bird abundance across the ranges of road exposure recorded for each species, while holding all other continuous covariates at the mean values of the counts of that species. For the two categorical covariates (BBS square and dominant habitat type for each 200-m transect section), I used the BBS square with the smallest absolute random effect size (closest to the average BBS square) and the habitat with the largest number of counts for that species.

To test whether species characteristics were associated with different directions and magnitudes of road exposure effects on bird abundance, I modelled the relationships between the relative effect size of road exposure and five chosen characteristics: mean body mass; migratory tendency; an index of habitat specialisation; national population size; and long-term national population trend (1970-2016). I extracted mean body masses from Robinson (2005) and migratory tendency data (in categorical form – resident or migrant) from McInerny et al. (2018). I obtained an index of how specialised or generalised a species is in its habitat use from Davey et al. (2012), national population estimates for Great Britain from Musgrove et al. (2013) and long-term trend data from DEFRA (2018). I also obtained relative brain mass estimates, which I calculated from data provided in Moller & Erritzoe (2017); however, I excluded this measure from subsequent analyses due to its correlation with mean body mass and because these data were available for fewer species. I performed the Generalized Estimating Equation using the R package "zelig" (Choirat et al. 2018). Within this, I incorporated taxonomic family as a grouping factor to account for any non-independence between species resulting from phylogenetic relatedness. To increase the influence of species with more precise estimates of the effect of road exposure, I also weighted each species by 1/variance of the effect size of road exposure.

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Discussion

Findings and limitations

Bird populations in Great Britain have experienced dramatic changes over the past half-century and many species have seen severe declines (DEFRA 2019a). Documented causes of these include changes in habitat, agricultural practises and climate (Eglington and Pearce-Higgins 2012; Burns et al. 2016; Hayhow et al. 2017; Oliver et al. 2017), but the past 50 years have seen many other changes too. Britain has a dense road network, even by global standards (**Figure 1**), the total length of which has increased by 23% since 1970 (DfT 2018a). In that year, the mean annual number of vehicle miles undertaken on roads in Britain was 125 billion. By 2018, it had risen to 328 billion, an increase of > 160% (DfT 2019). In this thesis, I set out to explore the possibility of roads in Britain being a contributor to changes in bird populations. By quantifying associations, firstly between road exposure and detectability of birds, and secondly between road exposure and abundance of birds, I uncovered strong spatial correlations between roads and bird populations across Britain, thus supporting the possibility of a causal link between the two.

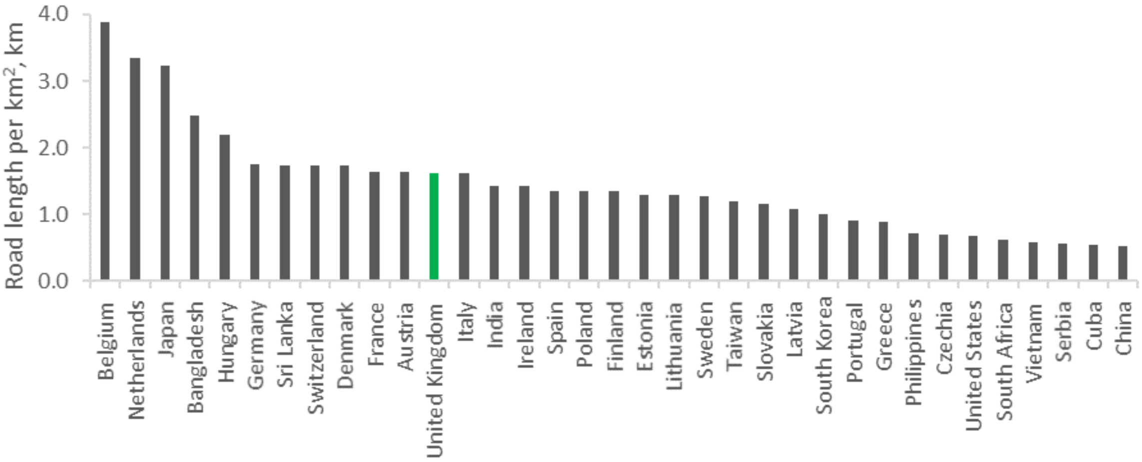

Figure 1. Estimated road length/km^2 for countries with area > 30,000 km^2 (n = 132) and road length/km^2 > 0.5 km, with the United Kingdom highlighted in green. Data extracted from CIA (2020a, 2020b) and include paved and unpaved roads; note there is likely some discrepancy in measurements of road lengths between countries.

In Chapter 2, I used data from nearly 20,000 UK Breeding Bird Survey (BBS) transect sections across Britain to assess the associations between road exposure and detectability of 51 bird species. I found that, while some birds were easier to detect with increasing road exposure, others were more difficult. These patterns are likely due to a combination of noise impacts and bird behavioural changes. These quantifications allowed me, in Chapter 3, to assess associations between road exposure and abundance of the same 51 bird species, whilst accounting for associations between road exposure and detectability, a factor frequently overlooked in prior studies. Importantly, in both chapters, I spatially optimised the relationship between distance from road and road exposure separately for each species, allowing a higher-resolution understanding of the species-specific associations with roads. As in Chapter 2, I considered higher and lower level traffic roads separately, incorporating traffic volume in the road exposure calculations for the former. For minor roads (lower level traffic), 28 species had significant associations between abundance and road exposure, most of which were positive. For major roads (higher level traffic), only eight species had significant associations between abundance and road exposure, most of which were negative. The mean maximum distances up to which these associations were detectable were 460 m and 350 m for negative and positive associations with minor roads respectively and 330 m and 570 m for negative and positive associations with major roads respectively. Interestingly, four species had significant positive associations with minor roads and significant negative associations with major roads, in line with my hypothesis that the noise produced by major roads may cause greater avoidance by birds than that produced by minor roads.

Whilst I felt it important to distinguish between road types, as their impacts likely differ (Forman et al. 2002; Reijnen and Foppen 2006; Silva et al. 2012), garnering accurate results for major roads proved difficult and I believe the effect sizes I obtained may be underestimates. Major roads make up only 13% of Britain's total road length (DfT 2018a) and, while 47% of BBS transect sections used in this study were within 100 m of a minor road, only 9% were within 100 m of a major road. My ability to estimate associations between major road exposure and both detectability and bird abundance correctly was therefore limited, an issue likely exacerbated by the inclusion of traffic data. Both Chapters 2 and 3 were also restricted by a need for large sample sizes for the detectability models to converge successfully, which is why I could analyse only 51 species.

In Chapter 4, I overcame these limitations by analysing associations between road exposure and bird abundance without incorporating detectability or traffic, and, initially, without differentiating between road types. This allowed analysis of a further 24 rarer species, giving a total of 75. I confirmed through a post hoc analysis that not accounting for detectability only changed the effect sizes of my results slightly and most likely would not have resulted in any significant effect direction changes. Of the 75 species tested, 25 had strongly significant negative associations with road exposure and 22 had strongly significant positive associations with road exposure. The mean maximum distances up to which associations between road exposure and bird abundance were detectable were 700 m for negative associations and 500 m for positive associations. The larger distance of the former, compared to those found in Chapter 3, was mostly due to a greater number of significant species with larger distances, as opposed to large variation in distances between the chapters for individual species. Overall, I found species with larger national populations to have generally higher abundance with increasing road exposure, whilst the opposite was true for rarer species. I also found smaller-bodied and migratory species to be more negatively associated with road exposure.

Choosing to analyse all road types together in Chapter 4 navigated around the sample size and data spread issues for major roads encountered in Chapter 3 but did not allow consideration of variation between road types. I therefore ran separate analyses of major and minor roads for a smaller number of species which had both large sample sizes and significant associations with all roads together. Most species had significant negative associations with major roads, including several that had significant positive associations with minor roads, in keeping with my results from Chapter 3. Combined results from both chapters are summarised in **Table 1**.

Table 1. Associations with roads found for each species in both Chapters 3 and 4. Only significant associations are featured, and the direction and significance level are given for each.

Scientific name	**Common name**	**C3: major roads**	**C3: minor roads**	**C4: all roads**	**C4: major roads**	**C4: minor roads**
Acrocephalus schoenobaenus	Sedge warbler			Negative, $P < 0.0007$		
Acrocephalus scirpaceus	Reed warbler			Negative, $P < 0.0007$		
Aegithalos caudatus	Long-tailed tit					
Alauda arvensis	Eurasian skylark			Negative, $P < 0.0007$	Negative, $P < 0.05$	Negative, $P < 0.05$
Alectoris rufa	Red-legged partridge			Negative, $P < 0.0007$		
Anas platyrhynchos	Mallard		Negative, $P < 0.001$	Negative, $P < 0.0007$	Negative, $P < 0.05$	Negative, < 0.05
Anser anser	Greylag goose			Negative, $P < 0.0007$		
Anthus pratensis	Meadow pipit		Negative, $P < 0.001$	Negative, $P < 0.0007$	Negative, $P < 0.05$	Negative, $P < 0.05$
Anthus trivialis	Tree pipit			Negative, $P < 0.05$		
Apus apus	Common swift					
Ardea cinerea	Grey heron			Negative, $P < 0.05$		
Aythya fuligula	Tufted duck			Negative, $P < 0.0007$		
Branta canadensis	Canada goose			Negative, $P < 0.0007$		
Buteo buteo	Common buzzard		Negative, $P < 0.001$	Negative, $P < 0.0007$		
Carduelis cabaret	Lesser redpoll					
Carduelis carduelis	European goldfinch		Positive, $P < 0.001$	Positive, $P < 0.0007$		
Certhia familiaris	Eurasian treecreeper			Negative, $P < 0.05$		
Chloris chloris	European greenfinch		Positive, $P < 0.001$	Positive, $P < 0.0007$	Positive, $P < 0.05$	Positive, $P < 0.05$
Chroicocephalus ridibundus	Black-headed gull					

Columba livia domestica	Feral pigeon		Positive, $P < 0.001$	Positive, $P < 0.0007$	Negative, $P < 0.05$	Positive, $P < 0.05$
Columba oenas	Stock dove			Negative, $P < 0.0007$		
Columba palumbus	Common woodpigeon		Positive, $P < 0.001$	Positive, $P < 0.0007$		
Corvus corone	Carrion crow			Negative, $P < 0.05$		
Corvus frugilegus	Rook	Positive, $P < 0.001$	Positive, $P < 0.001$	Positive, $P < 0.0007$	Positive, $P < 0.05$	Positive, $P < 0.05$
Corvus monedula	Eurasian jackdaw			Positive, $P < 0.0007$	Positive, $P < 0.05$	Positive, $P < 0.05$
Cyanistes caeruleus	Blue tit		Positive, $P < 0.001$	Positive, $P < 0.0007$	Negative, $P < 0.05$	Positive, $P < 0.05$
Cygnus olor	Mute swan			Negative, $P < 0.0007$		
Delichon urbicum	Common house martin		Positive, $P < 0.001$	Positive, $P < 0.0007$		
Dendrocopos major	Great spotted woodpecker			Negative, $P < 0.0007$		
Emberiza citrinella	Yellowhammer		Positive, $P < 0.001$	Negative, $P < 0.05$	Negative, $P < 0.05$	Positive, $P < 0.05$
Emberiza schoeniclus	Common reed bunting		Negative, $P < 0.001$	Negative, $P < 0.0007$		
Erithacus rubecula	European robin		Positive, $P < 0.001$	Positive, $P < 0.0007$		
Falco tinnunculus	Common kestrel					
Fringilla coelebs	Common chaffinch	Negative, $P < 0.001$	Positive, $P < 0.001$	Positive, $P < 0.0007$	Negative, $P < 0.05$	Positive, $P < 0.05$
Fulica atra	Eurasian coot		Negative, $P < 0.001$	Negative, $P < 0.0007$		
Gallinula chloropus	Common moorhen			Negative, $P < 0.0007$		
Garrulus glandarius	Eurasian jay					
Haematopus ostralegus	Eurasian oystercatcher					
Hirundo rustica	Barn swallow		Positive, $P < 0.001$	Positive, $P < 0.0007$		
Lagopus lagopus	Red grouse			Negative, $P < 0.0007$		
Larus argentatus	Herring gull					
Larus canus	Common gull			Positive, $P < 0.0007$		
Larus fuscus	Lesser black-backed gull			Positive, $P < 0.0007$		
Linaria cannabina	Common linnet	Negative, $P < 0.001$		Negative, $P < 0.0007$	Negative, $P < 0.05$	Negative, $P < 0.05$
Motacilla alba	Pied/white wagtail			Positive, $P < 0.05$		
Motacilla flava	Yellow wagtail			Negative, $P < 0.0007$		
Muscicapa striata	Spotted flycatcher					
Numenius arquata	Eurasian curlew					
Oenanthe oenanthe	Northern wheatear			Negative, $P < 0.0007$		
Parus major	Great tit		Positive, $P < 0.001$	Positive, $P < 0.0007$		
Passer domesticus	House sparrow	Negative, $P < 0.001$	Positive, $P < 0.001$	Positive, $P < 0.0007$	Negative, $P < 0.05$	Positive, $P < 0.05$
Passer montanus	Tree sparrow			Positive, $P < 0.0007$		

Perdix perdix	Grey partridge					
Periparus ater	Coal tit					
Phasianus colchicus	Ring-necked pheasant	Negative, $P < 0.001$	Negative, $P < 0.001$	Negative, $P < 0.0007$	Negative, $P < 0.05$	Negative, $P < 0.05$
Phylloscopus collybita	Common chiffchaff			Negative, $P < 0.05$	Negative, $P < 0.05$	Negative, $P < 0.05$
Phylloscopus trochilus	Willow warbler	Negative, $P < 0.001$		Negative, $P < 0.0007$		
Pica pica	Eurasian magpie					
Picus viridis	European green woodpecker			Negative, $P < 0.0007$		
Prunella modularis	Dunnock		Positive, $P < 0.001$	Positive, $P < 0.0007$		
Pyrrhula pyrrhula	Eurasian bullfinch			Positive, $P < 0.0007$		
Regulus regulus	Goldcrest		Negative, $P < 0.001$			
Sitta europaea	Eurasian nuthatch			Negative, $P < 0.05$		
Spinus spinus	Eurasian siskin					
Streptopelia decaocto	Eurasian collared dove		Positive, $P < 0.001$	Positive, $P < 0.0007$	Negative, $P < 0.05$	Positive, $P < 0.05$
Sturnus vulgaris	Common starling	Negative, $P < 0.001$	Positive, $P < 0.001$	Positive, $P < 0.0007$		
Sylvia atricapilla	Eurasian blackcap		Negative, $P < 0.001$	Negative, $P < 0.05$		
Sylvia borin	Garden warbler					
Sylvia communis	Common whitethroat			Positive, $P < 0.05$		
Sylvia curruca	Lesser whitethroat					
Tadorna tadorna	Common shelduck			Negative, $P < 0.0007$		
Troglodytes troglodytes	Eurasian wren		Positive, $P < 0.001$	Positive, $P < 0.05$		
Turdus merula	Common blackbird	Negative, $P < 0.001$	Positive, $P < 0.001$	Positive, $P < 0.0007$	Negative, $P < 0.05$	Positive, $P < 0.05$
Turdus philomelos	Song thrush		Positive, $P < 0.001$	Positive, $P < 0.0007$		
Turdus viscivorus	Mistle thrush					
Vanellus vanellus	Northern lapwing			Negative, $P < 0.0007$		

While Chapter 4 allowed a better understanding of the generality of the issue than Chapter 3, by including a broader range of species, that came at a cost in terms of analysis resolution, most importantly the loss of detectability incorporation. Comparing the results of Chapters 3 and 4 however show that, without exception, the directions of effects did not change between the two for species included in both, allowing increased confidence in both sets of results. The post hoc analysis undertaken in Chapter 4 which reran the analyses of 48 species with detectability included showed only slight shifts in the effect sizes, none of which were enough to alter significance. This suggests that, although detectability should ideally be incorporated for improved result accuracy, the associations between roads and bird abundance dominate over those between roads and detectability.

Although my analyses covered a large area and used high-resolution data, they were still fundamentally correlative in nature. I found strongly significant patterns between road exposure and bird abundance but cannot say how much the former is causing the latter. In addition, I tested only monotonic relationships between road exposure and both detectability and bird abundance, which may have concealed more complex associations. However, my results are, for the most part, in line with those of other studies (summarised in **Table 2**), with those that differ largely arising from studies that focused solely on major roads or considered areas within only a relatively short distance from a road. I therefore feel I can have confidence in my analytical approaches and findings.

Table 2. A comparison of the species-specific results from Chapters 3 & 4 with those of other studies

Scientific name	**Common name**	**Author**	**Date**	**Finding**	**My findings (Chapters 3 & 4; C3 & C4)**
Alauda arvensis	Eurasian skylark	Helldin & Seiler	2003	**Lower abundance** within major road-effect zone; defined as 285 m from road.	**Lower abundance** with increasing exposure to all roads (C4), minor roads (C4) and major roads (C4); effect distances 1150-1540 m.
		Milsom *et al.*	2000	**Lower likelihood of presence** closer to roads.	
		Morelli *et al.*	2015	**Higher occurrence** with increasing road coverage within 100 m radius.	
		Reijnen *et al.*	1996	**Lower density** of breeding birds with higher traffic noise; effect distances 100-490 m.	
Anthus pratensis	Meadow pipit	Helldin & Seiler	2003	**Lower abundance** within major road-effect zone; defined as 285 m from road.	**Lower abundance** with increasing exposure to all roads (C4), minor roads (C3; C4) and major roads (C4); effect distances 270-420 m.
		Milsom *et al.*	2000	**Lower likelihood of presence** closer to roads.	
		Reijnen *et al.*	1996	**Lower density** of breeding birds with higher traffic noise; effect distances 25-90 m.	
Anthus trivialis	Tree pipit	Kuitunen *et al.*	1998	**Lower abundance** closer to highways; compared 25 m and 200 m from the roads.	**Lower abundance** with increasing exposure to all roads (C4); effect distances 1540 m.
		Reijnen *et al.*	1995a	**Lower density** of breeding birds with higher traffic noise; effect distances ~50-100 m.	
Buteo buteo	Common buzzard	Bautista *et al.*	2004	**Higher abundance** closer to a major road than further away but decreased with increasing traffic.	**Lower abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 320-580 m.
		Reijnen *et al.*	1995a	**Lower density** of breeding birds with higher traffic noise; effect distances ~1500-2800 m.	
Carduelis carduelis	European goldfinch	Morelli *et al.*	2015	**Higher occurrence** with increasing road coverage within 100 m radius.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 330-380 m.
		Santos *et al.*	2016	Higher than expected roadkill:abundance ratio (both major and minor type roads combined).	
Certhia familiaris	Eurasian treecreeper	Rheindt	2003	**Lower abundance** closer to a motorway; compared 100 m and 950 m from the road.	**Lower abundance** with increasing exposure to all roads (C4); effect distances 770-1420 m.
Chloris chloris	European greenfinch	Brotons & Herrando	2001	**Lower probability of occurrence** within 2 km of a highway.	**Higher abundance** with increasing exposure to all roads (C4), minor roads (C3; C4) and major roads (C4); effect distances 440-660 m.
		Fernández-Juricic	2000	**Lower density** with higher traffic load in a city.	
		Morelli *et al.*	2015	**Higher occurrence** with increasing road coverage within 100 m radius.	

		Palomino & Carrascal	2007	**Higher abundance** closer to road; effect distance up to 510 m.	
Columba livia domestica	Feral pigeon	Palomino & Carrascal	2007	**Higher abundance** closer to road; effect distance up to 510 m.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3; C4), but **lower abundance** with increasing exposure to major roads (C4); effect distances 70-740 m.
Columba palumbus	Common wood pigeon	Brotons & Herrando	2001	**Lower probability of occurrence** within 500 m of a local road.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 300-920 m.
		Reijnen *et al.*	1995a	**Lower density** of breeding birds in plots adjacent to major roads than those ~400 m away.	
			1995b	**Lower density** of breeding birds in plots adjacent to a major road than those ~700 m away. **Lower density** of breeding birds with higher traffic noise.	
Corvus corone	Carrion crow	Palomino & Carrascal	2007	**Lower abundance** closer to road; effect distance up to 490 m.	**Lower abundance** with increasing exposure to all roads (C4); effect distances 580-770 m.
Corvus monedula	Eurasian jackdaw	Palomino & Carrascal	2007	**Lower abundance** closer to road; effect distance up to 490 m.	**Higher abundance** with increasing exposure to all roads (C4), minor roads (C4) and major roads (C4); effect distances 120-580 m.
Cyanistes caeruleus	Blue tit	Reijnen *et al.*	1995a	**Lower density** of breeding birds with higher traffic noise; effect distances ~790-1750 m.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3; C4), but **lower abundance** with increasing exposure to major roads (C4); effect distances 180-2300 m.
		Rheindt	2003	**Higher abundance** closer to a motorway; compared 100 m and 950 m from the road.	
		Santos *et al.*	2016	Higher than expected roadkill:abundance ratio (both major and minor type roads combined).	
Dendrocopos major	Great spotted woodpecker	Helldin & Seiler	2003	**Lower abundance** within major road-effect zone; defined as 245 m from road. **Lower abundance** with decreasing distance from major roads.	**Lower abundance** with increasing exposure to all roads (C4); effect distances 770-1150 m.
		Morelli *et al.*	2015	**Lower occurrence** with increasing road coverage within 100 m radius.	
		Reijnen *et al.*	1995a	**Lower density** of breeding birds in plot areas closer to major roads.	
		Rheindt	2003	**Lower abundance** closer to a motorway; compared 100 m and 950 m from the road.	
		Wiacek *et al.*	2015	**Lower abundance** closer to a busy road; compared 60 m and 560 m from the road.	
Emberiza schoeniclus	Common reed bunting	Reijnen *et al.*	1995b	**Lower density** of breeding birds with higher traffic noise.	**Lower abundance** with increasing exposure to all roads (C4) and minor roads (C3),
Erithacus rubecula	European robin	Byrkjedal *et al.*	2012	Closer to road streetlights at night-time.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 400-660 m.
		Fuller *et al.*	2007	Birds sang more during the night in noisier urban areas.	
		Reijnen *et al.*	1995b	**Lower density** of breeding birds in plots adjacent to a major road than those ~700 m away.	
		Rheindt	2003	**Lower abundance** closer to a motorway; compared 100 m and 950 m from the road.	

