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Variation in abundances of common bird species associated with roads

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Abstract

1. 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 utilizing 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.
2. We use data from across Great Britain to analyse the relationships between roads and the spatial distributions of bird populations. We model counts of 51 common and widespread species from the U.K. Breeding Bird Survey in relation to road exposure, which we calculated for each count site using the density, distance and traffic volume of all roads within a 5-km radius. In these models, we incorporate other factors known to affect bird populations, including agricultural intensity, human population, habitat and climate. Importantly, we also account for differences in detectability of birds near to roads.
3. 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).
4. For species with significant effects of road exposure, we 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.
5. *Synthesis and applications*. Our 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. Our 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.

KEYWORDS
anthropogenic noise, bird populations, Breeding Bird Survey, Great Britain, infrastructure impacts, road ecology, road exposure

1 | 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 kilometres 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 (Meyer, Kaniovski, & Scheffran, 2012; WEC, 2011), more than double the 2015 figure (OICA, 2015). Much of this expansion is expected in emerging economies, such as China and India (Dulac, 2013; van der Ree, Smith, & Grilo, 2015), which still have areas with comparatively low road density. Many nations with longer histories of industrialization 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. Benítez-López, Alkemade, & Verweij, 2010; Fahrig & Rytwinski, 2009). The road-effect zone—the area over which the ecological effects of roads extend (Forman & Deblinger, 2000)—can be up to several kilometres wide (Benítez-López et al., 2010; Clarke, Liley, Sharp, & Green, 2013; Reijnen, Foppen, & Meeuwsen, 1996), encompassing large portions of many countries. For example, >80% of Great Britain falls within 1 km of a paved road (S.C. Cooke, 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. Benítez-López et al., 2010; Fahrig & Rytwinski, 2009; Kociolek, Clevenger, St. clair, & Proppe, 2011), with stronger effects seen near those with heavier traffic volume (e.g. Bautista et al., 2004; Peris & Pescador, 2004; Reijnen & Foppen, 2006; Reijnen et al., 1996). 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, Foppen, Braak, & Thissen, 1995; Rheindt, 2003), and has been shown to cause abundance declines even when other potential mechanisms are removed (McClure, Ware, Carlisle, Kaltenecker, & Barber, 2013; Ware, McClure, Carlisle, & Barber, 2015). Noise can disrupt the ability of birds to communicate (Habib, Bayne, & Boutin, 2006; Leonard & Horn, 2012; Lohr, Wright, & Dooling, 2003; Rheindt, 2003) and to detect prey or predators (Slabbekoorn & Ripmeester, 2008). This may reduce breeding success (Halfwerk, Holleman, Lessells, & Slabbekoorn, 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 (Erritzoe, Mazgajski, & Rejt, 2003; Forman & Alexander, 1998; Hernandez, 1988) and this may reduce abundance near roads (Jack, Rytwinski, Fahrig, & Francis, 2015). Light pollution, known to affect the timing of circannual events such as breeding and physiological changes (de Molenaar, Saunders, & Jonkers, 2006; Dominoni, Quetting, & Partecke, 2013), may also affect populations around roads (Day, 2003; de Molenaar, Jonkers, & Sanders, 2000; Kociolek et al., 2011). Other processes by which roads may negatively affect birds include chemical pollution (Kociolek et al., 2011; Mineau & Brownlee, 2005), which may reduce breeding success (Fry, 1995) and bird health (Llacuna, Gorriz, Durfort, & Nadal, 1993); and habitat fragmentation, due to avoidance of edge habitat around roads, or reluctance to cross the road itself (Develey & Stouffer, 2001; Laurance, Stouffer, & Laurance, 2004; Rich, Dobkin, & Niles, 1994; 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 (Dean & Milton, 2003; Fahrig & Rytwinski, 2009; Lambertucci, Speziale, Rogers, & Morales, 2009; Meunier, Verheyden, & Jouventin, 2000; Yamac and Kirazli, 2012). For some species, roads provide food (in the form of road-kill; Dean & Milton, 2003; Knight & Kawashima, 1993; Laursen, 1981), grit and heat (Erritzoe et al., 2003; Whitford, 1985; Yosef, 2009). Powerlines, many of which run alongside roads, can also provide perches (Knight & Kawashima, 1993; Meunier et al., 2000; Morelli, Beim, Jerzak, Jones, & Tryjanowski, 2014). In addition, roads can increase habitat heterogeneity, due to creation of varied edge habitat along roadsides (Helldin & Seiler, 2003; Meunier, Verheyden, & Jouventin, 1999), 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, Papp, Bókony, & Lendvai, 2008). Barn owls *Tyto alba* are also frequently involved in collisions, and it has been suggested that this can affect population numbers (Borda-de-Água, Grilo, & Pereira, 2014; Massemin & Zorn, 1998). There is potential, therefore, for roads to act as ecological traps for some species (Reijnen & Foppen, 1994; Schlaepfer, Runge, & Sherman, 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, here we analyse bird populations across Great Britain with respect to road exposure, which we 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 practices and land management; habitat loss and degradation; and climate change (Burns et al., 2016; Eglington & Pearce-Higgins, 2012; 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 our analyses, we also account for the impacts of roads on detectability (Cooke et al., 2019), a factor important, yet often overlooked, in studies of this nature.