Fringilla coelebs	Common chaffinch	Morelli *et al.*	2015	**Higher occurrence** with increasing road coverage within 100 m.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3; C4), but **lower abundance** with increasing exposure to major roads (C3; C4); effect distances 210-2300 m.
		Reijnen *et al.*	1995a	**Lower density** of breeding birds with higher traffic noise; effect distances ~1500-2800 m.	
			1995b	**Lower density** of breeding birds with higher traffic noise.	
		Rheindt	2003	**Higher abundance** closer to a motorway; compared 100 m and 950 m from the road.	
Fulica atra	Eurasian coot	Reijnen *et al.*	1996	**Lower density** of breeding birds with higher traffic noise; effect distances 20-75 m.	**Lower abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 640-840 m.
Hirundo rustica	Barn swallow	Palomino & Carrascal	2007	**Higher abundance** closer to road; effect distance up to 510 m.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 260-270 m.
Linaria cannabina	Common linnet	Peris & Pescador	2004	**Lower breeding density** near high traffic road compared to lower traffic road.	**Lower abundance** with increasing exposure to all roads (C4), minor roads (C4) and major roads (C3; C4); effect distances 230-2300 m.
Motacilla flava	Yellow wagtail	Milsom *et al.*	2000	**Lower likelihood of presence** closer to roads.	**Lower abundance** with increasing exposure to all roads (C4); effect distances 510 m.
		Morelli *et al.*	2015	**Higher occurrence** with increasing road coverage within 100 m radius.	
Oenanthe oenanthe	Northern wheatear	Peris & Pescador	2004	**Lower breeding density** near high traffic road, compared to low traffic.	**Lower abundance** with increasing exposure to all roads (C4); effect distances 840-1540 m.
Parus major	Great tit	Brotons & Herrando	2001	**Lower probability of occurrence** within 2 km of a highway.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 140-1050 m.
		Fernández-Juricic	2000	**Lower density** with higher traffic load in a city.	
		Grunst *et al.*	2020	Nestlings closer to (minor type) roads have shorter telomeres.	
		Halfwerk *et al.*	2011	**Smaller clutch size and fewer fledglings** with higher traffic noise	
		Holm & Laursen	2011	**Fewer fledglings** near roads with fast and frequent traffic.	
		Mockford & Marshall	2009	Songs had higher minimum frequencies in noisier, urban territories.	
		Morelli *et al.*	2015	**Higher occurrence** with increasing road coverage within 100 m radius.	
		Rheindt	2003	**Lower abundance** closer to a motorway; compared 100 m and 950 m from the road.	
		Santos *et al.*	2016	Higher than expected roadkill:abundance ratio (both major and minor type roads combined).	
		Slabbekoorn & den Boer-Visser	2006	Songs were shorter and faster, and had higher minimum frequencies in urban environments.	
		Slabbekoorn & Peet	2003	Songs had higher minimum frequencies in noisier, urban environments.	
		Wiacek *et al.*	2015	**Higher abundance** closer to a busy road; compared 60 m and 560 m from the road.	
Passer domesticus	House sparrow	Brotons & Herrando	2001	**Higher probability of occurrence** within 500 m of a major road.	**Higher abundance** with increasing exposure to all roads

		Palomino & Carrascal	2007	**Higher abundance** closer to road; effect distance up to 510 m.	(C4) and minor roads (C3; C4), but **lower abundance** with increasing exposure to major roads (C3; C4); effect distances 260-510 m.
		Peris & Pescador	2004	**Higher breeding density** near high traffic road, compared to low traffic.	
Passer montanus	Tree sparrow	Gamalo & Baril	2018	**Higher abundance** closer to a highway, measured along a 500 m transect.	**Higher abundance** with increasing exposure to all roads (C4); effect distances 290 m.
Phasianus colchicus	Ring-necked pheasant	Reijnen *et al.*	1995a	**Lower density** of breeding birds in plots adjacent to major roads than those ~400 m away. **Lower density** of breeding birds with higher traffic noise/visibility; effect distances ~45-90 m.	**Lower abundance** with increasing exposure to all roads (C4), minor roads (C3; C4) and major roads (C3; C4); effect distances 590-2300 m.
			1995b	**Lower density** of breeding birds in plots adjacent to a major road than those ~700 m away. **Lower density** of breeding birds with higher traffic noise.	
Phylloscopus collybita	Common chiffchaff	Reijnen *et al.*	1995a	**Lower density** of breeding birds in plots with high noise load adjacent to major roads than those ~400 m away.	**Lower abundance** with increasing exposure to all roads (C4), minor roads (C4) and major roads (C4); effect distances 70-1150 m.
			1995b	**Lower density** of breeding birds in plots adjacent to a major road than those ~700 m away, and in plot areas closer to a major road.	
		Rheindt	2003	**Lower abundance** closer to a motorway; compared 100 m and 950 m from the road.	
Phylloscopus trochilus	Willow warbler	Foppen & Reijnen	1994	Larger dispersal distances, directed away from the road, of yearling males within 200 m of a highway.	**Lower abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 1050-2300 m.
		Kuitunen *et al.*	1998	**Lower abundance** closer to highways; compared 25 m and 200 m from the roads.	
		Reijnen & Foppen	1991	Male site-tenacity lower, and dispersal distances larger, within 200 m of a highway.	
			1994	**Lower density** of older males, and lower proportion of successful yearling males, within 200 m of a highway.	
		Reijnen *et al.*	1995a	**Lower density** of breeding birds in plots adjacent to major roads than those ~400 m away and in plot areas closer to major roads when car visibility is high. **Lower density** of breeding birds with higher traffic noise/visibility; effect distances ~180-1750 m.	
			1995b	**Lower density** of breeding birds in plots adjacent to a major road than those ~700 m away, and in plot areas closer to a major road. **Lower density** of breeding birds with higher traffic noise.	
Picus viridis	European green woodpecker	Morelli *et al.*	2015	**Lower occurrence** with increasing road coverage within 100 m radius.	**Lower abundance** with increasing exposure to all roads (C4); effect distances 260-1420 m.
Regulus regulus	Goldcrest	Helldin & Seiler	2003	**Lower abundance** within major road-effect zone; defined as 245 m from road.	**Lower abundance** with increasing exposure to minor roads (C3); effect distances 180-840 m.
		Reijnen *et al.*	1995a	**Lower density** of breeding birds in plots adjacent to major roads than those ~400 m away, and in plot areas	

				closer to major roads. **Lower density** of breeding birds with higher traffic noise; effect distances ~100-120 m.	
Sitta europaea	Eurasian nuthatch	Rheindt	2003	**Lower abundance** closer to a motorway; compared 100 m and 950 m from the road.	**Lower abundance** with increasing exposure to all roads (C4); effect distances 2170-2300 m.
		Wiacek *et al.*	2015	**Lower abundance** closer to a busy road; compared 60 m and 560 m from the road.	
Sturnus vulgaris	European starling	Walthers & Barber	2019	Traffic noise (major road level) has no effect on nestling physiological stress.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3), but **lower abundance** with increasing exposure to major roads (C3); effect distances 280-1150 m.
Sylvia atricapilla	Eurasian blackcap	Brotons & Herrando	2001	**Lower probability of occurrence** within 2 km of a highway.	**Lower abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 920-1600 m.
		Reijnen *et al.*	1995a	**Lower density** of breeding birds in plots with high noise load/visibility of cars adjacent to major roads than those ~400 m away and in plot areas closer to major roads when car visibility is high. **Lower density** of breeding birds with higher traffic noise, in plots of high noise load.	
		Rheindt	2003	**Lower abundance** closer to a motorway; compared 100 m and 950 m from the road.	
		Santos *et al.*	2016	Higher than expected roadkill:abundance ratio (both major and minor type roads combined).	
Sylvia communis	Common whitethroat	Morelli *et al.*	2015	**Higher occurrence** with increasing road coverage within 100 m radius.	**Higher abundance** with increasing exposure to all roads (C4); effect distances 100-130 m.
		Reijnen *et al.*	1995b	**Lower density** of breeding birds in plots adjacent to a major road than those ~700 m away.	
Troglodytes troglodytes	Eurasian wren	Morelli *et al.*	2015	**Lower occurrence** with increasing road coverage within 100 m radius.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 140-230 m.
		Reijnen *et al.*	1995a	**Lower density** of breeding birds with higher traffic noise; effect distances ~30-60 m.	
			1995b	**Lower density** of breeding birds in plots adjacent to a major road than those ~700 m away, and in plot areas closer to a major road. **Lower density** of breeding birds with higher traffic noise.	
		Rheindt	2003	**Lower abundance** closer to a motorway; compared 100 m and 950 m from the road.	
		Santos *et al.*	2016	Lower than expected roadkill:abundance ratio (both major and minor type roads combined).	
Turdus merula	Common blackbird	Brotons & Herrando	2001	**Lower probability of occurrence** within 2 km of a highway.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3; C4), but **lower abundance** with increasing exposure to major roads (C3; C4); effect distances 130-920 m.
		Nemeth & Brumm	2009	Songs had higher minimum frequencies and intervals between songs were shorter in urban environments.	
		Peris & Pescador	2004	**Lower breeding density** near high traffic road compared to lower traffic road.	
		Reijnen *et al.*	1995b	**Lower density** of breeding birds in plots adjacent to a major road than those ~700 m away, and in plot areas	

				closer to a major road. **Lower density** of breeding birds with higher traffic noise.	
		Rheindt	2003	**Lower abundance** closer to a motorway; compared 100 m and 950 m from the road.	
Turdus philomelos	Song thrush	Reijnen *et al.*	1995a	**Lower density** of breeding birds in plot areas with high noise load closer to major roads.	**Higher abundance** with increasing exposure to all roads (C4) and minor roads (C3); effect distances 300-420 m.
			1995b	**Lower density** of breeding birds in plot areas closer to a major road. **Lower density** of breeding birds with higher traffic noise.	
		Rheindt	2003	**Lower abundance** closer to a motorway; compared 100 m and 950 m from the road.	
Vanellus vanellus	Northern lapwing	Helldin & Seiler	2003	**Lower abundance** within major road-effect zone; defined as 285 m from road.	**Lower abundance** with increasing exposure to all roads (C4); effect distances 1540 m.
		Reijnen *et al.*	1996	**Lower density** of breeding birds with higher traffic noise; effect distances 120-560 m.	
		van der Zande	1980	**Lower density** closer to both major and minor roads; effect distances 200-2000 m.	

Possible mechanisms behind my findings

As explained in the introduction of this thesis, noise is thought to be the most important mechanism by which roads affect birds (Reijnen et al. 1997; Rheindt 2003; McClure et al. 2013). Given the large distances over which I found the associations between roads and bird abundance to exist, it is likely that traffic noise is playing a major part. This idea is further supported by variation in associations between birds and different road types. As I predicted, more negative associations were found with major roads, which have much higher traffic levels and therefore greater noise loads, compared to minor roads. Road noise may also be the reason I found smaller-bodied and migrant species to be in relatively lower abundance around roads. Smaller-bodied birds have generally quieter communication which may be more masked by traffic noise (Ryan & Brenowitz 1985; Parris & Schneider 2009; Rheindt 2003), and it has previously been suggested that migrant birds may be less able to adapt to noise disturbance (Mammides et al. 2016; Laurance 2015).

Collisions with vehicles also kill large number of birds (Erritzoe et al. 2003), and this may be another factor behind our finding of more negative associations between roads and smaller-bodied birds, which are possibly more difficult for drivers to notice when they fly across roads. Collision mortality may also be more important for some species that appear able to tolerate human disturbance (and thus likely not repelled by roads) but are frequently killed on the roads, for example ring-necked pheasants and common buzzards (Project Splatter 2020). Roads also produce chemical pollution (Sanderfoot & Holloway 2017) and visual disturbances (Forman & Alexander 1998; Day 2003; Vliet et al. 2010; Kociolek et al. 2011), which may be impacting both birds that nest on roadsides, including some of the passerine species in this study, and nocturnal birds respectively.

Roads can also provide benefits – while artificial light can have a detrimental effect on some species, for others, it allows them a longer daily activity period (Byrkjedal et al. 2012). This may be behind our finding of higher abundance of European robins around roads. Additionally, roads can be sources of food, grit and heat, and powerlines, which are often co-located with roads, can provide perches and nesting structures (Morelli et al. 2014).

The impact of roadside habitat, versus that of the road itself, is difficult to tease out here. Britain has very few areas of lowland semi-natural habitat and so road verges containing hedgerows and trees may be important for some species. At the same time, edge habitat created by roads (Meunier et al. 1999; Helldin & Seiler 2003), or already in existence when the roads were built, may repel or attract species too. Although I incorporated habitat in my models, it was not captured at high enough resolution to account for subtle changes in roadside areas and therefore some of my findings, particularly the positive associations between minor roads and many bird species, may be largely down to habitat variation. In addition, roadside habitat may influence detectability to an extent perhaps not picked up by my detectability models, which may then have affected my later results. Nevertheless, the similarity of my results with and without detectability included suggest this impact is small, and the findings of previous studies that have controlled for the potential impacts of habitat (Reijnen et al. 1995; 1996), increase the probability that the associations, particularly the negative ones, that I found between roads and bird populations are not solely down to habitat variation. In addition, I found no significant differences between the relative effect size of roads for birds associated with different habitats, other than those occupying freshwater sites (**Figure 2**).

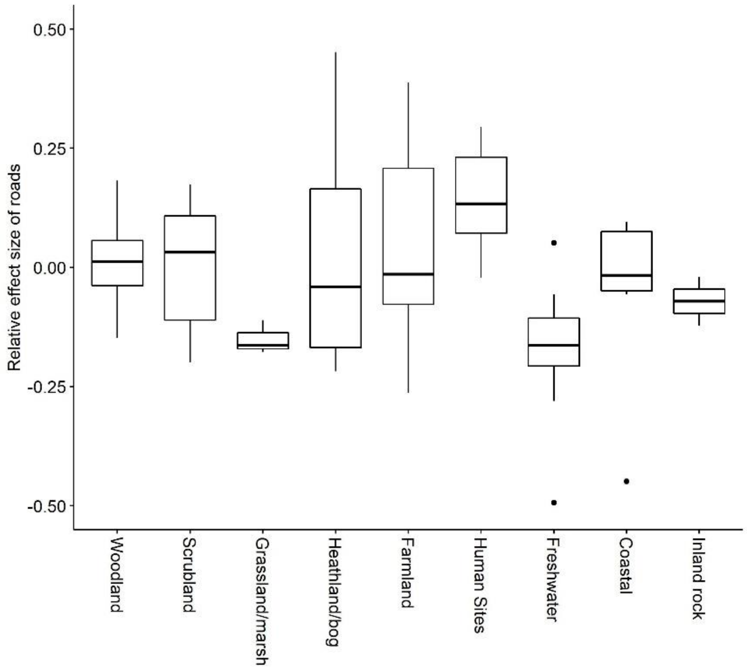

Figure 2. Relative road effect size for species associated with different habitats. For each of the 75 species, the habitat assigned was the one containing the highest proportion of observations of that species. The only habitat significantly different from any others was freshwater (Tukey's test: freshwater/woodland $P = 0.014$; freshwater/farmland $P = 0.02$; freshwater/human sites $P < 0.0001$).

Overall, behind the results of Chapters 3 and 4, it is likely that a combination of mechanisms is at play, along with habitat impacts, and that the relative importance of these varies in different areas and around different road types. It is likely that habitat variation is responsible for many of the positive associations between bird abundance and roads, while noise disturbance is likely to be driving most of the negative associations. As in both Chapters 3 and 4 I found some species to be associated positively with minor roads and negatively with major roads, it is possible that, even for species attracted to roads for habitat or other benefits, thresholds of traffic disturbance exist, beyond which the benefits of being near a road are outweighed by the costs.

Broader context and further research

Despite the correlative nature of my analyses, my results suggest that roads may modify bird populations on a large scale. However, given that I found some species to be in higher abundance with increasing road exposure, while others were in lower, it is not just population changes that should be considered but shifts in the structures of whole communities. My finding of species with larger national populations having generally higher abundance with increasing road exposure, while rarer species had lower abundance, suggests that roads may benefit generally common species at the expense of others. It is possible that roads contribute to the reduced national abundance of some species, or, conversely, rarer species may be more likely to be negatively impacted by, or avoid, roads and roadside habitat if their rarity is, in part, due to a reduced ability to thrive under human disturbance in general. Similar patterns have been identified in other human-disturbed environments, with urban (Clergeau et al. 2006; Newbold et al. 2018), agricultural (Finch et al. 2019) and warming (Thuiller et al. 2011; Davey et al. 2012) environments being linked to reduction of some species and simultaneous replacement by other species. It is suggested that these processes may be leading to simplification of biodiversity across large areas (McKinney & Lockwood 1999; Le Viol et al. 2012; McGill et al. 2015; Sullivan et al. 2016; Newbold et al. 2018). My results indicate that roads may contribute to this simplification effect, maintaining total bird numbers but reducing species richness and diversity, a suggestion backed by previous studies that found reduced avian diversity around roads (e.g. Rheindt 2003; Arevalo & Newhard 2010; Wiacek et al. 2015; Mammides et al. 2016; Gamalo & Baril et al. 2018; Senzaki et al. 2020).

To understand further the magnitude, and importance, of impacts of roads on birds in Britain, research focused on temporal trends will be important. The data I used in this study are available, in the same or similar formats, for the past 20 years. Moving forward, I plan to broaden out my analyses to consider how bird populations have changed in relation to changes in roads and traffic volumes over this time period. This will give some insight into how much roads could be responsible for bird population changes in Britain over the past half-century. Smaller-scale studies in Britain could help to tease apart the importance of impacts such as noise, light, and air pollution, and wildlife-vehicle collisions (the latter of which are already being monitored; Project Splatter; Schwartz et al. 2010). Studies comparing transects situated at differing distances from roads could also be helpful in determining the importance of these different mechanisms. In addition to this, those able to determine the level of causality between roads and variation in bird abundance would be very useful. Bird populations could be analysed in areas where roads have been opened or closed, or where traffic levels have varied contrarily. Ideally, higher-resolution habitat data should be captured, to establish how much of the effects seen are due to the influence of roadside habitat as opposed to the road itself. Looking further afield, there are likely many areas of the world with sufficient road and bird data in which a repeat of this work could be attempted. Given that Britain is not alone in having a dense road network (**Figure 1**), it would be interesting to see if patterns from this study hold in other countries, particularly those without typical western European landscapes. International collaborations with comparisons between different countries could yield a wealth of information on road impacts across different scales, species and habitats, which could help to inform mitigation efforts. Finally, studies that consider the structure of bird populations, and breeding success, will also be important as solely considering abundance overlooks the possibility of low-quality habitat, in which birds' productivity is limited, being occupied out of necessity in years of higher overall population abundance (Reijnen & Foppen 1995; Reijnen et al. 1997).

Mitigation

In a global, as well as a national context, these potential impacts of roads on bird populations and communities could be substantial. Yet, to date, roads have largely been overlooked as a threat to biodiversity at governmental level. The total global road length is expected to increase by nearly 60% by 2050 (Dulac 2013) and the number of vehicles using it is expected to double (WEC 2011; Meyer 2012), but few countries appear to consider road and traffic mitigation as a necessity. Only 10% of the 6th National Reports submitted for the Convention on Biological Diversity (via the Clearing-House Mechanism) mention roads as a threat to biodiversity (C. Maney, unpubl. data). In Britain, traffic levels are forecast to increase up to 51% (of the 2015 level) by 2050 (DfT 2018b). Highways England, the organisation responsible for major roads in Britain, recognises that roads and their surrounding areas have the potential both to negatively impact wildlife and to provide important habitats (Highways England 2015a), but the UK Government's 25-year Environment Plan (HM Government 2018a) predominantly mentions the impacts of roads, namely air pollution, litter and chemical run-off, only in terms of their direct impacts on people.

The best methods of mitigating road impacts are clearly to reduce the number of vehicles, by e.g. increasing available and affordable public transport, to reduce the number of roads and to plan their locations better. The mean effect distance of 700 m that I found for negative associations covers 72% of Great Britain and 41% of the total area of terrestrial protected sites. Considering just Special Protection Areas (SPAs; areas designated under the EU Birds Directive), 22% of their total area lies within 700 m of a road, though these figures vary by country (**Table 3**; **Figure 3**). That 41% of Britain's protected areas are already potentially being impacted by roads should be a matter for immediate attention and closure of non-essential roads near sensitive areas should be considered. The planning of new roads should also take into account, and ideally avoid, these areas.

Table 3. Percentage of total land area, protected areas and SPAs that lies within 700 m of a road.

	England	**Wales**	**Scotland**	**Great Britain**
Total area	87%	79%	45%	72%
Protected areas	54%	48%	19%	41%
SPAs	36%	26%	13%	22%

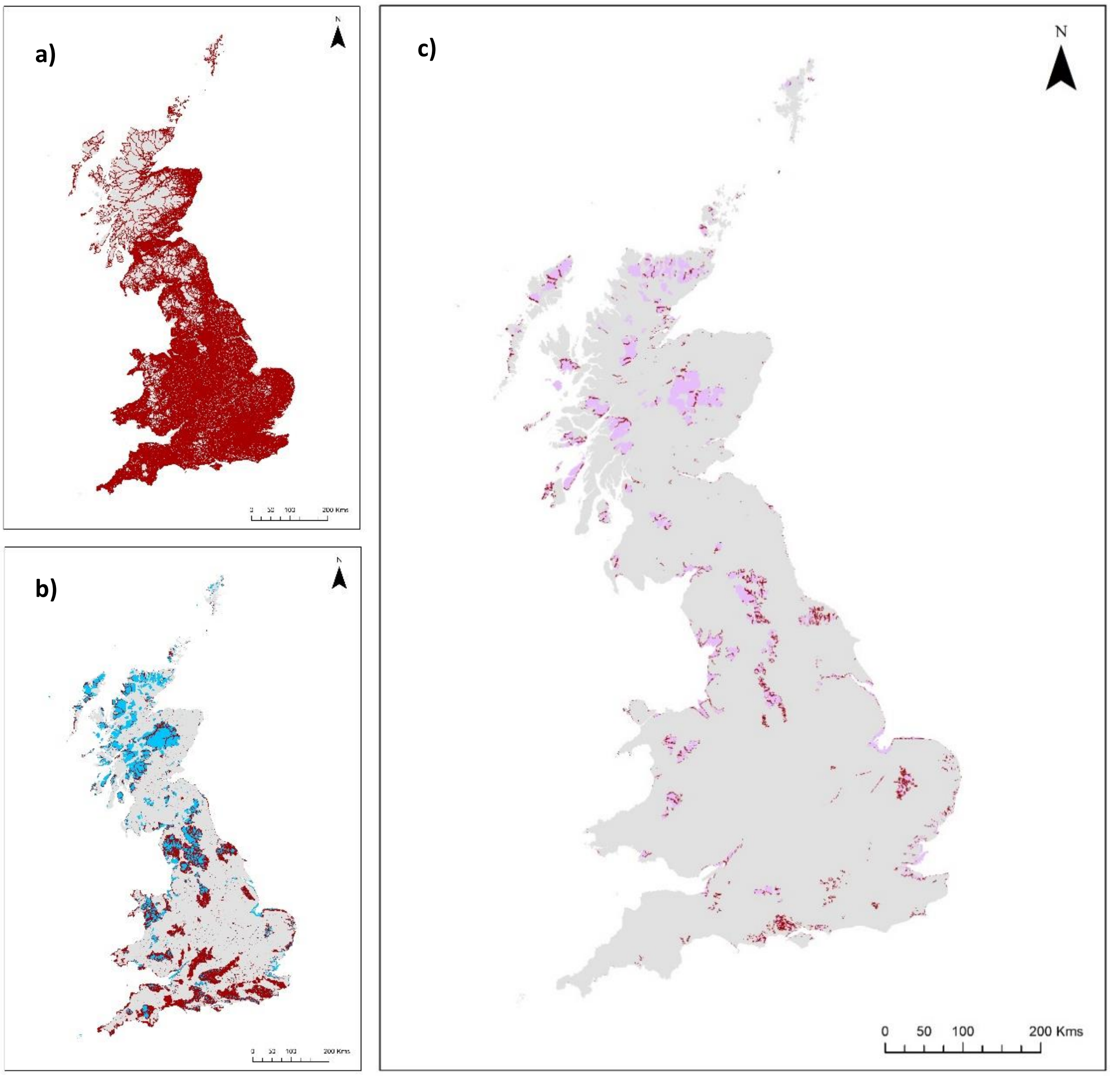

Figure 3. Areas of **a)** Great Britain, **b)** protected areas and **c)** SPAs that lie within 700 m of a road. Colour representation is as follows: grey is the land area of Great Britain; blue is protected areas; lilac is SPAs; and dark red is the affected areas of all three categories.

Secondary to these efforts, remaining impacts should be minimised as much as possible. For adequate mitigation of roads, an understanding of the relative importance of different impact mechanisms is usually necessary. However, given the scale of the potential impacts of roads on birds and other taxa, mitigation is likely required before a full understanding can be achieved.

Reijnen et al. (1997) suggested that, as noise is probably the most important road impact mechanism, measures to reduce the noise load would be a useful starting point. As we move toward the UK’s aim of combustion engine-powered car sales ceasing by 2035 (HM Government 2018b; BBC 2020), in favour of electric vehicles, we can expect traffic noise resulting from engines to decrease. However, much of this noise comes not from vehicle engines but from the interaction between tyres and the road surfaces, particularly at higher speeds (Li 2018). There is good evidence to suggest this can be reduced by the use of “low noise road surfacing”, which is produced using smaller aggregate material (Highways England 2015b) or by the inclusion of rubber in the road surface. The latter can simultaneously be a good use of old tyres (Kehagia & Mavridou 2014), which can cause environmental issues if simply discarded (Guardian 2002). Speed reductions in sensitive areas, particularly during the breeding season, should also be considered. Artificial noise barriers can also be used (Ishizuka & Fujiwara 2004), but these must be designed in ways such that they do not worsen the issue of habitat fragmentation by preventing wildlife from crossing roads, i.e. in conjunction with wildlife bridges and tunnels. Unfortunately, the ability of hedgerows to dampen road noise is limited (van Renterghem et al. 2014) but thick tree lines can be of some use (Dobson & Ryan 2000; Samara & Tsitsoni 2011; van Renterghem et al. 2015) if planted correctly and, if these are grown over the top of the road, they can reduce barrier effects (Goosem 2007). New roads may also be sunk into the surrounding area to reduce the distance over which noise disturbance reaches (as well as mortality to some extent; Erritzoe et al. 2003), but there is limited evidence as to the efficacy of this method.

In terms of mitigation for birds, it is not only the amplitude and distance of noise that should be taken into account, but also its frequency. Previous studies have shown species that have songs or calls with frequencies overlapping those of traffic noise to be more likely to avoid road areas and some species to shift the frequencies of their vocalisations (e.g. Mockford & Marshall 2009; Nemeth & Brumm 2009; Parris & Schneider 2009; Hu & Cardoso 2010; Francis et al. 2011). As there are concerns that the reduced noise of electric vehicles may increase the risk of vehicle collisions with people, some electric cars produce artificial noise (BBC 2019). If this use of artificial noise is to become widespread, the frequency of that noise, in the context of impacts on wildlife, should be considered. In addition, when any noise-reducing methods are implemented, opportunities should be taken to measure the effect this mitigation has on road impacts on wildlife.

Whilst the use of hedgerows as road noise attenuators is limited, both hedgerows and trees can reduce visual disturbance, provide important habitats and potentially function as ecological corridors. In some cases, they have the potential to reduce collisions, by encouraging birds to fly higher over the roads (Erritzoe et al. 2003). However, there is a risk of roadside habitats functioning as population sinks, attracting birds and other wildlife that then suffer collisions, predation or reduced health or breeding success due to their increased proximity to the road (Pescador & Peris 2007; Orlowski 2008; Holm & Laursen 2011; Sanderfoot & Holloway 2017; Grunst et al. 2020). Improving roadside habitat therefore needs implementing alongside other mitigation measures. Alternatively, compensation could be attempted by the creation of new habitats in areas away from roads (Reijnen et al. 1997; Reijnen & Foppen 2006) but in countries such as Britain, few such areas exist.

Birds are not unique in their sensitivity to roads. Roads can affect individuals and populations of many taxa, including mammals, amphibians, fish and invertebrates (Fahrig & Rytwinski 2009; Benitez-Lopez et al. 2010; Crovo et al. 2015; Muñoz et al. 2015). It is also becoming increasingly evident that humans are not exempt either. Road products, in particular noise and air pollution, have been linked to increases in various illnesses in people, including strokes and cardiovascular, allergic and respiratory diseases (Maheswaran & Elliott 2003; Krzyżanowski et al. 2005; Ndrepepa & Twardella 2011). Some mitigation is already being undertaken to reduce these impacts on people in Britain, through schemes such as the Clean Air Strategy (DEFRA 2019b), DEFRA's Noise Action Plan for Roads (DEFRA 2019c) and Highways England's Noise Insulation Scheme (gov.uk 2019), and in the planning of some new roads (A14 Improvement Scheme; Highways England 2015b), but as of yet there are no broad scale aims to reduce the full suite of impacts of roads on wildlife and the environment. Rather than impacts on people and various taxa being considered separately, a multi-species (including humans) approach to road mitigation (Polak et al. 2019) could be more effective and efficient and this should be considered as imperative, both in Britain and further afield.

Conclusion

This study represents the first in-depth, high-resolution and broad-scale analysis of the spatial relationships between roads and bird populations. I found that detectability of birds in field surveys varies with exposure to roads, that many bird species change in abundance as road exposure increases, and that roads could be contributing to broad-scale simplification of avian communities. Future studies to pull apart the importance of different mechanisms, for example noise, from that of roadside habitat in Britain would be helpful, as would those better able to determine extents of causality, as opposed to correlation, between roads and bird populations. Regardless, given my results and those of previous studies, along with the current reach of the global road network and the expected growths in both total road length and traffic volume, an increased focus on mitigation of road impacts on birds, other wildlife, and people, is of urgent necessity.

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Appendix A. Methodology

Bird data

To produce bird count estimates for this study, I obtained data from the UK Breeding Bird Survey (BBS). For this survey 1-km squares are selected from those in the British National Grid using a stratified random sampling design (BTO 2019). Surveyors are only recruited if able to identify all British bird species by sight and sound, meaning BBS data is not significantly affected by surveyor experience (Eglington *et al*. 2010). Each square is surveyed annually in two early morning visits during the breeding season (early visit: beginning of April to mid-May; late visit: mid-May to end-June). On each visit, the surveyor walks two 1-km transects, each divided into five 200-m transect sections. These transects mostly do not run alongside roads (64% of the transect sections used in this analysis did not follow a paved road along any part of them). While walking a transect, surveyors note every bird they see or hear in each transect section, along with the estimated perpendicular distance of each bird from the transect (recorded as one of four distance bands: 0-25 m; 25-100 m; > 100 m; flying over the area). They also record the dominant habitat type in each 200-m transect section as one of nine broad classes: woodland (dominated by trees generally taller than 5 m); scrubland (dominated by woody shrubs or young trees shorter than 5 m); semi-natural grassland and marsh (dominated by grasses or by wet communities dominated by rushes/sedges/reeds etc); heathland and bogs; farmland (enclosed fields); human sites (areas associated with people i.e. buildings, parks and gardens); water bodies (freshwater); coastal; and inland rock. For full methods see BTO (2019).

For my analyses, I extracted counts from BBS squares that had been surveyed every year from 2012-2014 inclusive. I selected three years to increase the sample size of counts for each species and to average-out the effect of annual population fluctuations whilst avoiding long-term abundance changes. Within each square, I excluded transect sections that did not have both habitat and route data recorded. I then extracted counts of birds in the distance bands 0-25 m and 25-100 m, excluding those from the other two bands as they did not have both lower and upper distance limits.

Chapter 2

To produce the final data for the distance sampling models in Chapter 2, I then performed the following. Within the counts for each species, I removed those from habitat types with total count < 20. As a level of pseudoreplication was expected, for each species I calculated the correlation between counts at transect sections in 2012 and 2013, and in 2013 and 2014. If the mean of these two (Pearson's) correlation coefficients was ≥ 0.6, a cut-off considered to be sufficiently conservative, I used only data from 2013 for that species, otherwise data from all three years were used. Following this, I extracted species with total count > 1,000, as preliminary analyses indicated this to be a minimum threshold requirement for model convergence. This resulted in a final dataset of 63 bird species with survey visit and year specific raw bird count values for each of 19,909 200-m transect sections in 2,034 BBS squares spread widely across Britain (**Figure A1**).

Chapter 3

For Chapter 3 I used the 51 species that I was able to analyse successfully in Chapter 2. Taking the dataset that was produced before any Chapter 2 specific modifications, for each species I chose one focal survey visit to represent its breeding abundance – the early visit for resident species and the late visit for migrant species. I used counts from that visit to calculate the mean annual bird count in each transect section for that species, summing over both distance bands, and averaging over years. Where transect sections had multiple habitats recorded across the years, I assigned a single habitat to each section, using the procedure outlined in **Figure A2**. My final dataset contained counts from 19,709 200-m transect sections, in 2,033 1-km BBS squares.

Following this, for each species, I removed any transect sections with habitats that had been excluded for that species in the production of the distance sampling models in Chapter 2 (i.e. those with total count < 20). This process gave us mean annual bird count estimates for all 51 species around each 200-m transect section. As I chose to use counts within 100 m of each transect section (from the 0-25 m and 25-100 m distance bands), each mean annual count estimate pertained to a maximum area of 200 m x 200 m.

Chapter 4

In preparing data for Chapter 4, I used the same methods as for Chapter 3, except I included all species with a total mean annual bird count > 100 and retained all habitat categories in the data for each species, to maximise the sample sizes. I excluded two winter flocking species: fieldfare *Turdus pilaris* and golden plover *Pluvialis apricaria*, as their flocks can persist into the start of the breeding season, potentially affecting model results. I also removed any transects with mean annual counts > 10 for three wading bird species: Eurasian curlew *Numenius arquata*, northern lapwing *Vanellus vanellus* and Eurasian oystercatcher *Haematopus ostralegus*, to exclude counts from non-breeding flocks.

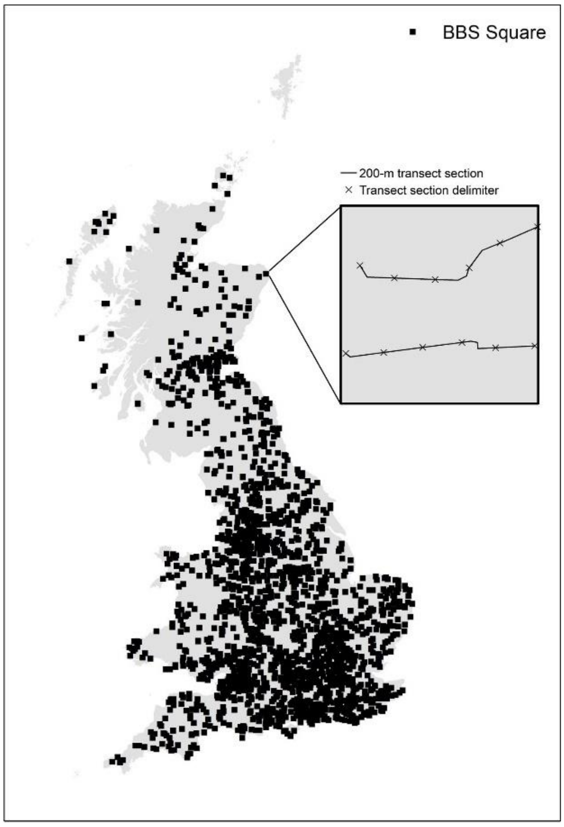


Figure A1. Locations of BBS squares used in this study with an inset example of the layout of a BBS square, crossed by two 1-km transects.

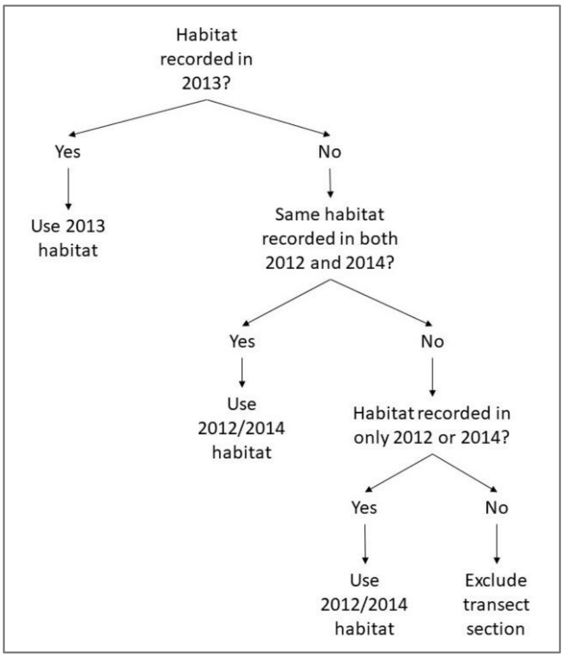


Figure A2. Procedure used to assign a single habitat class to transect sections with multiple habitats recorded across the three-year period.

Road data

Road maps

I obtained shapefiles for all roads in every region of Great Britain, excluding the Isles of Scilly, from the Ordinance Survey Open Data's (OS Open Data 2016) Meridian 2 dataset for January 2013 (Meridian 2 v1.2 Release 1 2013), supplied by Global Mapping Ltd (Global Mapping Ltd 2016). There are five classifications of roads in Great Britain: motorways; A-roads; B-roads; classified unnumbered (known informally as C-roads); and unclassified roads (known informally as D-roads) (DfT 2012). I combined all motorways and A-roads into one shapefile – major roads – and all B-, C- and D-roads into another shapefile – minor roads.

Major road traffic data

I obtained traffic data for major roads but was unable to do the same for minor roads as data are collected for only a small selection of minor roads. For major roads, I downloaded traffic data from the Department for Transport's Traffic Counts website in the form of estimated annual average daily flow values (AADF; DfT 2016). These are the number of motorised vehicles passing specific points (traffic count points) in the road network each day and are obtained through a combination of manual and automated traffic counts. Each traffic count point covered a section of road delimited by two section junctions (**Figure A3**). For each traffic count point, I calculated the mean of the annual average daily flow (AADF) for all motor vehicles from 2012-2014 inclusive.

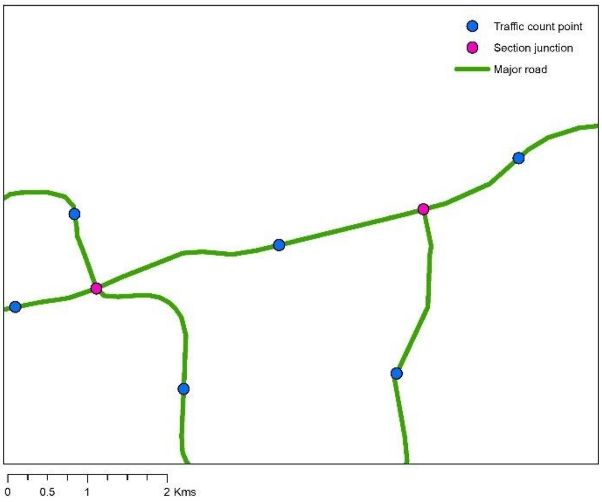


Figure A3. Traffic count points and section junctions along major roads.

I identified 297 (1.6%) traffic count points that were missing data for one or more years, had changed location, or showed sudden changes in traffic levels due to road alterations or upgrades. To process these points, I used the following protocol:

1. I established whether the roads had been closed in any year, using a combination of online information and printed road maps. If they had been, I listed the AADF for them as zero in that year.
2. Where the roads had been upgraded or altered during the three years, or the traffic count points/links had moved, I used only the AADF data from 2013.
3. I used interpolation to provide AADF estimates for any remaining gaps in the data.

I then combined (i.e. dissolved) all the individual roads in the previously created major roads shapefile. Following this, I split them at each traffic section junction, to define the road sections relating to each traffic count point (**Figure A4**). I then attributed the traffic count data to its corresponding road sections and searched for errors. Methods to do this included calculating, and identifying, large distances between each traffic count point or section junction and the nearest major road section, and identifying unexpectedly short road sections. Short road sections were often slip roads, which would cause duplication in the traffic data or incorrect divides between sections. I also visually inspected high-density road areas, i.e. cities, where errors were more common. I then corrected all identified errors (**Figure A5**).

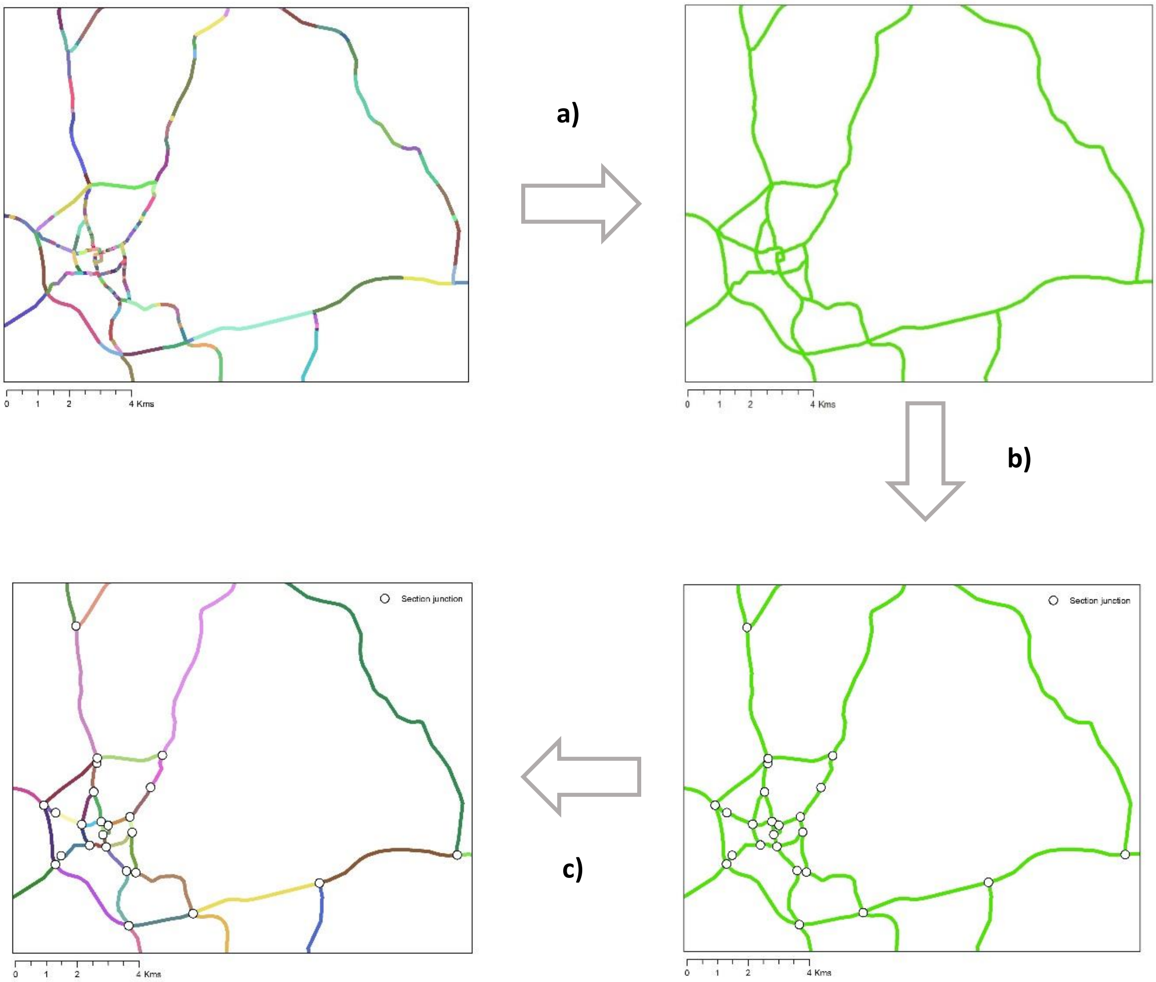


Figure A4. The process of a) combining all major roads before b) overlaying section junctions and c) splitting the roads at each section junction. Different shades of green represent different major road sections.

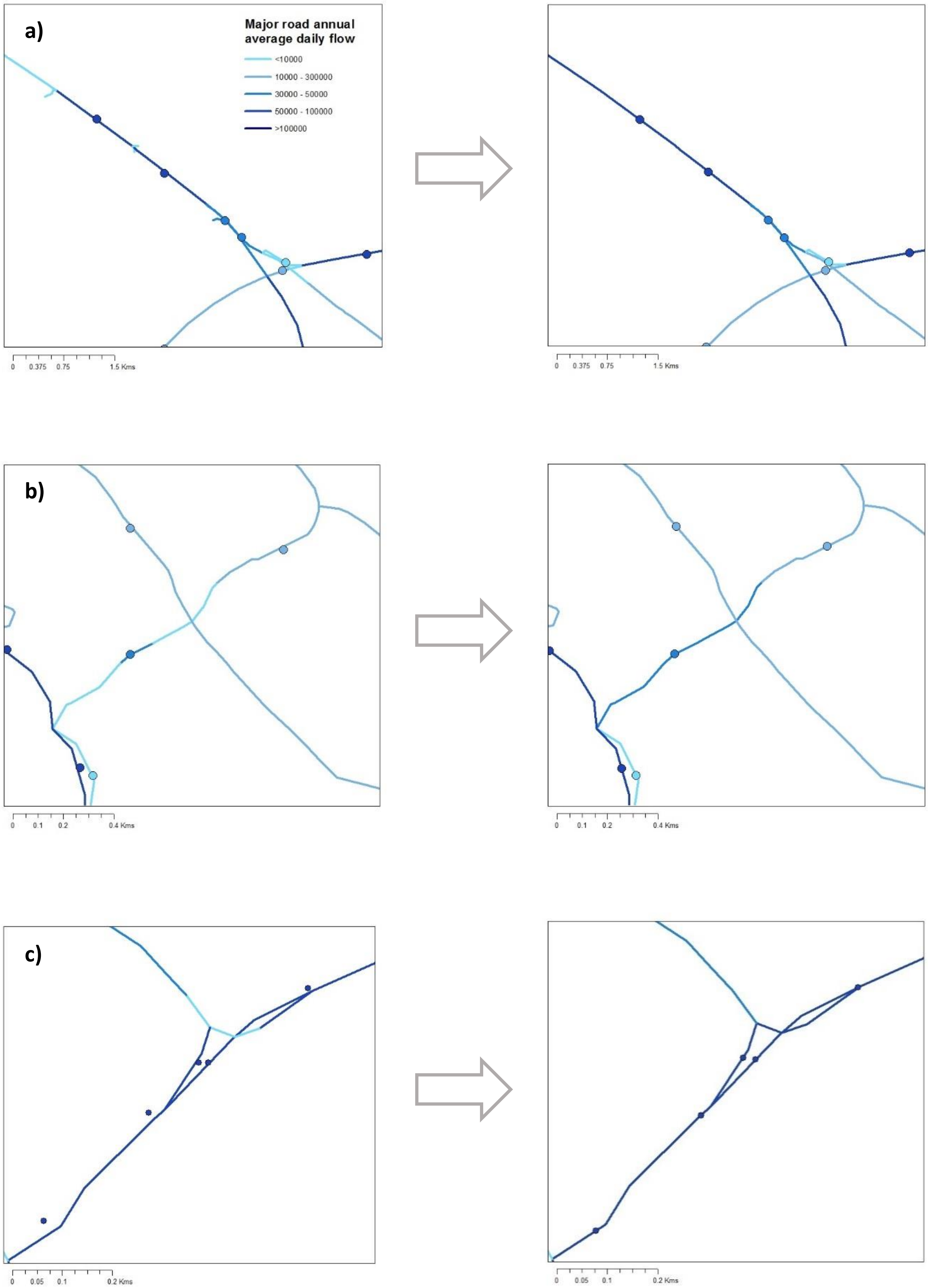


Figure A5. Examples of the editing required to create the final major road shapefiles. Traffic count points are pictured as circles, major roads as lines. In a) slip roads needed removing, in b) the incorrect short road section needed removing, and in c) the traffic count points needed aligning with the roads.

Calculating road exposure

Chapters 2 & 3

I placed points (hereafter kernel points) at intervals of 100 m along every road (**Figure A6**). For those on major roads, I attributed the traffic level of their corresponding road section to them. I then identified all kernel points within a 5-km radius of each BBS 200-m transect section midpoint (**Figure A7**). I chose this distance on the assumption that it was greater than the maximum distance that any effect of a road on an observer, or a bird, would reach.

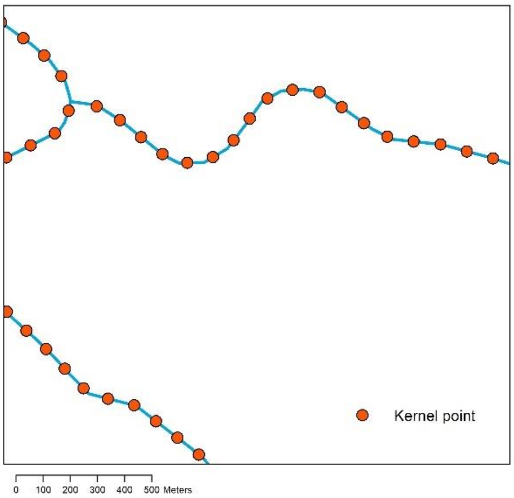


Figure A6. An example of a section of roads with kernel points placed every 100 m along them.

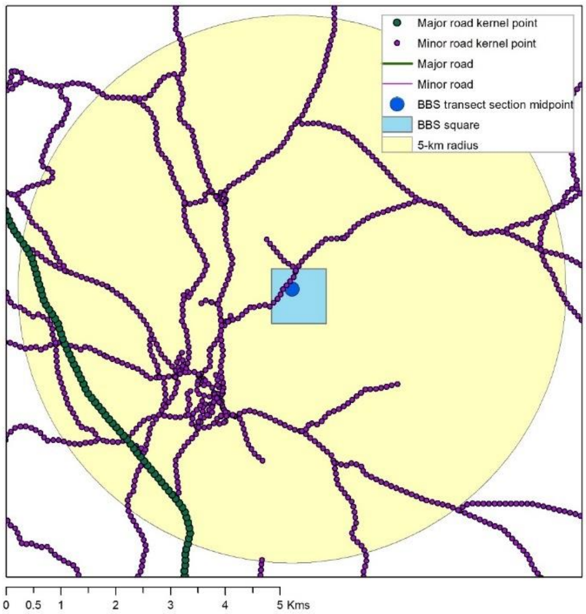


Figure A7. An example of the 5-km radius placed around the midpoint of a 200-m BBS transect section within a BBS square. This particular transect section midpoint has one major road within 5 km and several minor roads. The major and minor roads have kernel points placed along them, at every 100 m.

As some road impacts are likely to act on bird abundance/bird behaviour/observers in areas around roads (e.g. noise disturbance and habitat effects), but others only on or over the road surface itself (e.g. collisions and perching opportunities), I assumed a negative exponential relationship between distance from a road and the exposure of a transect midpoint to that road, with road exposure being highest on the road itself and declining with distance. I used the following formulae to calculate road exposure at each transect midpoint:

Exposure to major roads (MJE) = $\sum(t_i * \exp(-d_i * k_{major}))$

Exposure to minor roads (MNE) = $\sum(\exp(-d_i * k_{minor}))$

Where:

d_i *= distance from the midpoint of the transect section to kernel point i*
t_i *= traffic level at kernel point i, measured as annual average daily flow (AADF)*
k_{major} *= parameter determining the scale of the relationship between major road exposure and distance from a major road*
k_{minor} *= parameter determining the scale of the relationship between minor road exposure and distance from a minor road*

As k_{major} or k_{minor} increases, road exposure at distance d decreases (**Figure A8**). The values of k_{major} and k_{minor} were optimised using bisection searches applied within the distance sampling (Chapter 2) or GAMM (Chapter 3) framework by running multiple models with a range of k_{major}/k_{minor} values and selecting those that produced the models with the highest log-likelihood (**Figure A9**). For both k_{major} and k_{minor} I chose limits of 1 and 100 as these assume that road exposure (when not weighted by traffic) approaches zero at approximate distances of 5 km and 0.05 km respectively, which I thought were above and below the distance expected. I did not evenly space the k values, due to the non-linear relationship between k and distance, but tested values of: 1-20 in increments of 1; 25-45 in increments of 5; and 50-100 in increments of 10. If no peak in log-likelihood could be identified, I excluded that road type from the analysis for that species.

Chapter 4

For Chapter 4, I adopted a slightly simpler approach for calculating road exposure. I calculated road exposure for all road types together and did not include any traffic data as they are only available for major roads. I optimised the single k parameter for each species separately, as in the previous chapters, this time using the below formula. I did not use a bisection search for parameter optimisation, but instead chose the optimum *k* value produced from the first procedure of testing the range of values from 1-100.

Exposure to roads = $\sum(\exp(d_i * -k))$

Where:

d_i *= distance from the midpoint of the transect section to kernel point i*

k = parameter determining the scale of the relationship between road exposure and distance from a road

If no peak in log-likelihood could be identified, I did not continue with the analysis for that species. This resulted in three species being excluded: corn bunting *Emberiza calandra*, common redstart *Phoenicurus phoenicurus* and Eurasian magpie *Pica pica*. I later removed one further species, ring-necked parakeet *Psittacula krameria*, as a reliable model for this species could not be produced, leaving 75 species in the analysis.