2 | MATERIALS AND METHODS

Our analytical framework involved modelling spatially explicit bird count data in relation to the proximity and traffic volume of nearby roads. We also incorporated other predictors known, or thought likely, to influence bird counts, including the impacts of roads on detectability (Cooke et al., 2019). We used all areas and island groups of England, Scotland and Wales, except for the Isles of Scilly which we excluded due to limited traffic data. We 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. We provide a graphical overview of our methods in Figure S1.1.

2.1 | Data collation and preparation

2.1.1 | Bird counts

We 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 our analyses, we extracted observations from BBS squares that had been surveyed each year from 2012 to 2014 inclusive. These transects are surveyed in two visits each year, early and late in the breeding season. We chose to use observations from the early visit for resident species and the late visit for migrant species as these tend to contain the highest counts for each. We also extracted the dominant habitat type for each transect section.

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, Evans, Noble, Greenwood, & Gaston, 2008). Additionally, roads may impact both bird abundance and detectability, and these two effects are confounded in raw bird counts. We 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, we pooled all observations from two distance bands (0–25 m and 25–100 m) over the 3 years and used the R package MRDS (Laake, Borchers, Thomas, Miller, & Bishop, 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 Section 2.1.2 below for definitions) was not significantly associated with variation in detectability of a species, we 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 S5.1).

For each species, we 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 our

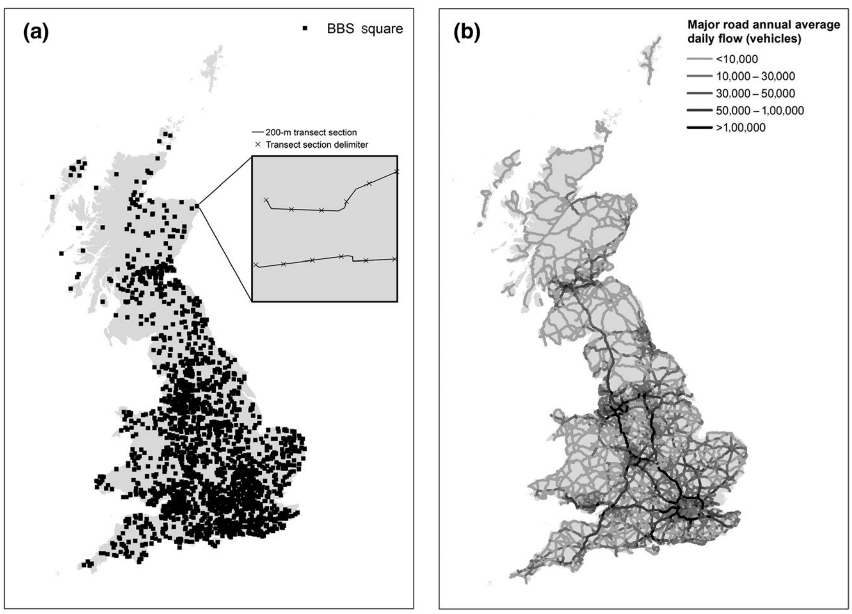

FIGURE 1 (a) Locations of Breeding Bird Survey (BBS) squares used in this study with an inset example of the layout of a BBS square, crossed by two 1-km transects, and (b) a map of major roads in Britain with their traffic volumes. First published in Cooke et al. (2019)