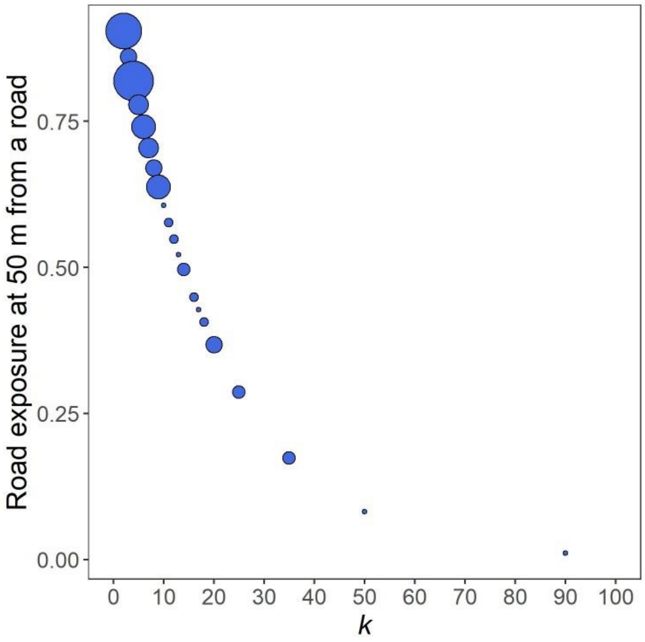
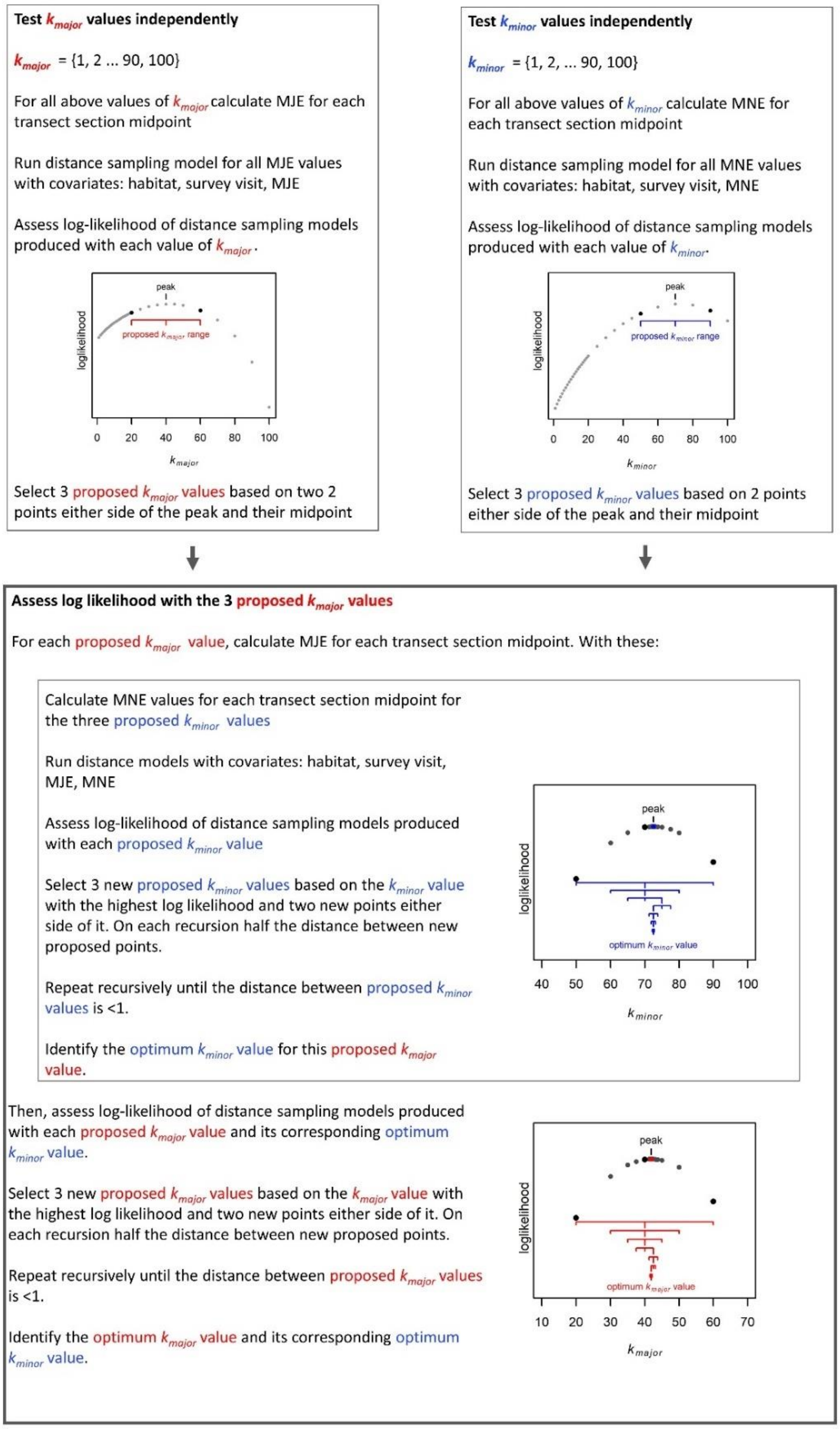


Figure A8. Road exposure at 50 m from a single road, for the optimum values of *k* identified for each of the 75 species analysed in Chapter 4. Point size represents the frequency of the *k* value.



Test k_{major} values independently

k_{major} = {1, 2 ... 90, 100}

For all above values of k_{major} calculate MJE for each transect section midpoint

Run distance sampling model for all MJE values with covariates: habitat, survey visit, MJE

Assess log-likelihood of distance sampling models produced with each value of k_{major} .

Select 3 proposed k_{major} values based on two 2 points either side of the peak and their midpoint

Test k_{minor} values independently

k_{minor} = {1, 2, ... 90, 100}

For all above values of k_{minor} calculate MNE for each transect section midpoint

Run distance sampling model for all MNE values with covariates: habitat, survey visit, MNE

Assess log-likelihood of distance sampling models produced with each value of k_{minor}.

Select 3 proposed k_{minor} values based on 2 points either side of the peak and their midpoint

Assess log likelihood with the 3 proposed k_{major} values

For each proposed k_{major} value, calculate MJE for each transect section midpoint. With these:

Calculate MNE values for each transect section midpoint for the three proposed k_{minor} values

Run distance models with covariates: habitat, survey visit, MJE, MNE

Assess log-likelihood of distance sampling models produced with each proposed k_{minor} value

Select 3 new proposed k_{minor} values based on the k_{minor} value with the highest log likelihood and two new points either side of it. On each recursion half the distance between new proposed points.

Repeat recursively until the distance between proposed k_{minor} values is <1.

Identify the optimum k_{minor} value for this proposed k_{major} value.

Then, assess log-likelihood of distance sampling models produced with each proposed k_{major} value and its corresponding optimum k_{minor} value.

Select 3 new proposed k_{major} values based on the k_{major} value with the highest log likelihood and two new points either side of it. On each recursion half the distance between new proposed points.

Repeat recursively until the distance between proposed k_{major} values is <1.

Identify the optimum k_{major} value and its corresponding optimum k_{minor} value.

Figure A9. An overview of the methods used to optimise the kernel density estimation parameters k_{major} and k_{minor} in Chapters 2 and 3.

Other covariates

In the GAMMs in both Chapters 3 and 4, I included a number of other covariates thought, or known, to affect bird populations. These included two proxy measures of agricultural intensity, along with human population density, temperature, rainfall and tree cover density.

Arable yield, which effectively captures a range of metrics describing agricultural intensity, can have a large effect on bird density (Donald et al. 2006). High-resolution yield data were not available for the whole of my study area, so I derived a proxy using CEH's 2015 Land Cover Map vector dataset (Rowland et al. 2017) from the Edina Environment Digimap Service (Edina 2018). I extracted the 'arable land' habitat class and calculated the proportion of arable land within 5-km buffers centred on the midpoint of each BBS 200-m transect section. To confirm that this was a suitable proxy for arable yield, I calculated the same measure for 2,254 1-km squares in the east and south of England, for which I was able to obtain yield estimates from Finch et al. (2019). These were derived independently using a combination of Farm Business Survey data (FBS 2019) and farm owner surveys. I found a strong positive correlation between the two (Pearson's correlation coefficient = 0.82). I also calculated the area of the largest arable polygon (corresponding to cropping unit or field) in each 5-km buffer as an additional measure of agricultural heterogeneity across my study area (Pearson's correlation coefficient with yield estimates = 0.34).

I obtained gridded local resident human population density estimates at a 1-km^2 spatial resolution, from the Centre for Ecology and Hydrology (Reis et al. 2017). I $\log_{10}$-transformed these data as I assumed the difference in potential impact from e.g. 1-1000 people would be greater than that from 10,000-11,000 people. To account for spatial variation in weather, I obtained temperature and rainfall data from the Met Office (Met Office 2018) for ten regions across Great Britain. I used these to calculate the mean temperature and rainfall during the survey season (April-June), in my three-year period. I obtained tree cover density estimates for 2012 (in the form of cover percentage from 0-100% at a spatial resolution of 100 m, estimated using high-resolution satellite data) from the Copernicus Land Monitoring Service (Copernicus 2018). To the midpoint of each 200-m BBS transect section, I then attributed the $\log_{10}$-transformed human population density of the 1-km grid square it lay in, the temperature and rainfall values for the region it was in, and the mean of the 100 m^2 tree cover density estimates within a surrounding 5-km buffer. My reasoning for incorporating tree cover density in this way was to capture habitat effects on a more landscape scale than the local habitats recorded in the BBS surveys and to match the distance over which the proportion of arable land and the road exposure variables were measured.

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Appendix B. Full results for Chapter 2

Here I provide the model outcomes for all species (**Table B1**) and estimated changes in detectability between the lowest and highest minor (**Table B2**) and major (**Table B3**) road exposure recorded for each species that showed significant associations. I also list the survey date and habitat coefficients for each species (**Table B4**). Finally, I provide the mean body mass and the proportion of birds first detected visually, as opposed to aurally, for all species that showed a significant negative association between minor road exposure and detectability (**Table B5**).

Table B1. Effect sizes of minor and major road exposure, and identified optimum K_{minor} and K_{major} values, for each species. The threshold significance level of 0.001 was determined by Bonferroni correction.

Scientific name	Common name	Convergence achieved?	K_{minor}	Effect size (coefficient)	Minor road exposure significance level	K_{major}	Effect size (coefficient)	Major road exposure significance level
Aegithalos caudatus	Long-tailed tit	Yes	80	-0.229	NS	5.8	9.26E-07	NS
Alauda arvensis	Eurasian skylark	No	-	-	-	-	-	-
Alectoris rufa	Red-legged partridge	Yes	17.8	0.292	$P < 0.001$	13.3	2.51E-06	NS
Anas platyrhynchos	Mallard	Yes	3.4	-0.020	$P < 0.001$	19	-4.84E-07	NS
Anser anser	Greylag goose	No	-	-	-	-	-	-
Anthus pratensis	Meadow pipit	Yes	2.5	0.009	NS	2.5	3.71E-06	$P < 0.001$
Aythya fuligula	Tufted duck	No	-	-	-	-	-	-
Branta canadensis	Canada goose	No	-	-	-	-	-	-
Buteo buteo	Common buzzard	Yes	39.3	1.019	$P < 0.001$	24	8.66E-06	NS
Carduelis carduelis	European goldfinch	Yes	28.8	-0.083	$P < 0.001$	31.3	1.02E-06	NS
Carduelis chloris	European greenfinch	Yes	2.8	0.006	$P < 0.001$	-	-	Not analysed
Certhia familiaris	Eurasian treecreeper	Yes	86.3	-1.153	NS	2.1	1.56E-07	NS
Chroicocephalus ridibundus	Black-headed gull	No	-	-	-	-	-	-
Columba livia domestica	Feral pigeon	Yes	8.1	-0.149	$P < 0.001$	51.9	-1.26E-05	NS
Columba oenas	Stock dove	Yes	28.6	0.475	$P < 0.001$	-	-	Not analysed
Columba palumbus	Common woodpigeon	Yes	11.7	-0.087	$P < 0.001$	-	-	Not analysed
Corvus corone	Carrion crow	Yes	3.4	-0.017	$P < 0.001$	-	-	Not analysed

Corvus frugilegus	Rook	Yes	7.1	-0.102	*P* < 0.001	42.3	-4.94E-05	*P* < 0.001
Corvus monedula	Eurasian jackdaw	Yes	5.6	-0.047	*P* < 0.001	-	-	Not analysed
Cyanistes caeruleus	Blue tit	Yes	30.1	-0.086	*P* < 0.001	16.3	-1.35E-06	NS
Cygnus olor	Mute swan	Yes	4.4	-0.021	NS	33.9	-1.16E-04	NS
Delichon urbicum	Common house martin	Yes	19.4	-0.216	*P* < 0.001	6.4	4.06E-06	NS
Dendrocopos major	Great spotted woodpecker	Yes	82.8	0.141	NS	-	-	Not analysed
Emberiza citrinella	Yellowhammer	Yes	4.8	0.010	NS	44.7	-6.48E-06	NS
Emberiza schoeniclus	Common reed bunting	Yes	11.7	0.075	NS	14.8	2.67E-05	NS
Erithacus rubecula	European robin	Yes	30.1	-0.089	*P* < 0.001	8.7	-9.61E-07	NS
Fringilla coelebs	Chaffinch	Yes	34.7	-0.163	*P* < 0.001	2.5	1.32E-07	NS
Fulica atra	Eurasian coot	Yes	2.5	-0.016	*P* < 0.001	14.8	8.55E-06	*P* < 0.001
Gallinula chloropus	Common moorhen	Yes	2.2	-0.008	*P* < 0.001	-	-	Not analysed
Garrulus glandarius	Eurasian jay	Yes	13.3	-0.168	*P* < 0.001	-	-	Not analysed
Haematopus ostralegus	Eurasian oystercatcher	No	-	-	-	-	-	-
Hirundo rustica	Barn swallow	Yes	17.8	-0.104	*P* < 0.001	11.7	2.25E-06	NS
Larus argentatus	European herring gull	No	-	-	-	-	-	-
Larus canus	Common gull	No	-	-	-	-	-	-
Larus fuscus	Lesser black-backed gull	No	-	-	-	-	-	-
Linaria cannabina	Common linnet	Yes	3.4	-0.012	*P* < 0.001	-	-	Not analysed
Motacilla alba	Pied/white wagtail	Yes	4.1	0.006	NS	31.6	3.02E-05	NS
Numenius arquata	Eurasian curlew	No	-	-	-	-	-	-
Oenanthe oenanthe	Northern wheatear	Yes	2.1	0.006	NS	8.1	1.34E-05	NS
Parus major	Great tit	Yes	39.3	-0.193	*P* < 0.001	34.7	-5.54E-06	NS
Passer domesticus	House sparrow	Yes	4.1	0.013	*P* < 0.001	83	-2.88E-05	NS
Passer montanus	Eurasian tree sparrow	No	-	-	-	-	-	-
Periparus ater	Coal tit	Yes	19.4	-0.087	NS	72.5	1.34E-05	NS
Phasianus colchicus	Ring-necked pheasant	Yes	4.1	0.058	*P* < 0.001	8.7	-4.19E-06	*P* < 0.001

Phylloscopus collybita	Common chiffchaff	Yes	35	-0.180	NS	14.9	-3.33E-07	NS
Phylloscopus trochilus	Willow warbler	Yes	70.3	-0.482	*P* < 0.001	43.8	-2.23E-05	NS
Pica pica	Eurasian magpie	Yes	5.6	-0.034	*P* < 0.001	4.1	-8.62E-07	*P* < 0.001
Picus viridis	European green woodpecker	Yes	11.7	-0.115	NS	6.6	-3.68E-06	NS
Prunella modularis	Dunnock	Yes	49.4	-0.225	*P* < 0.001	13.5	-3.99E-07	NS
Pyrrhula pyrrhula	Eurasian bullfinch	Yes	31.6	-0.218	*P* < 0.001	5.6	9.45E-07	NS
Regulus regulus	Goldcrest	Yes	45.4	-0.230	NS	31.6	1.77E-05	NS
Sitta europaea	Eurasian nuthatch	Yes	53.6	-0.099	NS	53.8	-6.94E-05	NS
Spinus spinus	Eurasian siskin	Yes	3.4	0.029	*P* < 0.001	11.3	-2.59E-06	NS
Streptopelia decaocto	Eurasian collared dove	Yes	19.4	-0.216	*P* < 0.001	66.3	1.67E-05	NS
Sturnus vulgaris	Common starling	Yes	9.3	-0.069	*P* < 0.001	7.5	1.20E-06	*P* < 0.001
Sylvia atricapilla	Eurasian blackcap	Yes	25.5	-0.200	*P* < 0.001	76.6	2.42E-05	NS
Sylvia borin	Garden warbler	Yes	-	-	Not analysed	16.3	7.73E-06	NS
Sylvia communis	Common whitethroat	Yes	36.2	-0.310	*P* < 0.001	2.5	1.57E-07	NS
Troglodytes troglodytes	Eurasian wren	Yes	31.9	-0.112	*P* < 0.001	-	-	Not analysed
Turdus merula	Common blackbird	Yes	24	-0.095	*P* < 0.001	4.1	-2.39E-07	NS
Turdus philomelos	Song thrush	Yes	25.5	-0.126	*P* < 0.001	8.8	-6.85E-07	NS
Turdus viscivorus	Mistle thrush	Yes	2.8	0.005	NS	4.5	-3.19E-07	NS
Vanellus vanellus	Northern lapwing	No	-	-	-	-	-	-

Table B2. Species that showed a significant association between minor road exposure and detectability with the estimated detectability of each at the minimum and maximum minor road exposure recorded for that species

Scientific name	Common name	Minimum exposure	Detectability at minimum exposure	Maximum exposure	Detectability at maximum exposure	Change in detectability	% Change
Alectoris rufa	Red-legged partridge	4.24E-38	0.49	2.23	0.7	0.22	0.45
Anas platyrhynchos	Mallard	8.04E-07	0.49	39.24	0.24	-0.26	-0.52
Buteo buteo	Common buzzard	5.70E-76	0.49	1.11	0.9	0.4	0.81
Corvus corone	Carrion crow	8.04E-07	0.63	44.89	0.31	-0.32	-0.5
Carduelis carduelis	European goldfinch	2.24E-61	0.35	2.35	0.29	-0.06	-0.16

Carduelis chloris	European greenfinch	1.65E-05	0.34	64.18	0.49	0.15	0.44
Columba livia domestica	Feral pigeon	5.81E-16	0.47	10.48	0.1	-0.37	-0.78
Columba oenas	Stock dove	6.53E-59	0.49	1.66	0.8	0.31	0.63
Columba palumbus	Common woodpigeon	0.00E+00	0.47	6.4	0.27	-0.19	-0.42
Corvus frugilegus	Rook	8.26E-06	0.86	9.63	0.64	-0.21	-0.25
Corvus monedula	Eurasian jackdaw	7.18E-04	0.53	15.56	0.26	-0.27	-0.5
Cyanistes caeruleus	Blue tit	3.09E-60	0.24	2.13	0.2	-0.04	-0.17
Delichon urbicum	Common house martin	5.04E-40	0.4	1.9	0.31	-0.09	-0.22
Erithacus rubecula	European robin	0.00E+00	0.34	2.25	0.28	-0.06	-0.18
Fringilla coelebs	Chaffinch	0.00E+00	0.39	2.01	0.28	-0.11	-0.27
Fulica atra	Eurasian coot	4.74E-05	0.63	64.88	0.32	-0.31	-0.5
Gallinula chloropus	Common moorhen	2.50E-04	0.43	81.6	0.22	-0.21	-0.49
Garrulus glandarius	Eurasian jay	2.26E-26	0.46	3.63	0.26	-0.2	-0.44
Hirundo rustica	Barn swallow	7.21E-37	0.36	2.79	0.27	-0.09	-0.25
Linaria cannabina	Common linnet	4.02E-07	0.37	28.87	0.27	-0.11	-0.28
Parus major	Great tit	1.33E-78	0.31	1.77	0.22	-0.09	-0.29
Passer domesticus	House sparrow	8.87E-03	0.27	31.51	0.38	0.11	0.41
Phasianus colchicus	Ring-necked pheasant	5.39E-08	0.59	18.39	0.92	0.32	0.55
Phylloscopus trochilus	Willow warbler	0.00E+00	0.43	0.91	0.28	-0.15	-0.35
Pica pica	Eurasian magpie	8.61E-11	0.56	18.24	0.33	-0.23	-0.41
Prunella modularis	Dunnock	9.62E-99	0.32	1.7	0.22	-0.1	-0.32
Pyrrhula pyrrhula	Eurasian bullfinch	5.05E-40	0.26	1.31	0.19	-0.06	-0.25
Spinus spinus	Eurasian siskin	0.00E+00	0.24	31.08	0.55	0.31	1.33
Streptopelia decaocto	Eurasian collared dove	2.67E-15	0.39	2.63	0.22	-0.17	-0.43
Sturnus vulgaris	Common starling	1.01E-13	0.46	7.85	0.27	-0.19	-0.41
Sylvia atricapilla	Eurasian blackcap	0.00E+00	0.35	1.81	0.25	-0.11	-0.3
Sylvia communis	Common whitethroat	2.78E-77	0.36	1.15	0.25	-0.11	-0.3
Troglodytes troglodytes	Eurasian wren	0.00E+00	0.37	2.13	0.29	-0.08	-0.21
Turdus merula	Common blackbird	1.78E-49	0.38	2.81	0.29	-0.09	-0.23
Turdus philomelos	Song thrush	4.92E-51	0.51	2	0.4	-0.11	-0.21

Table B3. Species that showed a significant association between major road exposure and detectability with the estimated detectability of each at the minimum and maximum major road exposure recorded for that species

Scientific name	**Common name**	**Minimum exposure**	**Detectability at minimum exposure**	**Maximum exposure**	**Detectability at maximum exposure**	**Change in detectability**	**% Change**
Anthus pratensis	Meadow pipit	0	0.32	417771.3	0.89	0.57	1.8

Corvus frugilegus	Rook	0	0.86	40797.35	0.49	-0.37	-0.43
Fulica atra	Eurasian coot	0	0.63	124878.7	0.93	0.3	0.47
Phasianus colchicus	Ring-necked pheasant	0	0.59	286590.7	0.2	-0.4	-0.67
Pica pica	Eurasian magpie	0	0.56	662641.2	0.34	-0.21	-0.39
Sturnus vulgaris	Common starling	0	0.46	330302.8	0.63	0.17	0.37

Table B4. Survey date and habitat coefficients extracted from the distance sampling model for each species. Within each species, only habitat types with sufficient sample sizes (total count > 20) were tested. The reference habitat type was woodland and the threshold significance level of 0.001 was determined with Bonferroni correction.

		Aegithalos caudatus		***Alectoris rufa***		***Anas platyrhynchos***		***Anthus pratensis***		***Buteo buteo***	
		Effect size	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**
Habitat	**Scrubland**	0.118	No	-0.099	No	0.323	No	0.171	No	0.350	No
	Semi-natural grassland and marsh	-0.029	No	0.120	No	0.338	Yes	0.091	No	0.532	No
	Heathland and bogs	0.219	No	-	-	0.120	No	0.195	No	-	-
	Farmland	0.012	No	0.015	No	0.068	No	-0.001	No	0.057	No
	Human sites	0.068	No	-0.044	No	0.214	Yes	-	-	0.046	No
	Water-bodies (freshwater)	-0.041	No	0.908	No	0.019	No	0.047	No	0.294	No
	Coastal	-	-	6.485	No	0.883	Yes	0.140	No	-	-
	Inland rock	-	-	-	-	-	-	0.011	No	-	-
Survey visit (late)		-0.057	No	-0.178	Yes	-0.032	No	0.003	No	0.020	No

Carduelis carduelis		***Carduelis chloris***		***Certhia familiaris***		***Columba livia domestica***		***Columba oenas***		***Columba palumbus***		***Corvus corone***	
Effect size	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**
0.037	No	0.145	No	-0.231	No	-	-	0.276	No	0.131	No	-0.279	Yes
-0.004	No	0.178	No	-0.196	No	-	-	-0.324	No	0.111	No	-0.021	No
0.111	No	0.467	No	-	-	-	-	-	-	0.491	No	-0.002	No
-0.126	Yes	-0.095	No	-0.008	No	0.296	No	-0.029	No	0.089	Yes	0.073	No
-0.116	Yes	-0.091	No	-0.075	No	0.376	No	0.004	No	0.001	No	-0.072	No
0.016	No	-0.204	Yes	-0.230	No	-0.587	No	0.473	No	-0.111	Yes	-0.065	No
0.328	No	0.326	No	-	-	-	-	-	-	0.346	No	0.245	No
1.066	No	-	-	-	-	-	-	-	-	-	-	-0.059	No
0.040	Yes	-0.028	No	-0.057	No	-0.026	No	-0.016	No	-0.015	No	-0.092	Yes

Corvus frugilegus		*Corvus monedula*		*Cyanistes caeruleus*		*Cygnus olor*		*Delichon urbicum*		*Dendrocopos major*		*Emberiza citrinella*	
Effect size	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**
0.444	No	0.311	No	-0.108	No	4.012	No	0.350	No	-0.231	No	-0.047	No
7.604	No	0.333	No	-0.032	No	-1.128	No	0.124	No	0.406	No	-0.145	No
1.626	No	0.198	No	0.005	No	-	-	-	-	0.002	No	1.046	No
0.688	Yes	0.233	Yes	-0.093	Yes	-1.052	No	0.196	No	-0.173	Yes	-0.268	No
0.154	Yes	0.062	No	-0.064	No	-0.649	No	-0.023	No	-0.202	Yes	-0.099	No
6.237	No	0.137	No	-0.129	No	-1.178	No	-0.281	No	-0.205	No	-0.084	No
5.610	No	-0.318	No	-	-	-	-	6.963	No	-	-	-	-
-	-	0.046	No	-	-	-	-	-	-	-	-	-	-
0.146	Yes	-0.046	No	-0.031	No	-0.479	Yes	0.108	No	-0.240	Yes	0.119	Yes

Emberiza schoeniclus		***Erithacus rubecula***		***Fringilla coelebs***		***Fulica atra***		***Gallinula chloropus***		***Garrulus glandarius***		***Hirundo rustica***	
Effect size	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**
-0.035	No	-0.038	No	0.007	No	0.179	No	-0.159	No	0.009	No	0.179	No
-0.156	No	0.066	No	0.086	No	-0.031	No	0.169	No	0.024	No	-0.003	No
-0.202	No	0.128	No	0.204	No	-	-	-	-	0.585	No	0.333	No
-0.316	No	-0.107	Yes	-0.174	Yes	0.137	No	0.050	No	-0.081	No	-0.065	No
-0.331	No	-0.088	Yes	-0.037	No	0.177	No	0.044	No	-0.101	No	-0.162	No
-0.318	No	-0.198	Yes	-0.146	No	-0.133	No	-0.387	Yes	-0.398	Yes	-0.178	No
0.678	No	-	-	0.449	No	4.539	No	-	-	-	-	-	-
-	-	0.582	No	-	-	-	-	-	-	-	-	-	-
0.190	Yes	-0.019	No	0.089	Yes	-0.095	No	-0.125	No	-0.016	No	-0.018	No

Linaria cannabina		*Motacilla alba*		*Oenanthe oenanthe*		*Parus major*		*Passer domesticus*		*Periparus ater*		*Phasianus colchicus*	
Effect size	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**
-0.257	No	-0.132	No	-	-	-0.081	No	-0.110	No	-0.015	No	0.175	No
-0.027	No	-0.031	No	-0.217	No	0.029	No	-0.405	No	0.465	No	-0.135	No
-0.050	No	0.162	No	-0.297	No	0.138	No	1.094	No	0.215	No	0.610	No
-0.371	Yes	-0.110	No	-0.207	No	-0.109	Yes	-0.068	No	-0.064	No	-0.215	Yes
-0.289	Yes	-0.134	No	-0.858	No	-0.042	No	-0.265	Yes	-0.057	No	-0.023	No
-0.203	No	0.033	No	-	-	-0.130	Yes	0.028	No	-0.066	No	0.378	No
-0.218	No	-0.229	No	-	-	-	-	-0.320	Yes	-	-	-	-
0.099	No	-	-	0.048	No	-0.132	No	-	-	-	-	-	-
-0.036	No	-0.017	No	0.110	No	-0.081	Yes	0.010	No	-0.087	Yes	-0.070	No

Phylloscopus collybita		***Phylloscopus trochilus***		***Pica pica***		***Picus viridis***		***Prunella modularis***		***Pyrrhula pyrrhula***		***Regulus regulus***	
Effect size	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**
-0.108	No	0.008	No	-0.083	No	-0.008	No	0.127	No	0.044	No	0.141	No
-0.003	No	0.129	No	-0.037	No	0.256	No	0.318	No	0.328	No	0.145	No
0.096	No	0.038	No	0.776	No	-0.343	No	0.465	No	-	-	0.735	Yes
-0.117	No	0.038	No	0.014	No	-0.103	No	-0.005	No	-0.043	No	0.066	No
-0.014	No	0.194	No	-0.100	No	0.018	No	0.040	No	0.068	No	0.065	No
-0.191	No	-0.271	No	-0.223	No	-0.091	No	0.026	No	-0.214	No	-0.020	No
-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	0.344	No	-	-	-	-
0.030	No	0.014	No	-0.080	No	-0.354	Yes	-0.027	No	-0.041	No	0.001	No

Sitta europaea		***Spinus spinus***		***Streptopelia decaocto***		***Sturnus vulgaris***		***Sylvia atricapilla***		***Sylvia borin***		***Sylvia communis***	
Effect size	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**
0.414	No	0.097	No	-0.100	No	-0.049	No	0.103	No	-0.331	Yes	0.132	No
-0.238	No	-0.128	No	-	-	0.154	No	-0.076	No	0.166	No	-0.190	No
-	-	-0.348	No	-	-	0.374	No	-	-	0.047	No	0.368	No
-0.148	No	-0.058	No	-0.029	No	0.058	No	-0.083	No	-0.165	No	-0.251	Yes
-0.088	No	-0.381	No	-0.056	No	-0.124	No	-0.033	No	-0.086	No	-0.141	No
-0.012	No	-	-	-0.313	No	-0.048	No	-0.276	Yes	-0.393	Yes	-0.094	No
-	-	-	-	-	-	-0.103	No	-	-	-	-	0.296	No
-	-	-	-	-	-	-0.805	Yes	-	-	-	-	-	-
-0.241	Yes	0.000	No	-0.003	No	0.040	Yes	0.180	Yes	0.047	No	0.014	No

Troglodytes troglodytes		***Turdus merula***		***Turdus philomelos***		***Turdus viscivorus***	
Effect size	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**
-0.008	No	-0.001	No	-0.155	No	0.047	No
-0.022	No	-0.167	No	-0.227	No	0.329	No
0.158	No	0.256	No	-0.229	No	0.062	No
-0.182	Yes	-0.107	Yes	-0.143	Yes	-0.038	No
-0.055	No	-0.120	Yes	-0.107	No	-0.215	No
-0.261	Yes	-0.154	Yes	-0.236	Yes	-0.491	Yes
-0.237	No	0.222	No	-	-	-	-
-0.022	No	0.281	No	-	-	-	-
0.031	No	0.036	No	-0.035	No	-0.034	No

Table B5. Mean body mass (as recorded in Robinson 2005) and the proportion of birds first detected visually as opposed to aurally (as recorded in the 2014 BBS survey; Newson, S. E., unpubl. data), for all species that showed a significant association between minor road exposure and detectability.

Scientific name	**Common name**	**Family**	**Mean body mass/g**	**Proportion of birds detected visually**
Anas platyrhynchos	Mallard	Anatidae	1206.4	97.6
Buteo buteo	Common buzzard	Corvidae	508.7	89.1
Carduelis carduelis	European goldfinch	Fringillidae	15.8	66.3
Columba livia domestica	Feral pigeon	Columbidae	359.6	99.4
Columba palumbus	Common woodpigeon	Columbidae	507.4	87.0
Corvus frugilegus	Rook	Corvidae	452.3	92.9
Corvus monedula	Eurasian jackdaw	Corvidae	231.8	88.5
Cyanistes caeruleus	Blue tit	Paridae	10.9	54.8
Delichon urbicum	Common house martin	Hirundinidae	17.8	94.9
Erithacus rubecula	European robin	Muscicapidae	19.0	29.9
Fringilla coelebs	Chaffinch	Fringillidae	21.8	34.4
Fulica atra	Eurasian coot	Rallidae	880.0	95.1
Gallinula chloropus	Common moorhen	Rallidae	356.4	77.7
Garrulus glandarius	Eurasian jay	Corvidae	166.8	62.3
Hirundo rustica	Barn swallow	Hirundinidae	19.9	97.0
Linaria cannabina	Common linnet	Fringillidae	18.8	70.5
Parus major	Great tit	Paridae	18.6	49.5
Phylloscopus trochilus	Willow warbler	Phylloscopidae	8.9	10.0
Pica pica	Eurasian magpie	Corvidae	212.9	80.9
Prunella modularis	Dunnock	Prunellidae	21.2	44.9
Pyrrhula pyrrhula	Eurasian bullfinch	Fringillidae	22.5	57.7
Streptopelia decaocto	Eurasian collared dove	Columbidae	204.8	73.8
Sturnus vulgaris	Common starling	Sturnidae	85.0	96.3
Sylvia atricapilla	Eurasian blackcap	Sylvidae	17.7	11.3
Sylvia communis	Common whitethroat	Sylvidae	13.8	29.8
Troglodytes troglodytes	Eurasian wren	Troglodytidae	9.9	8.5
Turdus merula	Common blackbird	Turdidae	101.8	62.7
Turdus philomelos	Song thrush	Turdidae	74.9	20.8

Appendix C. Full results for Chapter 3

Here I provide the model parameters and outcomes for all species, along with the covariates included in the distance sampling model for each species (**Table C1**). For species that had shown a significant effect of both major and minor road exposure on detectability, I used the distance sampling model produced in Chapter 2, which incorporated both of these covariates (as well as habitat and survey visit). If one or neither road exposure type was shown to be significant on detectability of a species, I reproduced its distance sampling model excluding those covariates. As significant road exposure effects on detectability of two species (meadow pipit *Anthus pratensis* and Eurasian siskin *Spinus spinus*) were considered Type I errors in Chapter 2, I also excluded road exposure from the distance sampling models for these.

I also graphically present the estimated changes in abundance across the values of major and minor road exposure calculated for each species with a significant association (calculated using its k_{major}/k_{minor} value) (**Figure C1**). Finally, I present the model results for all other covariates (**Table C2**).

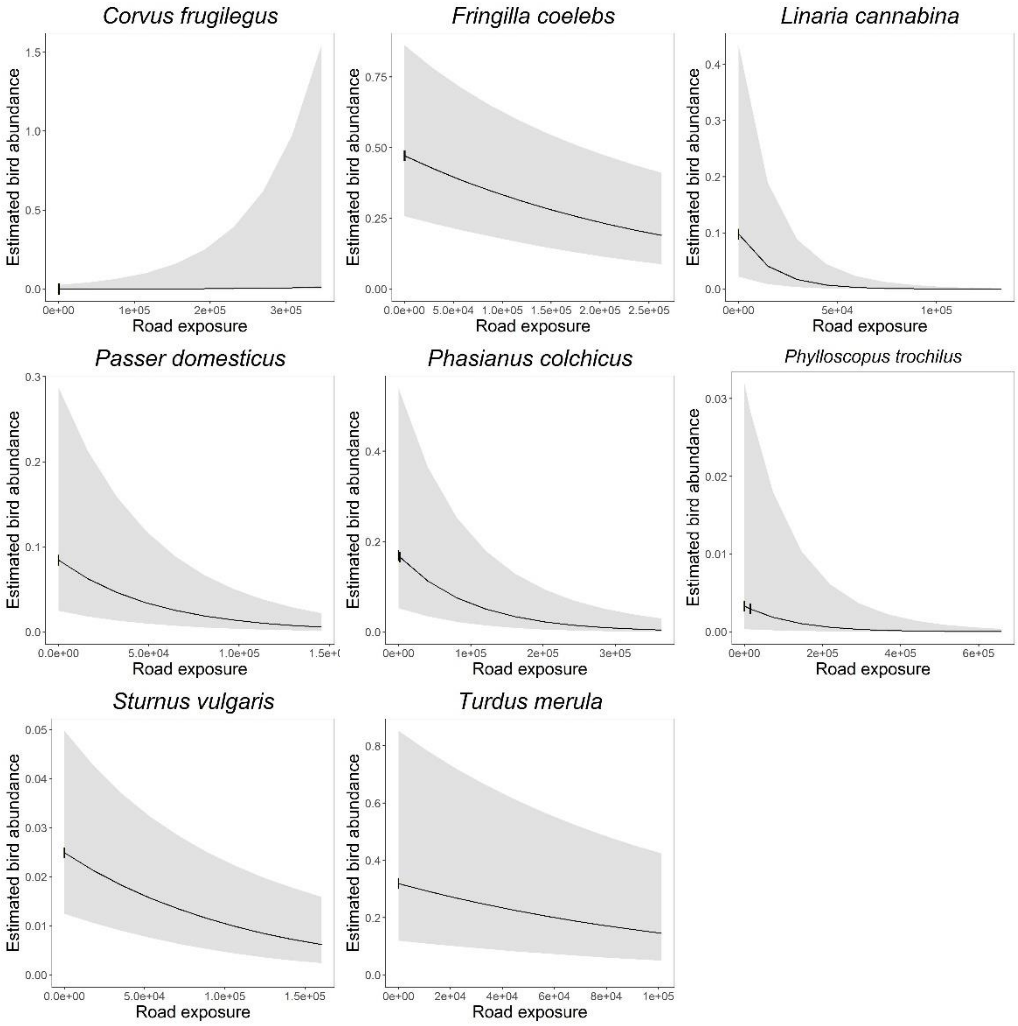
Table C1. Model parameters and detectability model covariates used for each species, along with significance and effect sizes of associations between bird abundance and both major and minor road exposure, and k_{major} and k_{minor} values used. Distance sampling model covariates include habitat (H), survey visit (V), major road exposure (Mj) and minor road exposure (Mn). Cells contain "-" if it was not possible to test major or minor road exposure due to the lack of existence of an optimum value of k_{minor} and k_{major} (See **Appendix A** for further details). The threshold significance level of 0.001 was determined by Bonferroni correction.

Scientific name	**Common name**	**Survey visit**	**Prop. arable land fit**	**Distance sampling model covariates**	k_{major}	**Major road exposure effect size (coefficient)**	**Major road exposure significance level**	k_{minor}	**Minor road exposure effect size**	**Minor road exposure significance level**
Aegithalos caudatus	Long-tailed tit	Early	Linear	HV	-	-	-	13.1	0.047	NS
Alectoris rufa	Red-legged partridge	Early	Quad.	HVMn	26.3	-1.36E-05	NS	68.8	-0.572	NS
Anas platyrhynchos	Mallard	Early	Linear	HVMn	7.5	-5.64E-07	NS	26.9	-0.270	$P < 0.001$
Anthus pratensis	Meadow pipit	Early	Linear	HV	-	-	-	17	-0.313	$P < 0.001$
Buteo buteo	Common buzzard	Early	Linear	HVMn	-	-	-	14.5	-0.649	$P < 0.001$
Carduelis carduelis	European goldfinch	Early	Linear	HVMn	-	-	-	14.1	0.434	$P < 0.001$
Certhia familiaris	Eurasian treecreeper	Early	Linear	HV	4.4	-2.15E-06	NS	3.3	-0.030	NS
Chloris chloris	European greenfinch	Early	Linear	HVMn	10	1.69E-06	NS	10.5	0.236	$P < 0.001$

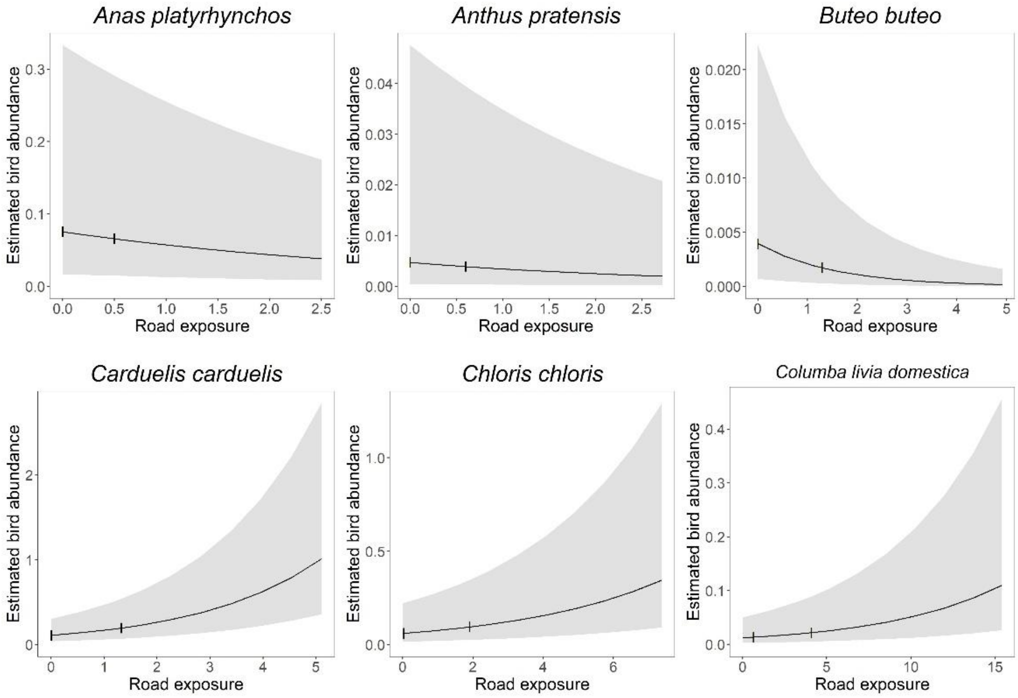
Columba livia domestica	Feral pigeon	Early	Linear	HVMn	87.5	-8.37E-06	NS	6.3	0.142	*P* < 0.001
Columba oenas	Stock dove	Early	Quad.	HVMn	25	-7.31E-05	NS	2.3	-0.019	NS
Columba palumbus	Common woodpigeon	Early	Linear	HVMn	15.3	-1.57E-06	NS	7	0.112	*P* < 0.001
Corvus corone	Carrion crow	Early	Linear	HVMn	6	-1.55E-07	NS	7.5	-0.027	NS
Corvus frugilegus	Rook	Early	Linear	HVMjMn	8.1	1.15E-05	*P* < 0.001	8.1	0.190	*P* < 0.001
Corvus monedula	Eurasian jackdaw	Early	Linear	HVMn	-	-	-	7.8	0.124	*P* < 0.001
Cyanistes caeruleus	Blue tit	Early	Linear	HVMn	12.5	-1.74E-06	NS	6.6	0.062	*P* < 0.001
Cygnus olor	Mute swan	Early	Linear	HV	10.4	-1.93E-05	NS	3.3	-0.046	NS
Delichon urbicum	Common house martin	Late	Linear	HVMn	3.3	-2.38E-06	NS	8.9	0.236	*P* < 0.001
Dendrocopos major	Great spotted woodpecker	Early	Linear	HV	4	-6.56E-07	NS	4.4	-0.045	NS
Emberiza citrinella	Yellowhammer	Early	Quad.	HV	47.2	-7.80E-05	NS	28.8	0.338	*P* < 0.001
Emberiza schoeniclus	Common reed bunting	Early	Linear	HV	59.5	7.02E-05	NS	3.3	-0.099	*P* < 0.001
Erithacus rubecula	European robin	Early	Linear	HVMn	-	-	-	11.5	0.102	*P* < 0.001
Fringilla coelebs	Chaffinch	Early	Linear	HVMn	10.5	-3.46E-06	*P* < 0.001	21.5	0.308	*P* < 0.001
Fulica atra	Eurasian coot	Early	Linear	HVMjMn	7.3	-3.56E-06	NS	5.5	-0.146	*P* < 0.001
Gallinula chloropus	Common moorhen	Early	Linear	HVMn	-	-	-	4.4	-0.038	NS
Garrulus glandarius	Eurasian jay	Early	Linear	HVMn	23.6	5.37E-07	NS	12.3	0.006	NS
Hirundo rustica	Barn swallow	Late	Linear	HVMn	-	-	-	17.3	0.494	*P* < 0.001
Linaria cannabina	Common linnet	Early	Quad.	HVMn	19	-5.89E-05	*P* < 0.001	20	0.128	NS
Motacilla alba	Pied/white wagtail	Early	Linear	HV	3.3	-1.91E-06	NS	19.6	0.201	NS
Oenanthe oenanthe	Northern wheatear	Late	Linear	HV	5.5	-4.01E-06	NS	3.3	-0.125	NS
Parus major	Great tit	Early	Linear	HVMn	4.4	2.16E-07	NS	33.8	0.339	*P* < 0.001
Passer domesticus	House sparrow	Early	Linear	HVMn	17.6	-1.85E-05	*P* < 0.001	9.8	0.385	*P* < 0.001
Periparus ater	Coal tit	Early	Linear	HV	9	1.70E-06	NS	2.3	-0.014	NS

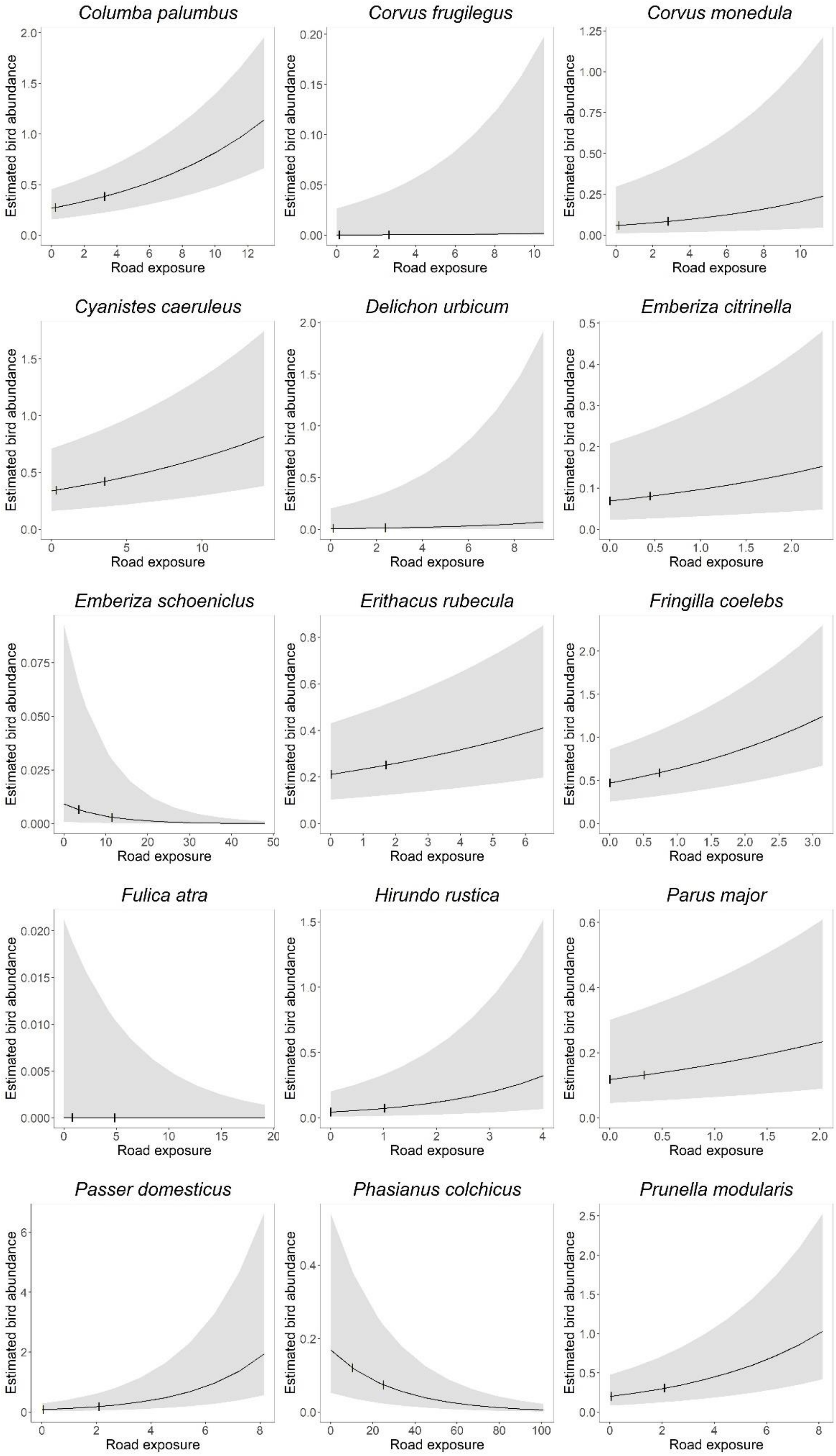
Phasianus colchicus	Ring-necked pheasant	Early	Linear	HVMjMn	7.8	-9.95E-06	*P* < 0.001	2.1	-0.033	*P* < 0.001
Phylloscopus collybita	Common chiffchaff	Late	Linear	HV	70.3	-3.86E-05	NS	7.6	-0.045	NS
Phylloscopus trochilus	Willow warbler	Late	Linear	HVMn	4.4	-7.97E-06	*P* < 0.001	3.3	-0.021	NS
Pica pica	Eurasian magpie	Early	Linear	HVMjMn	20	-1.01E-06	NS	-	NA	-
Picus viridis	European green woodpecker	Early	Linear	HV	17.5	-4.26E-05	NS	3.3	-0.048	NS
Prunella modularis	Dunnock	Early	Linear	HVMn	4.5	-2.66E-07	NS	9.8	0.202	*P* < 0.001
Pyrrhula pyrrhula	Eurasian bullfinch	Early	Linear	HVMn	7.8	2.99E-06	NS	15	0.231	NS
Regulus regulus	Goldcrest	Early	Linear	HV	-	-	-	5.5	-0.100	*P* < 0.001
Sitta europaea	Eurasian nuthatch	Early	Linear	HV	2.1	-7.91E-07	NS	2.1	-0.006	NS
Spinus spinus	Eurasian siskin	Early	Linear	HV	31.3	4.70E-06	NS	-	NA	-
Streptopelia decaocto	Eurasian collared dove	Early	Linear	HVMn	44.5	-4.34E-05	NS	7.8	0.297	*P* < 0.001
Sturnus vulgaris	Common starling	Early	Linear	HVMjMn	16.3	-8.67E-06	*P* < 0.001	4.4	0.086	*P* < 0.001
Sylvia atricapilla	Eurasian blackcap	Late	Linear	HVMn	2.9	5.54E-07	NS	4.5	-0.031	*P* < 0.001
Sylvia borin	Garden warbler	Late	Linear	HV	32.2	-0.00017	NS	6.6	-0.098	NS
Sylvia communis	Common whitethroat	Late	Quad.	HVMn	-	-	-	47.2	0.343	NS
Troglodytes troglodytes	Eurasian wren	Early	Linear	HVMn	-	-	-	32.5	0.142	*P* < 0.001
Turdus merula	Common blackbird	Early	Linear	HVMn	23.5	-7.73E-06	*P* < 0.001	5.9	0.089	*P* < 0.001
Turdus philomelos	Song thrush	Early	Linear	HVMn	15.3	6.34E-06	NS	14.1	0.132	*P* < 0.001
Turdus viscivorus	Mistle thrush	Early	Linear	HV	3.3	-2.50E-07	NS	2.1	-0.004	NS