analyses. We then used our distance sampling models to produce species- and transect-specific estimates of detectability. We produced these estimates to use as offsets in our analyses, so that we 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, we allowed estimation of undetected birds in sites where the count was zero. For more detail on the survey methodology and our calculation of mean bird counts see Appendix S2.

2.1.2 | Road exposure

For the midpoint of each 200-m BBS transect section, we estimated the exposure of that point to roads—hereafter road exposure. This was calculated from the density, distance and traffic volume of all roads within a 5-km radius, using the following methods. We 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. We 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.

We 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 motorized 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). We were not, however, able to incorporate traffic flow data for minor roads as the DfT collects only a limited sample of data for these. We then calculated the mean AADF across the 3 years and combined these data with the major road shapefile (Figure 1; Appendix S3).

We 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. We 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, we 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, we 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), we 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, we chose two values of k—identified in preliminary analyses as being above and below the range of plausible values, which we used to estimate road exposure at the midpoint of every 200-m BBS transect section. We 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 S4.

2.1.3 | Other covariates

To account for other factors that we expected to affect bird abundance, we 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 ($r = 0.68$). We 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 S2.

2.2 | Data analysis

We analysed the relationships 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). We 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: 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 relationships between proportion of arable land and bird count, we fitted proportion of arable land as a quadratic rather than linear relationship for five bird species (Table S5.1). We 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). We 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).

We assessed the significance of the results of each species by extracting the estimated effects (*E*), (i.e. the coefficients), and *SE* of major and minor road exposure. As we tested multiple species, we applied a Bonferroni correction, dividing our chosen critical alpha level (0.05) by the number of species tested ($n = 51$). We 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*. If these limits did not span zero, we accepted the effect as significant.

Where major or minor road exposure was significantly associated with bird abundance, we calculated the relative effect size to allow easier comparison between species. We 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 scale of associations between roads and bird abundance in real terms, we 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. We 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 observations of that species. For the two categorical covariates, we used the BBS square with the smallest absolute coefficient and the habitat with the largest number of observations.

In order to compare the scales of these changes with those associated with the proportion of arable land—which was not distance-optimized as the road exposure covariates were—we reran our 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. We 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.

3 | 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.

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* *Coloeus 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 S5.1)	*Linaria cannabina* *Phylloscopus trochilus*
	Significant negative association		*Buteo buteo* *Sylvia atricapilla* *Fulica atra* *Regulus regulus* *Anas platyrhynchos* *Anthus pratensis* *Emberiza schoeniclus*	*Phasianus colchicus*

[Correction added on 29 April 2020, after first online publication: The first two columns in Table 1 were amended in this version.]

Considering both road types together, the mean decrease in estimated abundance across the interquartile range of road exposure was 19% and mean increase 47%.

The abundance of eight species differed significantly with major road exposure (Figure 2). All except rook *Corvus frugilegus* showed reduced abundance with increased 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 Section 4).

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 S5.1 provides a graphical depiction of the predicted changes in abundance across the full ranges of road exposure values recorded.

Considering only species that showed a significant association between road exposure and abundance, the effect size was generally larger when the distance over which that effect acted (as determined by k_{major} or k_{minor}) was smaller (Pearson's r of absolute effect of major roads and k_{major} = 0.38 and of absolute effect of minor roads and k_{minor} = 0.47). 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 S4 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).