a) major road exposure



b) minor road exposure




Columba palumbus

Corvus frugilegus

Corvus monedula

Cyanistes caeruleus

Delichon urbicum

Emberiza citrinella

Emberiza schoeniclus

Erithacus rubecula

Fringilla coelebs

Fulica atra

Hirundo rustica

Parus major

Passer domesticus

Phasianus colchicus

Prunella modularis

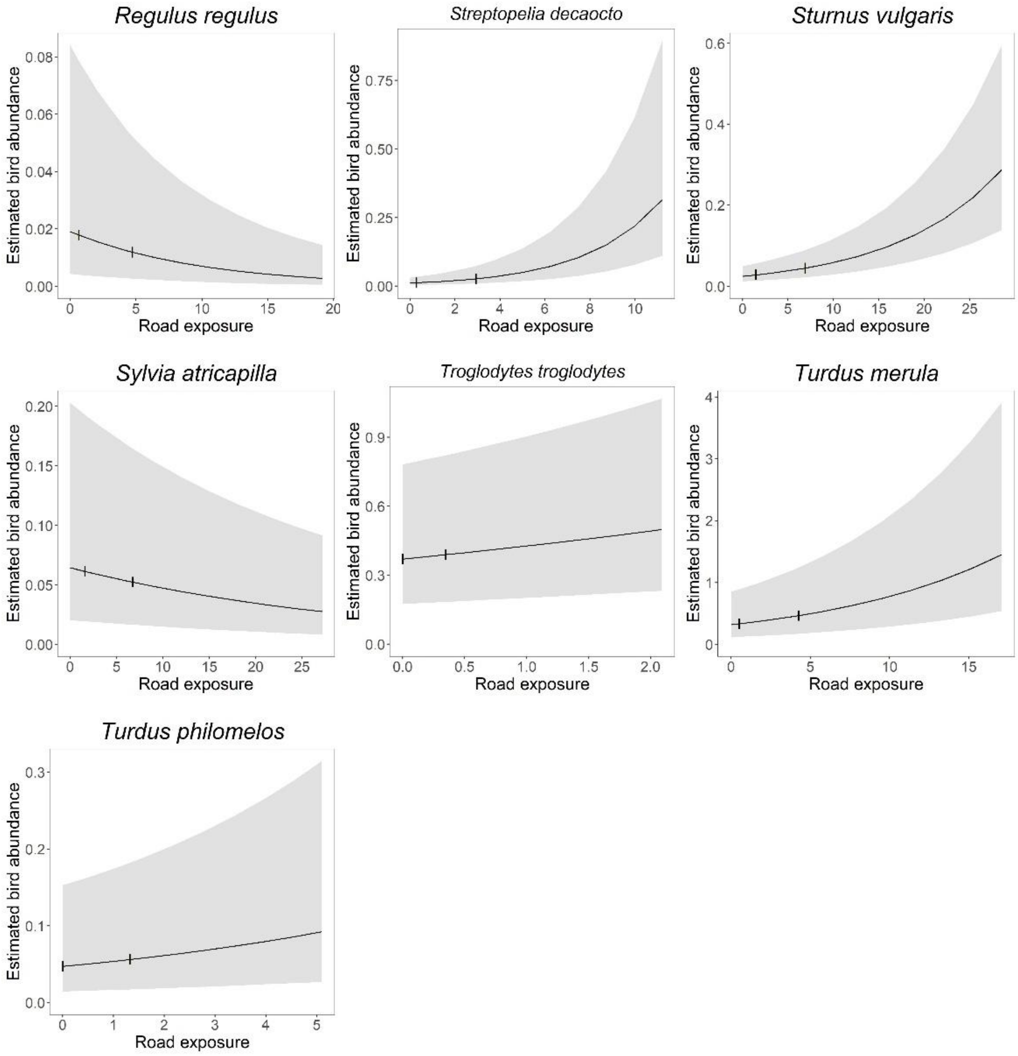


Figure C1. Estimated bird abundance for each species across the full range of (**a**) major road exposure and (**b**) minor road exposure. Major and minor road exposure ranges were calculated for each species using its value of k_{major} or k_{minor}. X-axes in (**a**) represent major road exposure, x-axes in (**b**) represent minor road exposure. Y-axes represent estimated number of birds within 100 m of a 200-m BBS transect. The 0.25 and 0.75 quartiles of road exposure for each species are indicated by the vertical lines. Only species with significant associations (determined using a Bonferroni correction) are featured here. Shaded areas denote 95% prediction intervals.

Table C2. Coefficients and significance for all other covariates included in the GAMM for each species. Within each species, only habitat types with sufficient sample sizes (total count > 20) were tested. The reference habitat category for all species is woodland and the threshold significance level of 0.001 was determined with Bonferroni correction. Effect sizes for the continuous covariates are not directly comparable as they were not standardised.

		Aegithalos caudatus		*Alectoris rufa*		*Anas platyrhynchos*		*Anthus pratensis*		*Buteo bute*
		Effect size	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**
Habitat	**Scrubland**	0.073	No	0.176	No	-0.442	No	1.498	Yes	-0.402
	Semi-natural grassland and marsh	-1.209	Yes	0.153	No	-0.173	No	2.727	Yes	-1.240
	Heathland and bogs	-1.695	Yes	-	-	-0.692	No	2.654	Yes	-
	Farmland	-0.704	Yes	1.132	Yes	0.068	No	1.537	Yes	-0.133
	Human sites	-0.572	Yes	0.187	No	0.240	No	-	-	-0.881
	Water-bodies (freshwater)	-0.045	No	-0.240	No	2.103	Yes	1.992	Yes	-18.534
	Coastal	-	-	0.830	No	0.330	No	2.069	Yes	-
	Inland rock	-	-	-	-	-	-	2.639	Yes	-
Prop. arable land		0.022	No	5.124	Yes	-0.204	No	-3.177	Yes	0.797
Prop. arable land^2		-	-	-4.161	Yes	-	-	-	-	-
Largest cropping unit		0.219	No	0.253	No	-0.171	No	-0.672	No	0.352
Human population density ($\log_{10}$)		-0.007	No	-0.172	Yes	0.028	No	-0.059	No	-0.060
Temperature		4.975	No	-2.367	No	-3.662	No	-1.597	No	-3.171
Rainfall		2.186	No	-3.324	No	-1.313	No	-1.586	No	-0.892
Tree cover density		0.507	No	0.582	No	-0.013	No	-0.635	No	-0.706

o	***Carduelis carduelis***		***Certhia familiaris***		***Chloris chloris***		***Columba livia domestica***		***Columba oenas***		***Columba palumbus***		***Corvus coro***
***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**
No	0.569	Yes	-2.048	No	0.956	Yes	-	-	0.076	No	-0.255	Yes	0.020
No	-0.359	No	-2.721	Yes	-0.102	No	-	-	-0.263	No	-0.826	Yes	-0.307
-	-1.441	Yes	-	-	-0.535	No	-	-	-	-	-1.426	Yes	-0.984
No	0.649	Yes	-1.629	Yes	0.530	Yes	1.164	Yes	0.127	No	-0.525	Yes	0.290
No	1.253	Yes	-1.561	Yes	1.529	Yes	1.951	Yes	0.128	No	-0.037	No	0.259
No	0.701	Yes	-0.969	No	1.115	Yes	2.389	Yes	-0.426	No	-0.110	No	0.298
-	-0.177	No	-	-	-0.755	No	-	-	-	-	-0.739	Yes	0.049
-	-1.358	No	-	-	-	-	-	-	-	-	-	-	0.006
No	0.620	Yes	-0.750	No	0.967	Yes	-0.896	No	2.350	No	1.363	Yes	-0.654
-	-	-	-	-	-	-	-	-	-2.623	No	-	-	-
No	0.041	No	-0.039	No	0.158	No	-0.541	No	-0.140	No	0.128	No	0.054
No	-0.030	No	-0.113	No	0.013	No	0.178	Yes	-0.016	No	0.063	Yes	0.063
No	4.364	No	-2.937	No	0.825	No	-1.922	No	-0.819	No	-1.211	No	-1.190
No	1.062	No	-2.240	No	0.306	No	0.338	No	0.624	No	1.239	No	0.438
No	0.414	No	0.999	No	0.668	No	0.433	No	-0.232	No	0.575	Yes	-0.035

ne	*Corvus frugilegus*		*Corvus monedula*		*Cyanistes caeruleus*		*Cygnus olor*		*Delichon urbicum*		*Dendrocopos major*		*Emberiza ci*
$P < 0.001$?	**Effect size**	**$P < 0.001$?**	**Effect size**	**$P < 0.001$?**	**Effect size**	**$P < 0.001$?**	**Effect size**	**$P < 0.001$?**	**Effect size**	**$P < 0.001$?**	**Effect size**	**$P < 0.001$?**	**Effect size**
No	-2.546	Yes	-1.174	Yes	-0.333	Yes	0.660	No	1.304	Yes	-0.381	No	1.715
No	-1.287	Yes	-0.585	Yes	-1.325	Yes	1.477	Yes	-0.122	No	-2.747	Yes	1.513
Yes	-4.091	Yes	-1.868	Yes	-1.909	Yes	-	-	-	-	-2.524	Yes	0.906
Yes	-0.608	Yes	0.096	No	-0.597	Yes	0.377	No	1.078	Yes	-1.299	Yes	1.832
Yes	-0.299	Yes	0.806	Yes	-0.328	Yes	0.945	No	2.093	Yes	-1.023	Yes	0.072
No	-0.832	Yes	0.183	No	-0.311	Yes	3.596	Yes	0.765	No	-1.770	Yes	0.222
No	-2.133	No	-0.357	No	-	-	-	-	0.990	No	-	-	-
No	-	-	0.498	No	-	-	-	-	-	-	-	-	-
Yes	1.667	Yes	0.088	No	-0.075	No	-0.671	No	1.651	Yes	-0.519	No	12.026
-	-	-	-	-	-	-	-	-	-	-	-	-	-9.804
No	0.088	No	-0.016	No	0.047	No	0.619	No	-0.467	No	-0.096	No	-0.083
Yes	-0.052	No	-0.018	No	0.000	No	0.157	No	-0.041	No	-0.029	No	-0.112
No	-9.833	Yes	-0.312	No	-0.250	No	-5.638	No	-4.071	No	0.987	No	3.194
No	-2.487	No	-0.654	No	-0.308	No	0.173	No	-1.344	No	0.417	No	2.792
No	-2.279	Yes	-0.585	No	0.160	No	-1.799	No	0.674	No	0.650	No	0.265

trinella	*Emberiza schoeniclus*		*Erithacus rubecula*		*Fringilla coelebs*		*Fulica atra*		*Gallinula chloropus*		*Garrulus glandarius*		*Hirundo rus*
***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**
Yes	1.590	No	-0.294	Yes	-0.143	No	0.202	No	0.000	No	-0.321	No	0.435
Yes	3.078	Yes	-1.527	Yes	-1.083	Yes	0.261	No	-0.107	No	-2.002	Yes	0.287
No	2.196	Yes	-1.730	Yes	-1.413	Yes	-	-	-	-	-2.188	Yes	-1.628
Yes	1.846	Yes	-0.744	Yes	-0.237	Yes	-0.580	No	-0.177	No	-1.497	Yes	1.218
No	0.577	No	-0.403	Yes	-0.174	Yes	0.327	No	0.604	No	-1.359	Yes	1.306
No	3.709	Yes	-0.364	Yes	-0.175	No	2.649	Yes	2.781	Yes	-1.095	No	0.764
-	2.174	Yes	-	-	-1.539	Yes	0.998	No	-	-	-	-	-
-	-	-	-1.337	Yes	-	-	-	-	-	-	-	-	-
Yes	1.397	No	-0.426	No	0.751	Yes	-0.669	No	-0.507	No	-0.811	No	0.499
Yes	-	-	-	-	-	-	-	-	-	-	-	-	-
No	0.716	Yes	0.056	No	-0.068	No	0.224	No	0.118	No	-0.660	No	-0.278
Yes	0.019	No	0.024	No	-0.082	Yes	0.151	Yes	0.099	No	0.058	No	-0.120
No	-3.958	No	-0.222	No	0.061	No	-4.653	No	-1.633	No	3.677	No	-2.766
Yes	1.494	No	0.630	No	0.142	No	0.005	No	-0.154	No	0.052	No	-0.336
No	0.936	No	0.184	No	0.206	No	-0.268	No	-0.600	No	0.600	No	-0.192

tica	*Linaria cannabina*		*Motacilla alba*		*Oenanthe oenanthe*		*Parus major*		*Passer domesticus*		*Periparus ater*		*Phasianus c*
$P < 0.001$?	**Effect size**	**$P < 0.001$?**	**Effect size**	**$P < 0.001$?**	**Effect size**	**$P < 0.001$?**	**Effect size**	**$P < 0.001$?**	**Effect size**	**$P < 0.001$?**	**Effect size**	**$P < 0.001$?**	**Effect size**
No	1.820	Yes	0.038	No	-	-	-0.311	Yes	0.995	Yes	-0.868	Yes	-0.076
No	1.907	Yes	0.329	No	2.233	No	-1.564	Yes	-0.788	Yes	-3.570	Yes	-0.520
Yes	1.839	Yes	-0.382	No	1.420	No	-2.349	Yes	-1.570	Yes	-2.524	Yes	-2.025
Yes	1.860	Yes	1.385	Yes	1.321	No	-0.544	Yes	1.100	Yes	-2.127	Yes	0.121
Yes	1.290	Yes	1.539	Yes	0.684	No	-0.497	Yes	2.328	Yes	-1.299	Yes	-0.575
No	2.094	Yes	1.321	Yes	-	-	-0.246	No	0.992	Yes	-1.710	Yes	-0.692
-	2.505	Yes	1.483	No	-	-	-	-	1.166	Yes	-	-	-
-	1.657	No	-	-	2.560	No	-0.715	No	-	-	-	-	-
No	4.516	Yes	-0.546	No	-7.790	No	-0.278	No	0.748	No	-1.032	No	0.706
-	-2.891	Yes	-	-	-	-	-	-	-	-	-	-	-
No	0.082	No	-0.453	No	0.349	No	0.037	No	-0.063	No	-0.110	No	-0.008
Yes	-0.096	Yes	-0.078	No	0.081	No	0.023	No	0.106	Yes	-0.053	No	-0.078
No	-1.783	No	4.132	No	-2.210	No	1.185	No	-1.020	No	3.591	No	-1.521
No	0.931	No	1.387	No	-3.886	No	0.355	No	0.588	No	-0.441	No	-2.409
No	1.038	Yes	-0.064	No	-6.216	No	-0.002	No	0.447	No	1.522	Yes	-0.055

olchicus	*Phylloscopus collybita*		*Phylloscopus trochilus*		*Pica pica*		*Picus viridis*		*Prunella modularis*		*Pyrrhula pyrrhula*		*Regulus reg*
***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**
No	0.128	No	0.583	Yes	0.374	No	0.322	No	0.710	Yes	0.592	No	-0.661
Yes	-1.194	Yes	-1.042	Yes	0.032	No	-0.679	No	-0.727	Yes	-2.030	Yes	-3.122
Yes	-1.693	Yes	-1.104	Yes	-1.398	Yes	0.020	No	-0.778	Yes	-	-	-3.372
No	-1.109	Yes	-1.158	Yes	0.211	No	-0.657	Yes	0.435	Yes	-0.702	Yes	-2.205
Yes	-1.192	Yes	-1.078	Yes	0.421	Yes	-0.148	No	0.569	Yes	-0.327	No	-0.868
Yes	-0.110	No	0.046	No	0.409	No	0.219	No	0.558	Yes	0.242	No	-1.077
-	-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	0.086	No	-	-	-
No	0.032	No	-1.781	Yes	-1.756	Yes	-1.660	No	0.737	Yes	0.115	No	-0.545
-	-	-	-	-	-	-	-	-	-	-	-	-	-
No	0.319	No	0.451	No	0.455	Yes	0.278	No	0.139	No	0.155	No	0.024
Yes	-0.009	No	-0.048	No	0.244	Yes	0.007	No	0.054	Yes	-0.079	No	-0.059
No	5.569	No	3.536	No	-4.046	No	-1.823	No	0.939	No	1.171	No	5.766
No	1.724	No	1.422	No	-0.094	No	0.663	No	0.860	No	3.063	No	0.166
No	0.077	No	0.500	No	0.098	No	-2.884	No	0.433	No	-0.245	No	0.976

ulus	*Sitta europaea*		*Spinus spinus*		*Streptopelia decaocto*		*Sturnus vulgaris*		*Sylvia atricapilla*		*Sylvia borin*		*Sylvia com*
***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**
Yes	-2.154	Yes	-0.418	No	0.776	No	0.425	No	-0.206	No	0.504	No	1.506
Yes	-2.194	Yes	-3.215	Yes	-	-	0.832	Yes	-1.498	Yes	-1.717	Yes	1.042
Yes	-	-	-2.119	Yes	-	-	-0.918	Yes	-	-	-1.880	No	0.547
Yes	-1.392	Yes	-1.839	Yes	0.476	Yes	0.784	Yes	-1.133	Yes	-1.341	Yes	1.174
Yes	-0.955	Yes	-1.327	Yes	1.986	Yes	1.635	Yes	-1.069	Yes	-1.701	Yes	0.167
Yes	-1.523	Yes	-	-	0.957	Yes	0.630	Yes	-0.140	No	0.525	No	1.328
-	-	-	-	-	-	-	0.737	No	-	-	-	-	0.660
-	-	-	-	-	-	-	-14.528	No	-	-	-	-	-
No	-1.353	No	-2.299	No	1.347	Yes	0.268	No	0.281	No	-0.644	No	6.493
-	-	-	-	-	-	-	-	-	-	-	-	-	-5.377
No	-0.636	No	-0.074	No	0.130	No	0.239	No	0.140	No	0.426	No	0.230
No	-0.034	No	-0.043	No	0.045	No	0.253	Yes	0.001	No	-0.094	No	-0.046
No	4.561	No	1.631	No	1.447	No	2.033	No	2.873	No	8.251	No	1.879
No	1.587	No	-0.370	No	0.915	No	1.551	No	0.827	No	1.168	No	0.215
No	0.614	No	1.415	No	0.033	No	0.183	No	0.051	No	-0.188	No	0.895

nunis	*Troglodytes troglodytes*		*Turdus merula*		*Turdus philomelos*		*Turdus viscivorus*	
***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**	**Effect size**	***P* < 0.001?**
Yes	-0.280	Yes	-0.066	No	0.032	No	-0.544	No
Yes	-1.250	Yes	-1.027	Yes	-1.421	Yes	-1.050	Yes
No	-1.356	Yes	-1.675	Yes	-2.085	Yes	-3.044	Yes
Yes	-0.783	Yes	-0.345	Yes	-1.057	Yes	-0.813	Yes
No	-0.672	Yes	0.197	Yes	-0.430	Yes	0.032	No
Yes	-0.049	No	-0.022	No	-0.383	No	-0.156	No
No	-1.723	Yes	-0.703	Yes	-	-	-	-
-	-0.344	No	-0.605	No	-	-	-	-
Yes	0.000	No	0.653	Yes	-0.423	No	-0.993	No
Yes	-	-	-	-	-	-	-	-
No	0.056	No	0.108	No	0.067	No	-0.140	No
No	0.012	No	0.045	Yes	-0.080	Yes	-0.001	No
No	-0.215	No	0.726	No	-2.056	No	1.340	No
No	0.538	No	0.373	No	-0.946	No	0.668	No
Yes	0.253	No	0.100	No	0.395	No	-0.762	No

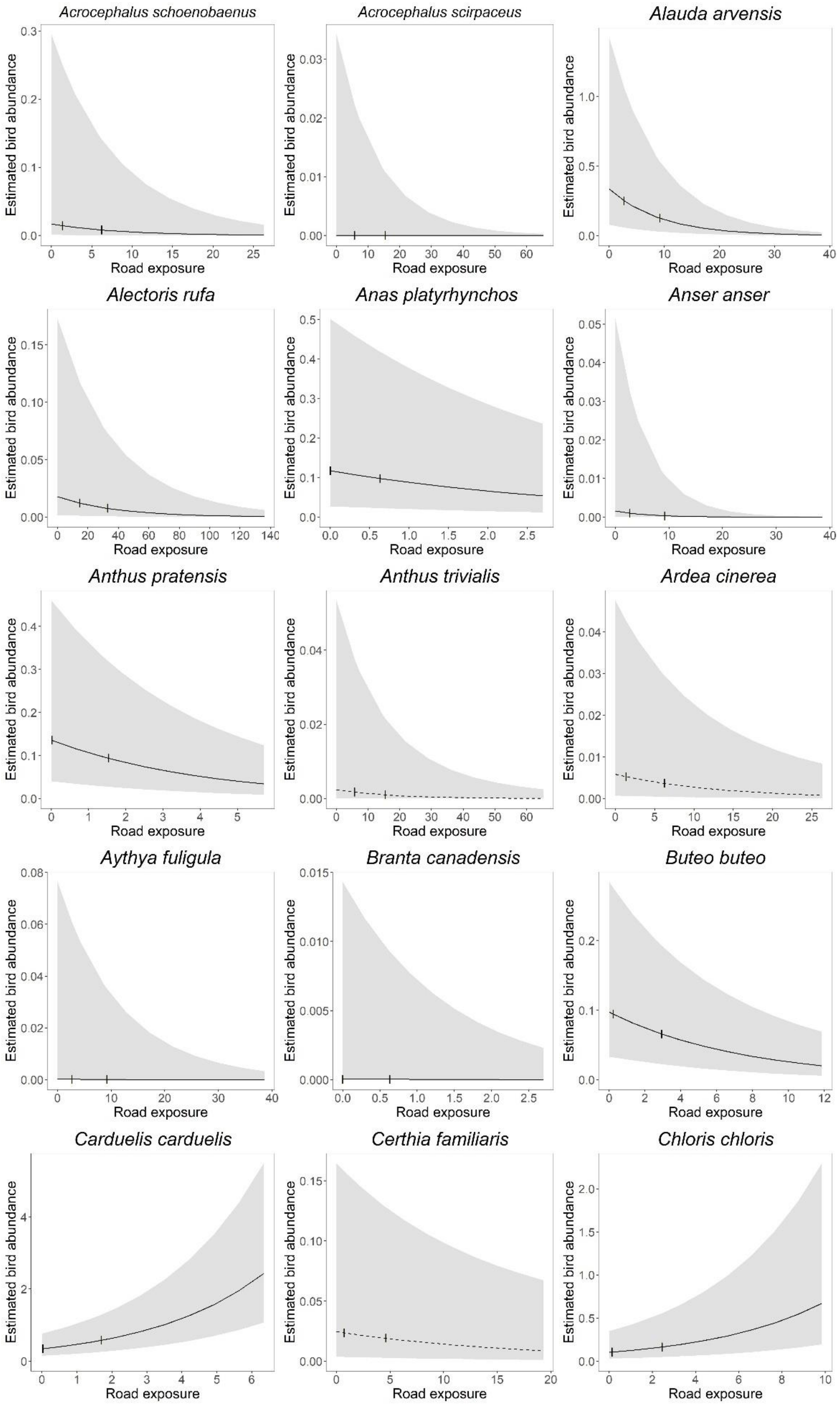
Appendix D. Full results for Chapter 4

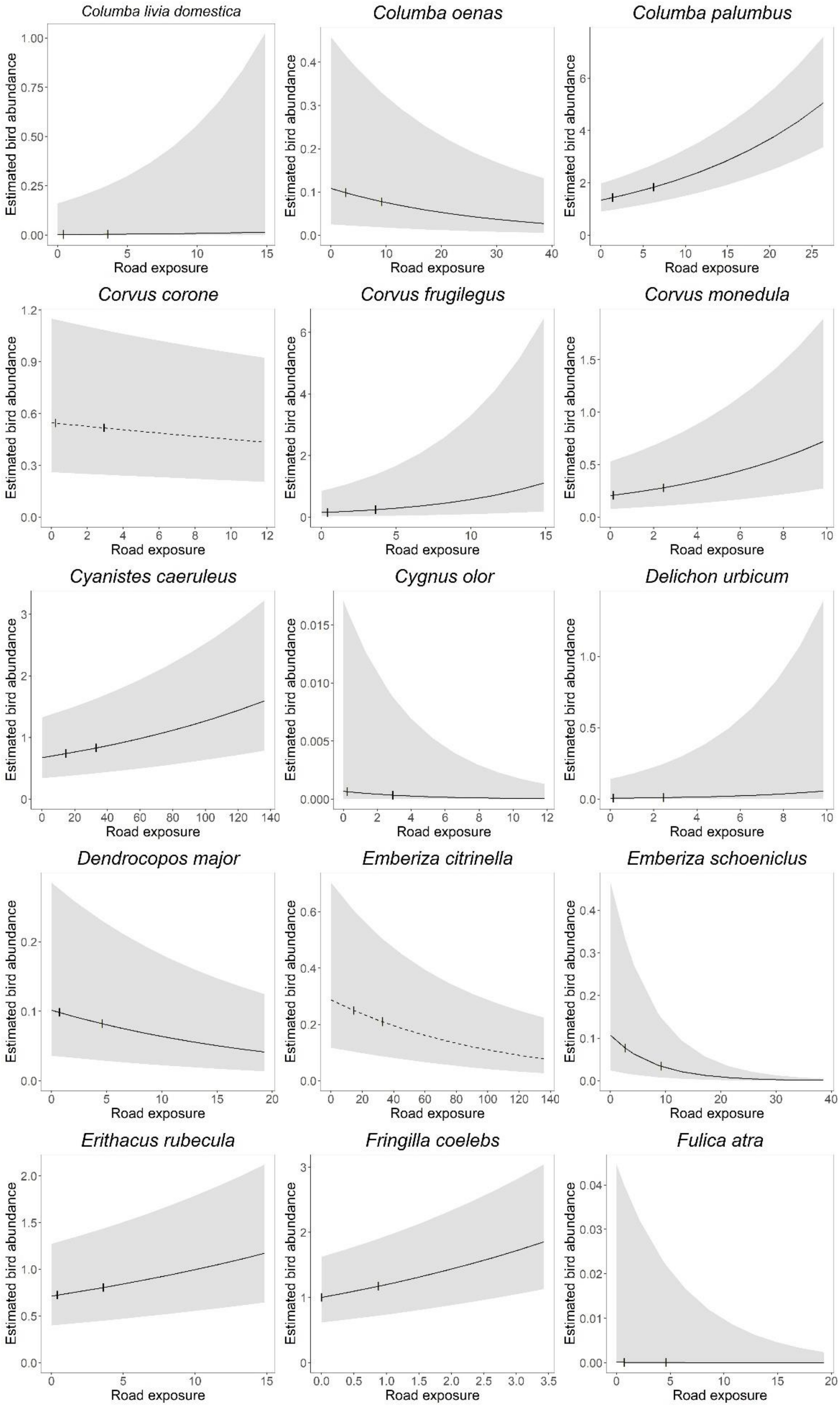
Here I provide the model parameters and road exposure results for all species (**Table D1**). I also graphically present the estimated changes in abundance across the ranges of road exposure calculated for each significant species (calculated using its *k* value) (**Figure D1**). Finally, I present the model results for all other covariates (**Table D2**).

Table D1. GAMM parameters and road exposure results for each species. The threshold significance level of 0.0007 was determined by Bonferroni correction.

Scientific name	Common name	Survey visit	Prop. arable land fit	*k*	Road exposure effect size (coefficient)	Significance level
Acrocephalus schoenobaenus	Sedge warbler	Late	Linear	5	-0.119	$P < 0.0007$
Acrocephalus scirpaceus	Reed warbler	Late	Linear	3	-0.075	$P < 0.0007$
Aegithalos caudatus	Long-tailed tit	Early	Linear	17	0.063	NS
Alauda arvensis	Eurasian skylark	Early	Quadratic	4	-0.107	$P < 0.0007$
Alectoris rufa	Red-legged partridge	Early	Quadratic	2	-0.026	$P < 0.0007$
Anas platyrhynchos	Mallard	Early	Linear	25	-0.288	$P < 0.0007$
Anser anser	Greylag goose	Early	Linear	4	-0.169	$P < 0.0007$
Anthus pratensis	Meadow pipit	Early	Linear	13	-0.243	$P < 0.0007$
Anthus trivialis	Tree pipit	Late	Linear	3	-0.058	<0.05
Apus apus	Common swift	Late	Linear	20	-0.136	NS
Ardea cinerea	Grey heron	Early	Linear	5	-0.075	$P < 0.05$
Aythya fuligula	Tufted duck	Early	Linear	4	-0.085	$P < 0.0007$
Branta canadensis	Canada goose	Early	Linear	25	-0.690	$P < 0.0007$
Buteo buteo	Common buzzard	Early	Linear	8	-0.133	$P < 0.0007$
Carduelis cabaret	Lesser redpoll	Early	Linear	14	-0.154	NS
Carduelis carduelis	European goldfinch	Early	Linear	12	0.308	$P < 0.0007$
Certhia familiaris	Eurasian treecreeper	Early	Linear	6	-0.054	$P < 0.05$
Chloris chloris	European greenfinch	Early	Linear	9	0.189	$P < 0.0007$
Chroicocephalus ridibundus	Black-headed gull	Early	Linear	9	-0.016	NS
Columba livia domestica	Feral pigeon	Early	Linear	7	0.123	$P < 0.0007$
Columba oenas	Stock dove	Early	Quadratic	4	-0.036	$P < 0.0007$
Columba palumbus	Common woodpigeon	Early	Linear	5	0.050	$P < 0.0007$
Corvus corone	Carrion crow	Early	Linear	8	-0.019	$P < 0.05$
Corvus frugilegus	Rook	Early	Linear	7	0.135	$P < 0.0007$
Corvus monedula	Eurasian jackdaw	Early	Linear	9	0.128	$P < 0.0007$
Cyanistes caeruleus	Blue tit	Early	Linear	2	0.006	$P < 0.0007$
Cygnus olor	Mute swan	Early	Linear	8	-0.228	$P < 0.0007$
Delichon urbicum	Common house martin	Late	Linear	9	0.228	$P < 0.0007$
Dendrocopos major	Great spotted woodpecker	Early	Linear	6	-0.046	$P < 0.0007$
Emberiza citrinella	Yellowhammer	Early	Quadratic	2	-0.010	$P < 0.05$

Emberiza schoeniclus	Common reed bunting	Early	Linear	4	-0.125	$P < 0.0007$
Erithacus rubecula	European robin	Early	Linear	7	0.033	$P < 0.0007$
Falco tinnunculus	Common kestrel	Early	Quadratic	4	-0.012	NS
Fringilla coelebs	Common chaffinch	Early	Linear	20	0.180	$P < 0.0007$
Fulica atra	Eurasian coot	Early	Linear	6	-0.154	$P < 0.0007$
Gallinula chloropus	Common moorhen	Early	Linear	7	-0.090	$P < 0.0007$
Garrulus glandarius	Eurasian jay	Early	Linear	8	-0.037	NS
Haematopus ostralegus	Eurasian oystercatcher	Early	Linear	12	0.066	NS
Hirundo rustica	Barn swallow	Late	Linear	18	0.443	$P < 0.0007$
Lagopus lagopus	Red grouse	Early	Linear	2	-0.046	$P < 0.0007$
Larus argentatus	Herring gull	Early	Linear	35	-0.064	NS
Larus canus	Common gull	Early	Linear	11	0.470	$P < 0.0007$
Larus fuscus	Lesser black-backed gull	Early	Linear	2	0.027	$P < 0.0007$
Linaria cannabina	Common linnet	Early	Quadratic	2	-0.017	$P < 0.0007$
Motacilla alba	Pied/white wagtail	Early	Linear	14	0.110	$P < 0.05$
Motacilla flava	Yellow wagtail	Late	Quadratic	9	-0.251	$P < 0.0007$
Muscicapa striata	Spotted flycatcher	Late	Linear	18	0.228	NS
Numenius arquata	Eurasian curlew	Early	Linear	35	0.107	NS
Oenanthe oenanthe	Northern wheatear	Late	Linear	3	-0.078	$P < 0.0007$
Parus major	Great tit	Early	Linear	6	0.028	$P < 0.0007$
Passer domesticus	House sparrow	Early	Linear	9	0.281	$P < 0.0007$
Passer montanus	Tree sparrow	Early	Quadratic	16	0.467	$P < 0.0007$
Perdix perdix	Grey partridge	Early	Quadratic	4	0.002	NS
Periparus ater	Coal tit	Early	Linear	20	-0.016	NS
Phasianus colchicus	Ring-necked pheasant	Early	Linear	2	-0.023	$P < 0.0007$
Phylloscopus collybita	Common chiffchaff	Late	Linear	6	-0.025	$P < 0.05$
Phylloscopus trochilus	Willow warbler	Late	Linear	2	-0.012	$P < 0.0007$
Picus viridis	European green woodpecker	Early	Linear	4	-0.034	$P < 0.0007$
Prunella modularis	Dunnock	Early	Linear	6	0.057	$P < 0.0007$
Pyrrhula pyrrhula	Eurasian bullfinch	Early	Linear	16	0.210	$P < 0.0007$
Regulus regulus	Goldcrest	Early	Linear	25	0.083	NS
Sitta europaea	Eurasian nuthatch	Early	Linear	2	-0.008	$P < 0.05$
Spinus spinus	Eurasian siskin	Early	Linear	90	0.319	NS
Streptopelia decaocto	Eurasian collared dove	Early	Linear	7	0.195	$P < 0.0007$
Sturnus vulgaris	Common starling	Early	Linear	4	0.063	$P < 0.0007$
Sylvia atricapilla	Eurasian blackcap	Late	Linear	5	-0.013	$P < 0.05$
Sylvia borin	Garden warbler	Late	Linear	50	-0.339	NS
Sylvia communis	Common whitethroat	Late	Quadratic	35	0.169	$P < 0.05$
Sylvia curruca	Lesser whitethroat	Late	Quadratic	14	0.119	NS
Tadorna tadorna	Common shelduck	Early	Linear	4	-0.270	$P < 0.0007$
Troglodytes troglodytes	Eurasian wren	Early	Linear	20	0.055	$P < 0.05$
Turdus merula	Common blackbird	Early	Linear	5	0.042	$P < 0.0007$
Turdus philomelos	Song thrush	Early	Linear	11	0.071	$P < 0.0007$
Turdus viscivorus	Mistle thrush	Early	Linear	10	0.047	NS
Vanellus vanellus	Northern lapwing	Early	Linear	3	-0.053	$P < 0.0007$


Acrocephalus schoenobaenus
Acrocephalus scirpaceus
Alauda arvensis
Alectoris rufa
Anas platyrhynchos
Anser anser
Anthus pratensis
Anthus trivialis
Ardea cinerea
Aythya fuligula
Branta canadensis
Buteo buteo
Carduelis carduelis
Certhia familiaris
Chloris chloris
Estimated bird abundance
Road exposure


Columba livia domestica

Columba oenas

Columba palumbus

Corvus corone

Corvus frugilegus

Corvus monedula

Cyanistes caeruleus

Cygnus olor

Delichon urbicum

Dendrocopos major

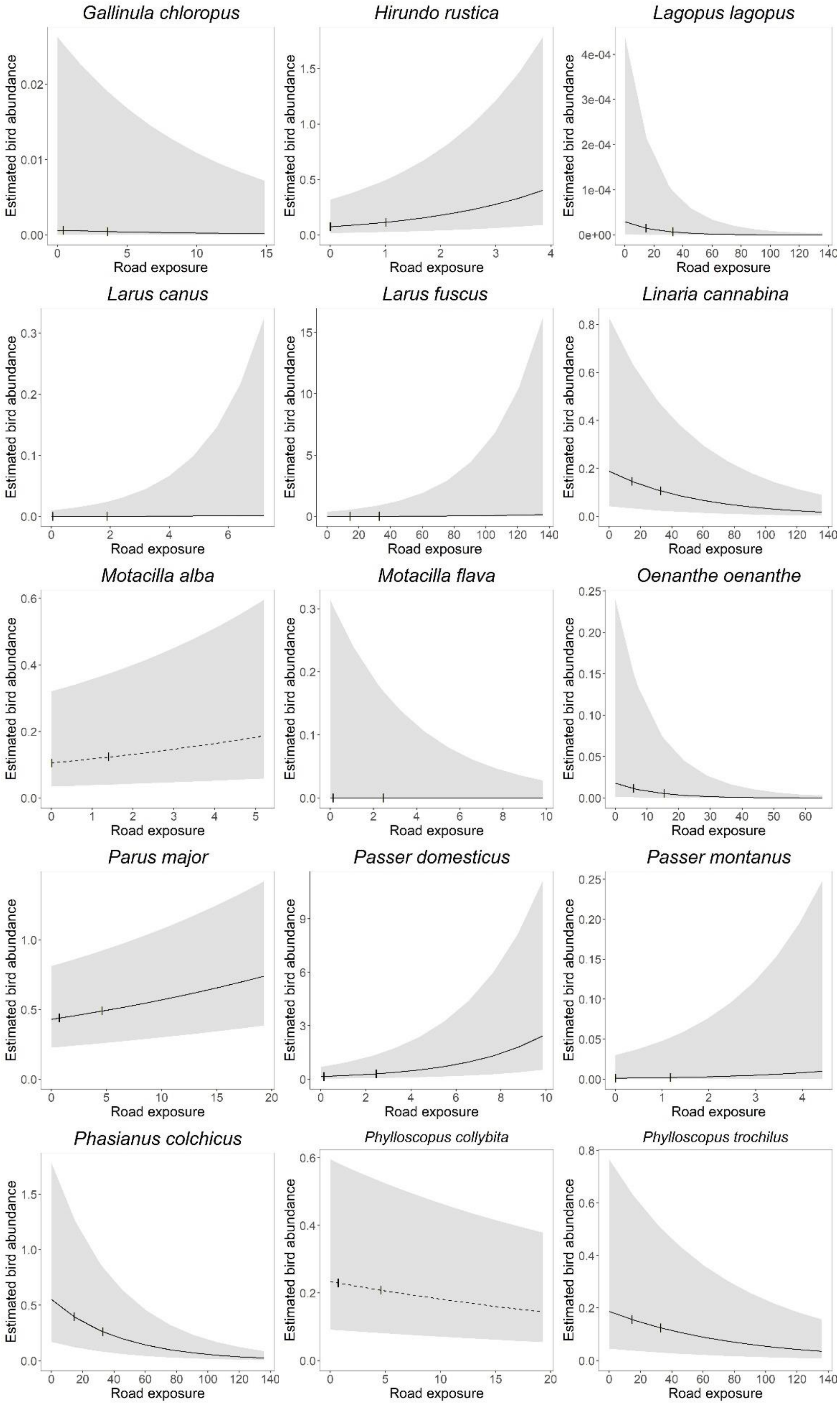
Emberiza citrinella

Emberiza schoeniclus

Erithacus rubecula

Fringilla coelebs

Fulica atra


Gallinula chloropus
Hirundo rustica
Lagopus lagopus
Larus canus
Larus fuscus
Linaria cannabina
Motacilla alba
Motacilla flava
Oenanthe oenanthe
Parus major
Passer domesticus
Passer montanus
Phasianus colchicus
Phylloscopus collybita
Phylloscopus trochilus
Estimated bird abundance
Road exposure
0.00
0.01
0.02
0
5
10
15
0.0
0.5
1.0
1.5
0
1
2
3
4
0e+00
1e-04
2e-04
3e-04
4e-04
0
20
40
60
80
100
120
140
0.0
0.1
0.2
0.3
0
2
4
6
0
5
10
15
0.0
0.2
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0.8
0.0
0.2
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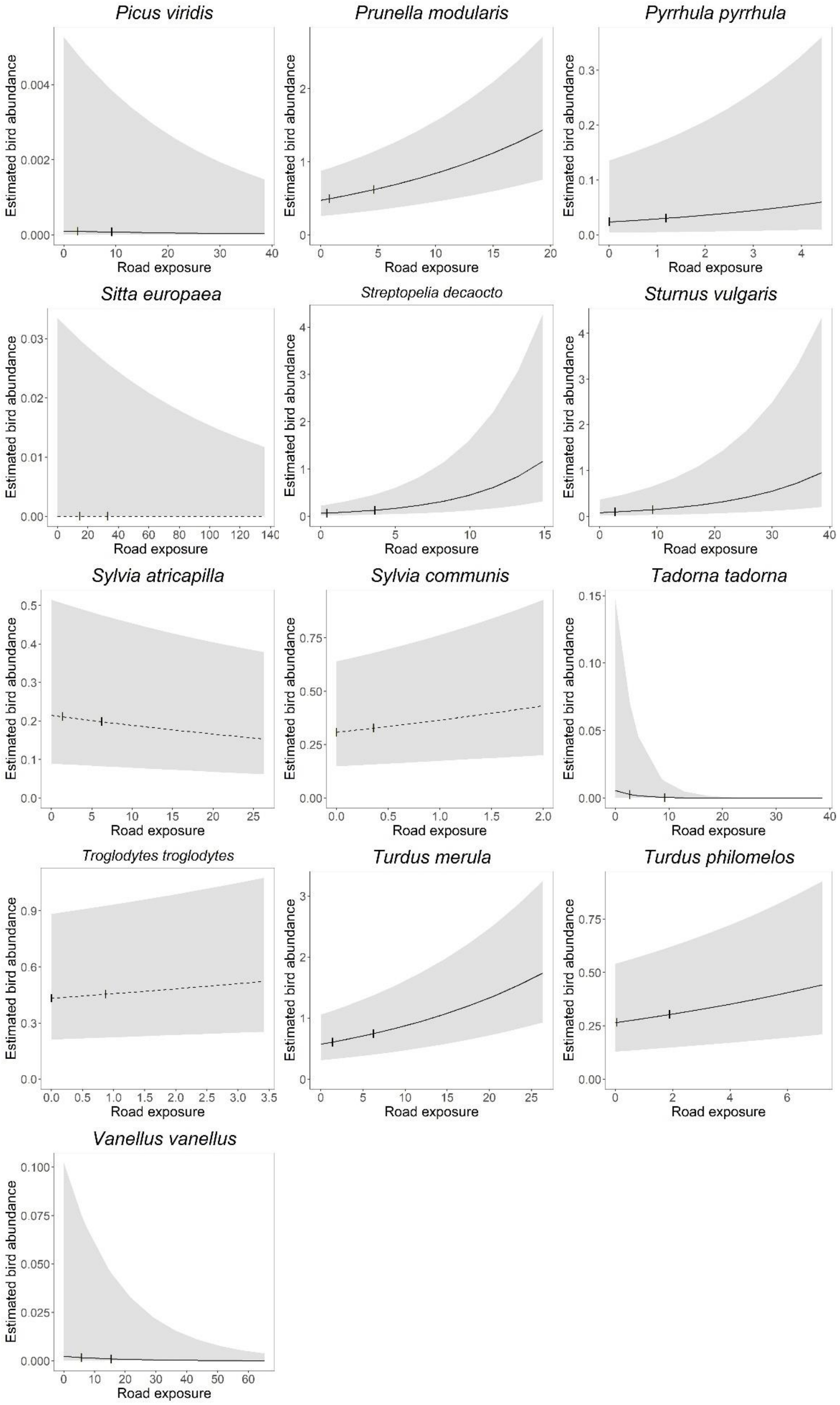


Figure D1. Estimated bird abundance across the full ranges of road exposure, as calculated for each species using its *k* value (which optimises the spatial scale between distance from road and road exposure). X-axes represent road exposure and Y-axes represent estimated bird abundance within 100 m of a 200-m BBS transect section. The 0.25 and 0.75 quartiles of road exposure for each species are indicated by the vertical lines. Only species with significant associations are shown here, and those that retained significance after Bonferroni correction are depicted by a solid, as opposed to dashed, line. Shaded areas denote 95% prediction intervals.

Table D2. Coefficients and significance (determined without Bonferroni correction) for all other covariates included in the GAMM for each species. The reference habitat category for all species is woodland. Effect sizes for the continuous covariates are not directly comparable as they were not standardised.

		Acrocephalus schoenobaenus		*Acrocephalus scirpaceus*		*Aegithalos caudatus*		*Alauda arvensis*		*Alectoris rufa*	
		Effect size	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**
Habitat	**Scrubland**	1.752	Yes	1.450	Yes	0.105	No	0.848	Yes	-0.035	No
	Semi-natural grassland and marsh	2.138	Yes	2.002	Yes	-1.219	Yes	2.117	Yes	-0.373	No
	Heathland and bogs	0.806	No	-24.501	No	-1.847	Yes	1.885	Yes	0.323	No
	Farmland	1.253	Yes	0.661	Yes	-0.614	Yes	1.567	Yes	0.978	Yes
	Human sites	0.882	Yes	0.367	No	-0.493	Yes	0.461	Yes	0.143	No
	Water-bodies (freshwater)	3.206	Yes	3.300	Yes	0.043	No	0.366	Yes	0.200	No
	Coastal	1.498	Yes	0.320	No	-1.149	Yes	1.208	Yes	0.887	No
	Inland rock	-23.758	No	-25.160	No	-1.976	No	2.105	Yes	0.479	No
Prop. arable land		1.561	Yes	-0.949	No	-0.084	No	2.907	Yes	5.031	Yes
Prop. arable land^2		-	-	-	-	-	-	-0.978	No	-4.137	Yes
Largest cropping unit		0.709	Yes	0.493	No	0.197	No	-0.132	No	0.152	No
Human population density ($\log_{10}$)		0.053	No	0.153	No	-0.001	No	-0.058	No	-0.191	Yes
Temperature		-0.108	No	-13.530	Yes	4.327	Yes	-0.006	No	-1.854	No
Rainfall		3.611	Yes	-4.393	No	2.186	Yes	0.171	No	-2.737	Yes
Tree cover density		1.627	Yes	1.753	Yes	0.264	No	0.008	No	0.207	No

Anas platyrhynchos		*Anser anser*		*Anthus pratensis*		*Anthus trivialis*		*Apus apus*		*Ardea cinerea*		*Aythya fuligula*	
Effect size	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**
-0.251	No	-0.176	No	1.240	Yes	0.977	Yes	1.170	Yes	0.095	No	1.498	Yes
0.121	No	0.166	No	2.394	Yes	-0.231	No	-0.740	No	0.106	No	0.400	No
-0.586	Yes	0.858	Yes	2.343	Yes	0.286	No	0.861	No	-0.550	No	-1.488	No
0.110	No	0.156	No	1.375	Yes	-1.280	Yes	-0.160	No	-0.227	No	-0.362	No
0.257	Yes	0.846	Yes	-0.182	No	-1.817	Yes	0.615	Yes	0.406	No	0.568	Yes
1.982	Yes	1.827	Yes	1.783	Yes	-0.828	No	0.877	Yes	2.478	Yes	3.389	Yes
0.648	Yes	0.731	No	1.933	Yes	-1.087	No	-1.799	No	1.038	No	0.396	No
-0.881	No	-26.734	No	2.221	Yes	0.408	No	0.585	No	-19.576	No	-27.951	No
-0.172	No	0.669	No	-3.111	Yes	-5.441	Yes	1.117	No	-0.417	No	0.198	No
-	-	-	-	-	-	-	-	-	-	-	-	-	-
-0.090	No	-0.609	No	-0.214	No	0.970	No	-0.316	No	-0.124	No	0.020	No
0.027	No	0.377	Yes	-0.165	Yes	-0.469	Yes	0.448	Yes	0.212	No	0.388	Yes
-3.501	Yes	8.862	No	-2.758	No	10.213	Yes	2.978	No	-2.038	No	-0.478	No
-1.177	No	1.164	No	-1.472	No	0.071	No	2.975	No	-1.104	No	-2.349	No
-0.033	No	0.782	No	-0.345	No	1.925	Yes	-0.217	No	-0.323	No	0.195	No

Branta canadensis		***Buteo buteo***		***Carduelis cabaret***		***Carduelis carduelis***		***Certhia familiaris***		***Chloris chloris***		***Chroicocephalus ridibundus***	
Effect size	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**
-0.151	No	-0.400	No	0.662	Yes	0.469	Yes	-1.749	Yes	0.633	Yes	0.314	No
0.659	Yes	-1.085	Yes	-1.231	Yes	-0.333	Yes	-2.067	Yes	-0.350	Yes	0.353	No
0.418	No	-1.140	Yes	-0.595	No	-1.206	Yes	-2.844	Yes	-0.470	Yes	0.581	No
0.201	No	-0.298	Yes	-0.944	Yes	0.501	Yes	-1.548	Yes	0.347	Yes	1.909	Yes
0.172	No	-1.031	Yes	-0.632	No	1.016	Yes	-1.652	Yes	1.074	Yes	1.684	Yes
2.366	Yes	-0.471	No	-1.333	No	0.671	Yes	-1.093	Yes	0.725	Yes	2.073	Yes
-0.239	No	-1.751	No	-25.135	No	-0.535	No	-18.898	No	-0.453	No	3.395	Yes
-23.284	No	-0.322	No	-0.287	No	-0.953	No	-18.870	No	-0.244	No	1.404	No
-0.735	No	0.920	Yes	-0.553	No	0.703	Yes	-0.250	No	0.798	Yes	-2.030	Yes
-	-	-	-	-	-	-	-	-	-	-	-	-	-
-0.751	Yes	-0.024	No	-2.167	Yes	-0.001	No	-0.030	No	0.185	No	0.154	No
-0.019	No	-0.184	Yes	-0.169	No	-0.074	Yes	-0.201	Yes	0.058	No	-0.273	Yes
-6.801	No	-3.072	No	0.089	No	4.258	Yes	0.390	No	-0.057	No	1.372	No
-2.145	No	-0.447	No	2.497	No	0.967	No	-0.322	No	-0.213	No	-0.228	No
0.346	No	0.033	No	1.298	Yes	0.388	Yes	0.671	No	0.544	Yes	1.032	No

Columba livia domestica		*Columba oenas*		*Columba palumbus*		*Corvus corone*		*Corvus frugilegus*		*Corvus monedula*		*Cyanistes caeruleus*	
Effect size	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**
1.034	Yes	-0.310	No	-0.222	Yes	-0.129	No	-2.119	Yes	-0.683	Yes	-0.282	Yes
0.131	No	-0.505	Yes	-0.798	Yes	-0.364	Yes	-0.704	Yes	-0.415	Yes	-1.248	Yes
-1.390	No	-1.909	Yes	-1.243	Yes	-0.864	Yes	-3.400	Yes	-1.716	Yes	-1.768	Yes
1.270	Yes	-0.149	No	-0.454	Yes	0.173	Yes	-0.256	Yes	0.161	Yes	-0.489	Yes
1.987	Yes	-0.186	No	-0.038	No	0.160	Yes	-0.223	Yes	0.694	Yes	-0.237	Yes
2.141	Yes	-0.289	No	-0.173	Yes	0.165	Yes	-0.313	Yes	0.213	Yes	-0.236	Yes
1.687	Yes	-0.952	No	-0.558	Yes	-0.119	No	-1.634	Yes	-0.284	No	-1.147	Yes
-18.020	No	-1.029	No	-0.859	Yes	0.000	No	-1.313	No	0.491	Yes	-1.623	Yes
-0.693	No	1.742	Yes	1.207	Yes	-0.406	Yes	1.603	Yes	0.240	No	0.094	No
-	-	-	-	-	-	-	-	-	-	-	-	-	-
-0.331	No	-0.220	No	0.108	No	0.010	No	0.079	No	-0.048	No	0.066	No
0.410	Yes	0.016	No	0.094	Yes	0.101	Yes	-0.130	Yes	-0.040	No	-0.013	No
-1.185	No	-2.040	No	-1.401	No	-0.661	No	-8.462	Yes	-0.080	No	0.672	No
0.450	No	-0.702	No	0.891	Yes	0.439	No	-2.288	No	-0.330	No	0.048	No
0.502	No	-0.117	No	0.480	Yes	-0.037	No	-2.107	Yes	-0.414	No	0.098	No