We also compared the estimated abundance changes with increasing road exposure, to those with increasing proportion of

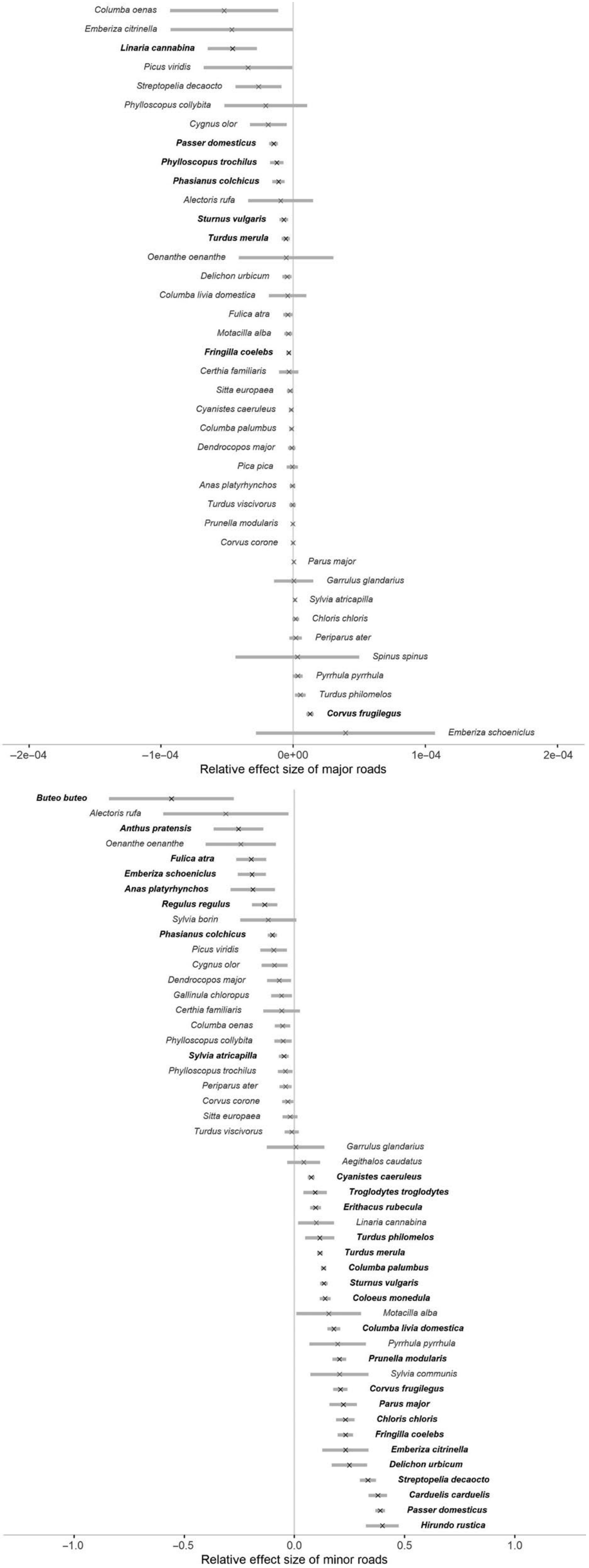

FIGURE 2 Associations between bird abundance and exposure of count sites to major roads and minor roads. For ease of comparison, the effect size for each species has been divided by the $\log_{10}$-transformed optimized parameter defining the spatial scale of the association: k_{major} for major roads 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 using a Bonferroni correction) are highlighted in black bold. Confidence intervals were calculated using a critical alpha of 0.05 and 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 S4 for further details). One species, *Sylvia borin*, is excluded from the major road graph due to particularly wide confidence limits

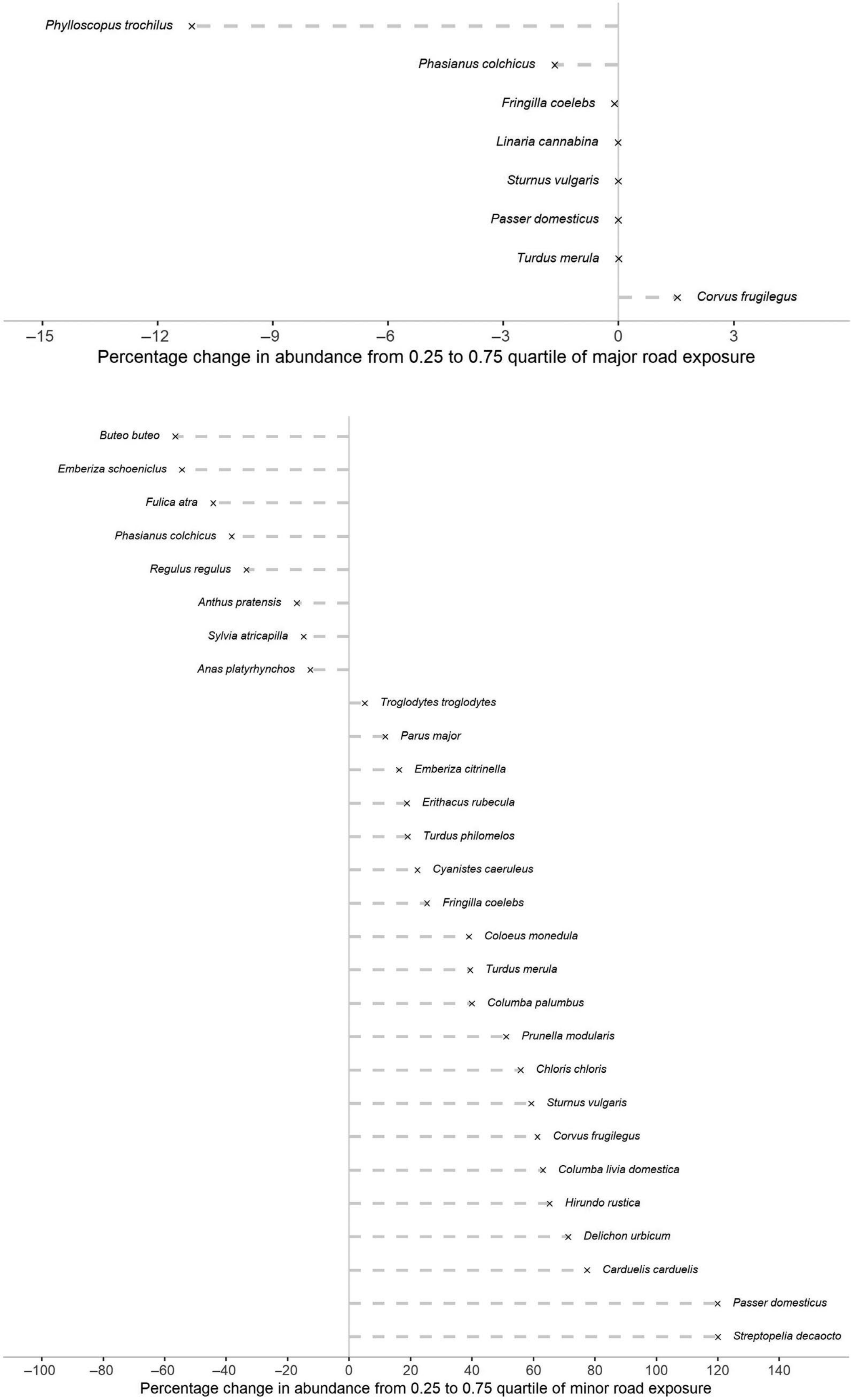

FIGURE 3 Predicted percentage changes in bird abundance with changing road exposure values. For both major and minor road exposure, we calculated the estimated change in bird abundance across the interquartile range of that covariate (quartiles 0.25–0.75), while holding all other covariates constant. Only species with significant associations between bird abundance and major/minor road exposure are included here. It is likely that our estimates for major roads are underestimated due to insufficient sample sizes and data spread

arable land (for species linearly related to proportion of arable land; n = 46). We did this using measures of road exposure which were not distance-optimized, 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-optimized 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 (M = 0.12) and that associated with minor road exposure (M = 0.16) were significantly different from the absolute mean change in abundance associated with the proportion of arable land (M = 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).