Cygnus olor		*Delichon urbicum*		*Dendrocopos major*		*Emberiza citrinella*		*Emberiza schoeniclus*		*Erithacus rubecula*		*Falco tinnunculus*	
Effect size	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**
0.986	Yes	1.268	Yes	-0.466	Yes	1.321	Yes	1.640	Yes	-0.256	Yes	0.518	No
1.428	Yes	-0.039	No	-1.937	Yes	0.933	Yes	2.363	Yes	-1.337	Yes	1.044	Yes
-21.694	No	-0.693	No	-1.804	Yes	0.830	Yes	1.552	Yes	-1.603	Yes	0.061	No
0.303	No	0.935	Yes	-1.013	Yes	1.350	Yes	1.406	Yes	-0.595	Yes	0.471	Yes
0.914	Yes	1.860	Yes	-0.836	Yes	-0.015	No	0.594	Yes	-0.364	Yes	0.052	No
3.267	Yes	0.813	Yes	-0.894	Yes	-0.123	No	2.893	Yes	-0.349	Yes	0.589	No
2.198	Yes	1.558	Yes	-1.786	Yes	-1.460	No	1.775	Yes	-1.831	Yes	-14.524	No
-21.863	No	-24.192	No	-2.193	Yes	1.142	No	1.837	Yes	-1.046	Yes	2.090	Yes
-0.288	No	1.724	Yes	0.010	No	12.048	Yes	1.181	Yes	-0.282	Yes	3.555	Yes
-	-	-	-	-	-	-9.849	Yes	-	-	-	-	-2.854	Yes
0.511	No	-0.318	No	-0.337	Yes	0.043	No	0.564	Yes	0.036	No	0.061	No
0.286	Yes	-0.139	No	-0.076	No	-0.190	Yes	0.080	No	0.040	Yes	-0.072	No
-6.139	No	-3.444	No	0.300	No	2.356	No	-0.357	No	0.422	No	1.885	No
-0.719	No	-1.238	No	0.050	No	2.379	Yes	2.359	Yes	0.640	Yes	2.285	No
-1.632	Yes	0.513	No	0.260	No	-0.093	No	0.357	No	0.115	No	0.314	No

Fringilla coelebs		*Fulica atra*		*Gallinula chloropus*		*Garrulus glandarius*		*Haematopus ostralegus*		*Hirundo rustica*		*Lagopus lagopus*	
Effect size	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**
-0.124	Yes	0.360	No	-0.144	No	-0.264	No	1.481	Yes	0.446	Yes	0.578	No
-1.048	Yes	0.345	No	-0.015	No	-1.572	Yes	1.380	Yes	0.274	No	1.036	Yes
-1.367	Yes	-1.575	Yes	-1.148	Yes	-1.580	Yes	1.141	Yes	-1.085	Yes	2.066	Yes
-0.253	Yes	-0.518	Yes	0.023	No	-1.243	Yes	1.711	Yes	1.084	Yes	-1.470	Yes
-0.211	Yes	0.418	Yes	0.501	Yes	-1.134	Yes	1.738	Yes	1.197	Yes	-17.520	No
-0.178	Yes	2.620	Yes	2.432	Yes	-1.084	Yes	2.767	Yes	0.804	Yes	-0.686	No
-1.338	Yes	1.408	Yes	-0.241	No	-17.379	No	3.371	Yes	0.716	No	-16.066	No
-1.193	Yes	-24.314	No	-18.430	No	-1.053	No	1.398	No	0.585	No	1.280	Yes
0.523	Yes	-0.148	No	0.027	No	-0.536	Yes	1.262	No	0.637	Yes	-6.360	Yes
-	-	-	-	-	-	-	-	-	-	-	-	-	-
-0.029	No	0.168	No	-0.004	No	-0.270	No	-1.214	No	-0.327	No	-3.034	No
-0.144	Yes	0.239	Yes	0.119	Yes	0.078	No	-0.197	No	-0.305	Yes	-0.045	No
0.042	No	-4.349	No	-1.752	No	0.108	No	0.113	No	-2.289	No	-0.636	No
0.096	No	-0.332	No	-0.142	No	-0.061	No	-3.106	No	-0.238	No	-1.298	No
0.178	No	-0.046	No	-0.241	No	0.597	Yes	1.616	Yes	-0.361	No	-3.940	Yes

Larus argentatus		***Larus canus***		***Larus fuscus***		***Linaria cannabina***		***Motacilla alba***		***Motacilla flava***		***Muscicapa striata***	
Effect size	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**
0.094	No	0.887	No	2.095	Yes	1.505	Yes	-0.096	No	0.805	No	-1.029	Yes
1.384	Yes	1.730	No	1.332	Yes	1.631	Yes	-0.125	No	2.208	Yes	-1.406	Yes
-0.265	No	1.045	No	2.446	Yes	1.447	Yes	-0.494	Yes	-17.805	No	-1.510	Yes
1.582	Yes	1.874	Yes	2.429	Yes	1.573	Yes	0.912	Yes	2.234	Yes	-0.947	Yes
2.229	Yes	-0.240	No	2.388	Yes	1.153	Yes	1.047	Yes	0.455	No	-0.470	No
1.794	Yes	1.112	No	3.316	Yes	1.624	Yes	0.871	Yes	0.901	No	-2.224	Yes
3.577	Yes	-31.884	No	4.038	Yes	1.933	Yes	1.219	Yes	-20.420	No	-19.561	No
1.709	No	-28.554	No	-24.371	No	1.513	Yes	0.452	No	-18.144	No	-20.002	No
-1.080	No	4.026	Yes	-0.444	No	4.517	Yes	-0.662	Yes	9.087	Yes	-0.158	No
-	-	-	-	-	-	-3.002	Yes	-	-	-4.467	Yes	-	-
1.130	Yes	-4.592	Yes	0.027	No	0.017	No	-0.142	No	0.426	No	-0.847	No
0.299	Yes	0.859	Yes	-0.052	No	-0.065	No	-0.227	Yes	-0.085	No	-0.503	Yes
8.124	No	10.869	No	5.665	No	-1.633	No	2.538	No	-6.317	No	4.149	No
0.880	No	2.091	No	-1.490	No	1.006	No	0.534	No	-4.762	No	-1.015	No
0.606	No	-3.273	No	0.485	No	0.987	Yes	-0.249	No	2.764	Yes	-0.088	No

Numenius arquata		*Oenanthe oenanthe*		*Parus major*		*Passer domesticus*		*Passer montanus*		*Perdix perdix*		*Periparus ater*	
Effect size	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**
1.083	No	0.753	No	-0.307	Yes	0.879	Yes	0.889	No	1.157	No	-0.803	Yes
1.823	Yes	2.359	Yes	-1.314	Yes	-0.454	Yes	-0.027	No	1.013	No	-2.823	Yes
1.858	Yes	1.570	Yes	-1.933	Yes	-1.101	Yes	-0.298	No	0.377	No	-2.048	Yes
1.380	Yes	1.342	Yes	-0.474	Yes	1.024	Yes	1.284	Yes	1.529	Yes	-1.674	Yes
-0.326	No	1.075	No	-0.409	Yes	2.156	Yes	1.866	Yes	-0.493	No	-0.993	Yes
0.124	No	1.949	Yes	-0.308	Yes	0.997	Yes	0.955	Yes	1.021	No	-1.496	Yes
3.394	Yes	2.553	Yes	-1.636	Yes	1.049	Yes	-21.881	No	1.498	No	-20.036	No
1.727	Yes	2.403	Yes	-0.821	Yes	-0.628	No	-20.959	No	-18.669	No	-2.820	Yes
-2.388	Yes	-3.973	Yes	-0.124	No	0.839	Yes	11.424	Yes	5.393	Yes	-0.628	Yes
-	-	-	-	-	-	-	-	-9.338	Yes	-2.808	No	-	-
-0.999	No	0.572	No	0.047	No	-0.038	No	-0.241	No	-0.014	No	-0.180	No
-0.221	Yes	0.298	Yes	0.017	No	0.241	Yes	-0.280	Yes	-0.152	No	-0.150	Yes
1.139	No	-0.101	No	1.684	Yes	-0.855	No	1.672	No	0.828	No	3.575	Yes
-2.161	No	-2.146	No	0.707	No	0.474	No	3.776	Yes	-3.432	No	-0.237	No
0.291	No	-4.151	Yes	-0.017	No	0.454	No	0.050	No	0.631	No	1.197	Yes

Phasianus colchicus		***Phylloscopus collybita***		***Phylloscopus trochilus***		***Picus viridis***		***Prunella modularis***		***Pyrrhula pyrrhula***		***Regulus regulus***	
Effect size	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**	**Effect size**	**$P < 0.05$?**
-0.043	No	0.031	No	0.497	Yes	0.181	No	0.422	Yes	0.341	No	-0.534	Yes
-0.616	Yes	-1.117	Yes	-0.768	Yes	-0.509	Yes	-0.653	Yes	-1.676	Yes	-2.096	Yes
-1.303	Yes	-1.579	Yes	-0.924	Yes	-0.177	No	-1.024	Yes	-2.272	Yes	-2.529	Yes
0.011	No	-0.878	Yes	-0.854	Yes	-0.569	Yes	0.283	Yes	-0.627	Yes	-1.707	Yes
-0.367	Yes	-0.875	Yes	-0.802	Yes	-0.661	Yes	0.396	Yes	-0.329	Yes	-0.796	Yes
-0.329	Yes	-0.160	No	0.071	No	0.020	No	0.287	Yes	0.022	No	-0.898	Yes
-1.323	Yes	-1.597	Yes	-1.325	Yes	-1.349	No	-0.258	No	-17.394	No	-3.227	Yes
-2.704	Yes	-1.386	Yes	-2.408	Yes	-17.048	No	0.000	No	-1.087	No	-2.328	Yes
0.694	Yes	0.149	No	-1.074	Yes	-0.778	Yes	0.658	Yes	0.343	No	-0.538	Yes
-	-	-	-	-	-	-	-	-	-	-	-	-	-
-0.021	No	0.225	Yes	0.144	No	-0.066	No	0.097	No	-0.036	No	-0.007	No
-0.152	Yes	-0.021	No	-0.060	No	-0.004	No	0.073	Yes	-0.153	Yes	-0.184	Yes
-1.060	No	3.400	Yes	3.431	Yes	-1.770	No	-0.196	No	2.962	No	3.500	Yes
-1.759	Yes	1.327	Yes	0.810	No	-0.133	No	0.292	No	2.615	Yes	0.305	No
-0.235	No	-0.002	No	0.366	No	-0.699	No	0.310	Yes	0.198	No	0.969	Yes

Sitta europaea		*Spinus spinus*		*Streptopelia decaocto*		*Sturnus vulgaris*		*Sylvia atricapilla*		*Sylvia borin*		*Sylvia communis*	
Effect size	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**
-1.256	Yes	-0.408	Yes	0.486	Yes	0.407	Yes	-0.068	No	0.524	Yes	1.226	Yes
-2.320	Yes	-2.898	Yes	-0.916	Yes	0.762	Yes	-1.163	Yes	-1.307	Yes	0.707	Yes
-2.573	Yes	-1.983	Yes	-0.684	Yes	-0.940	Yes	-2.074	Yes	-1.457	Yes	0.283	No
-1.250	Yes	-1.706	Yes	0.346	Yes	0.771	Yes	-0.810	Yes	-0.999	Yes	0.866	Yes
-0.795	Yes	-1.272	Yes	1.538	Yes	1.493	Yes	-0.832	Yes	-1.176	Yes	-0.044	No
-0.947	Yes	-1.712	Yes	0.727	Yes	0.638	Yes	-0.215	Yes	0.121	No	0.964	Yes
-1.691	Yes	-24.644	No	0.475	No	0.620	Yes	-1.921	Yes	-21.589	No	0.572	Yes
-21.738	No	-25.019	No	-13.869	No	-12.000	No	-1.546	Yes	-21.497	No	1.018	Yes
-1.427	Yes	-2.210	Yes	1.225	Yes	0.421	No	0.267	No	-0.480	No	5.772	Yes
-	-	-	-	-	-	-	-	-	-	-	-	-4.652	Yes
-0.397	No	-0.201	No	0.043	No	0.156	No	0.114	No	0.170	No	0.166	No
-0.112	No	-0.099	No	0.139	Yes	0.499	Yes	-0.028	No	-0.238	Yes	-0.073	Yes
2.748	No	1.833	No	0.200	No	1.546	No	2.130	No	7.115	Yes	1.037	No
0.011	No	0.035	No	0.155	No	1.115	No	0.707	No	1.054	No	0.067	No
0.181	No	1.503	Yes	0.166	No	0.081	No	0.176	No	0.306	No	0.772	Yes

Sylvia curruca		*Tadorna tadorna*		*Troglodytes troglodytes*		*Turdus merula*		*Turdus philomelos*		*Turdus viscivorus*		*Vanellus vanellus*	
Effect size	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**	**Effect size**	***P* < 0.05?**
1.867	Yes	-0.350	No	-0.221	Yes	-0.023	No	-0.043	No	-0.498	Yes	1.024	Yes
0.837	No	0.847	No	-1.082	Yes	-1.000	Yes	-1.210	Yes	-1.393	Yes	1.476	Yes
-0.407	No	-0.797	No	-1.154	Yes	-1.471	Yes	-1.808	Yes	-2.566	Yes	0.731	Yes
1.220	Yes	0.668	No	-0.653	Yes	-0.290	Yes	-0.770	Yes	-0.856	Yes	1.895	Yes
0.097	No	1.500	Yes	-0.555	Yes	0.140	Yes	-0.469	Yes	-0.364	Yes	0.429	No
1.402	Yes	2.749	Yes	-0.120	Yes	-0.091	No	-0.236	Yes	-0.548	Yes	1.913	Yes
-19.914	No	1.514	Yes	-1.277	Yes	-0.593	Yes	-1.732	Yes	-17.723	No	-0.234	No
-19.299	No	-24.767	No	-0.554	Yes	-0.655	Yes	-1.599	Yes	-18.445	No	2.278	Yes
3.788	Yes	1.967	Yes	-0.044	No	0.545	Yes	-0.147	No	-0.740	Yes	-1.040	Yes
-3.229	Yes	-	-	-	-	-	-	-	-	-	-	-	-
-0.100	No	-0.677	No	0.068	No	0.059	No	0.106	No	-0.091	No	0.266	No
-0.106	No	0.184	No	0.010	No	0.077	Yes	-0.096	Yes	-0.084	No	-0.022	No
1.614	No	5.700	No	0.416	No	0.834	No	-1.531	No	0.917	No	-3.273	No
0.984	No	1.956	No	0.524	No	0.460	No	-0.583	No	-0.465	No	-3.331	Yes
0.163	No	3.796	Yes	0.265	Yes	0.153	No	0.239	No	-0.479	No	-0.285	No

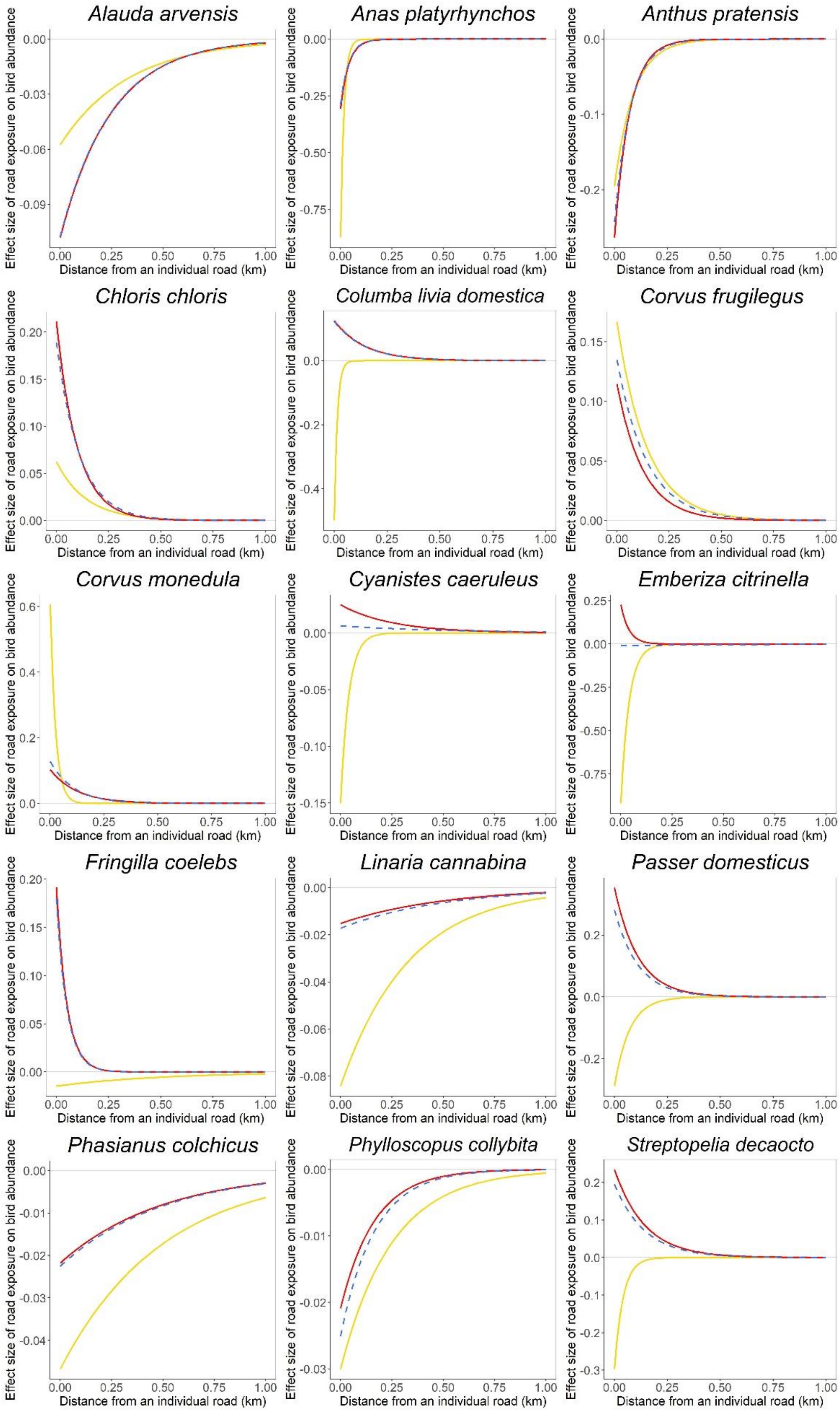
Appendix E. Chapter 4 sub-analyses

Analysis of major and minor roads separately

In my main analysis I did not differentiate between different road types due to the high sample sizes required (Cooke et al. 2020). However, I conducted an additional analysis of 29 species, estimating the associations between bird abundance and both major and minor roads in separate models. Of these, 16 had significant associations with both major and minor roads. In **Table E1** I present the GAMM results for these species, and in **Figure E1** I graphically compare the effect curves for major, minor and both road types together for each species.

Table E1. Effect sizes and *k* values for major and minor roads alongside those for the original associations with both road types together.

Scientific name	**Common name**	**Roads together**		**Major roads**		**Minor roads**	
		k	**Effect size**	***k***	**Effect size**	***k***	**Effect size**
Alauda arvensis	Eurasian skylark	4	-0.107	3	-0.057	4	-0.108
Anas platyrhynchos	Mallard	25	-0.288	60	-0.875	25	-0.306
Anthus pratensis	Meadow pipit	13	-0.243	11	-0.196	14	-0.264
Chloris chloris	European greenfinch	9	0.189	7	0.062	10	0.211
Columba livia domestica	Feral pigeon	7	0.123	70	-0.499	7	0.126
Corvus frugilegus	Rook	7	0.135	7	0.167	8	0.115
Corvus monedula	Eurasian jackdaw	9	0.128	40	0.605	8	0.103
Cyanistes caeruleus	Blue tit	2	0.006	25	-0.150	4	0.025
Emberiza citrinella	Yellowhammer	2	-0.010	25	-0.920	25	0.227
Fringilla coelebs	Common chaffinch	20	0.180	2	-0.015	20	0.191
Linaria cannabina	Common linnet	2	-0.017	3	-0.084	2	-0.015
Passer domesticus	House sparrow	9	0.281	14	-0.288	9	0.353
Phasianus colchicus	Ring-necked pheasant	2	-0.023	2	-0.047	2	-0.022
Phylloscopus collybita	Common chiffchaff	6	-0.025	4	-0.030	6	-0.021
Streptopelia decaocto	Eurasian collared dove	7	0.195	25	-0.297	7	0.235
Turdus merula	Common blackbird	5	0.042	35	-0.297	6	0.066


Alauda arvensis
Anas platyrhynchos
Anthus pratensis
Chloris chloris
Columba livia domestica
Corvus frugilegus
Corvus monedula
Cyanistes caeruleus
Emberiza citrinella
Fringilla coelebs
Linaria cannabina
Passer domesticus
Phasianus colchicus
Phylloscopus collybita
Streptopelia decaocto
Effect size of road exposure on bird abundance
Distance from an individual road (km)

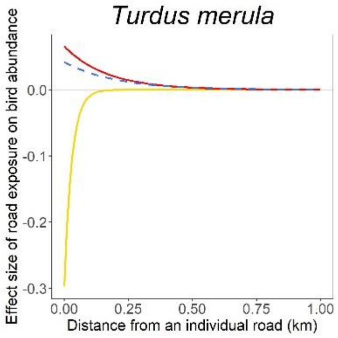


Figure E1. Effect curves for each species with distance from an individual road. The intercept is determined by the coefficient and the rate of decline is determined by the parameter '*k*', which defines the spatial scale of the relationship between distance from road and road exposure for each species. Effect curves for major roads are shown in yellow, minor roads in red and both road types together in dashed blue.

Comparison of results of common species with and without detectability incorporated

Cooke et al. 2019 demonstrated the importance of accounting for detectability in producing accurate estimates of the associations between road exposure and bird populations. As sample size limitations prevented us from doing so for all the species in our analysis, we reproduced the GAMMs for 50 common species with detectability incorporated, to ascertain the difference.

We fitted distance sampling models (using the R package "mrds"; Laake et al. 2017) to the count data for each species, using raw count at each 200-m transect section as the response and both habitat and road exposure as covariates. As the bird count data were from only two distance bands, we used a half-normal detection function with no adjustment. Within this set up, we optimised the spatial component of the road exposure variable, *k*, in the same way as in the main analysis – running iterations of the model with values of *k* from 1-100 and choosing the value that produced the peak log-likelihood (see **Appendix A** for details). We removed two species from this sub-analysis here as no optimum value of *k* could be identified. Using these distance sampling models, we estimated detectability at each 200-m BBS transect section. We then reproduced the GAMMs, analysing the associations between abundance and road exposure, for the remaining 48 species, but this time incorporating the estimated detectability as an offset. This resulted in only small modifications to the effect size estimates for all species and a change of effect direction for only two species, coal tit *Periparus ater*, and carrion crow *Corvus corone*, both of which did not have significant (after Bonferroni correction) associations between road exposure and abundance with or without detectability included (**Figure E2**).

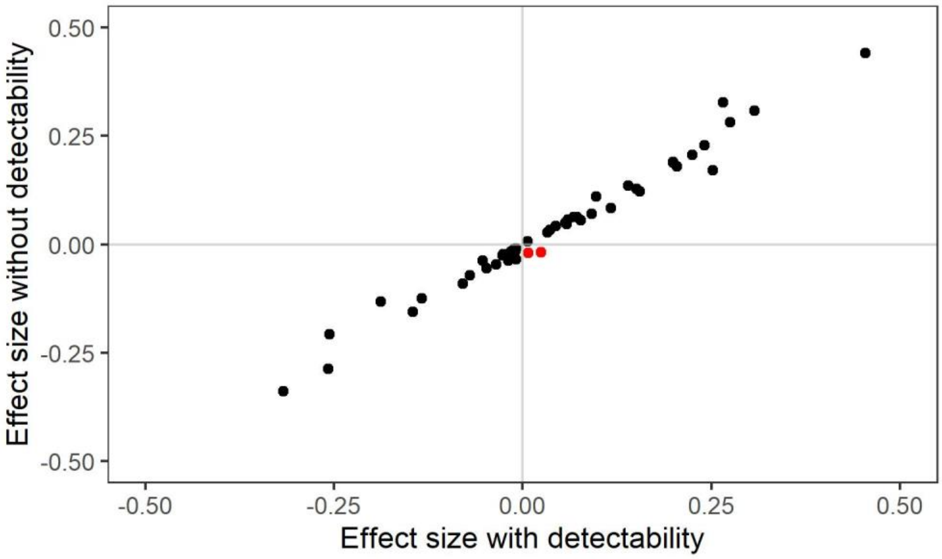


Figure E2. Comparison of effect sizes of road exposure on bird abundance with and without detectability included as an offset. Two species that showed changes in effect direction, coal tit and carrion crow, are shown in red.

References

Cooke et al. 2019. Road exposure and the detectability of birds in field surveys. *Ibis*.

Cooke et al. 2020. Variation in abundances of common bird species associated with roads. Journal of Applied Ecology

Laake, J., Borchers, D., Thomas, L., Miller, D. and Bishop, J. 2017. mrds: Mark-Recapture Distance Sampling. R package version 2.1.18. https://CRAN.R-project.org/package=mrds