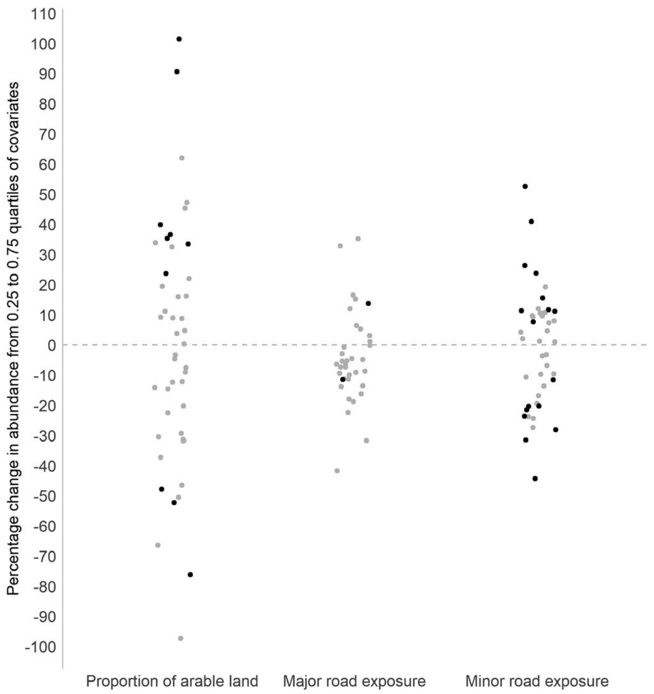

FIGURE 4 A comparison of estimated percentage changes in bird abundance across the interquartile ranges of proportion of arable land and road exposure covariates. In order to more accurately compare these covariates, major and minor road exposure here were included without distance optimization, to make 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 we fitted proportion of arable land as a linear effect are included here

4 | DISCUSSION

Over half (30/51) of the species we assessed showed significant positive or negative associations between road exposure and bird abundance. While seven of eight 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 (our proxy for yield), an important correlate of changes in bird populations (e.g. Burns et al., 2016). We 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 –1,500 m; Reijnen et al., 1996: 20 –1,700 m; Palomino & Carrascal, 2007: mean effect distance of 300 m; Mammides, Kounnamas, Goodale, & Kadis, 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, we believe our 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 our 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* (Helldin & Seiler, 2003; Reijnen et al., 1995), meadow pipit *Anthus pratensis* (Helldin & Seiler, 2003; Reijnen et al., 1995), ring-necked pheasant (Reijnen et al., 1995) and willow warbler (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 we found that only rooks were more prevalent with increasing major road exposure, 20 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; Morelli et al., 2015; Palomino and Carrascal, 2007), great tit *Parus major* (Helldin & Seiler, 2003; Wiącek, Polak, Kucharczyk, & Bohatkiewicz, 2015), house sparrow (e.g. Brotons & Herrando, 2001; Palomino & Carrascal, 2007; Peris & Pescador, 2004), 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 our 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 we found. While we are unable to say how much either the positive or negative variation we 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 we did (Reijnen et al., 1995, 1996).

Four of our species 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; Peris & Pescador, 2004; Reijnen & Foppen, 2006; Reijnen et al., 1996) and our 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 our study site, it is not possible to understand the broader implications of our findings. It may be that the associations we 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; Reijnen et al., 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, Ware, Carlisle, & Barber, 2017; Reijnen & Foppen, 1994).

In this study we were able only to consider common and widespread species, due to the large sample sizes that were required to estimate the associations between road exposure and detectability in Cooke et al. (2019). It is possible that many rarer species have lower abundance with both increasing major and minor road exposure and therefore our findings here should not be taken to be representative of British birds as a whole. However, even with this limitation, our results suggest that roads may modify local bird community structures, on a scale potentially comparable to that of agricultural activities. Given that our 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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AUTHORS' CONTRIBUTIONS

All authors contributed to the ideas and methodological design of this study. S.C.C. collated the data, lead the analysis and wrote the manuscript; A.J. provided guidance on the statistics and assisted with the figures; S.E.N. helped with the obtaining and sorting of the BBS data; A.B., A.J., S.E.N. and P.F.D. read and commented on draft versions of the manuscript and all authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via Apollo https://doi.org/10.17863/CAM.50140 (Cooke et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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