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Road exposure and the detectability of birds in field surveys

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Road ecology, the study of the impacts of roads and their traffic on wildlife, including birds, is a rapidly growing field, with research showing effects 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, we assess the relationships 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. We 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.

Keywords: anthropogenic noise, birds, Breeding Bird Survey, Monitoring, road ecology.

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, 2 km 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

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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 2009) 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 2004, 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. Clark & Karr 1979, Ferris 1979, Brotons & Herrando 2001, Peris & Pescador 2004, Arévalo & 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 estimate inaccurately 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 road exposure on detectability of birds. Some authors have accounted for the possibility of detectability being affected by road noise (McClure *et al.* 2013) whereas others have considered it unlikely in their studies (Rheindt 2003, Parris & Schneider 2009), but we are not aware of any empirical test of whether road exposure affects detectability.

This study therefore aims to assess the potential impact of road exposure on the detectability of birds in surveys. We use Great Britain as our 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 (Fig. 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 (Fig. 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, we predict that road exposure 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. We test this prediction by fitting distance sampling models to BBS count data for 63 common species, with 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), we are able to analyse associations between roads and detectability independent of those between roads and bird abundance.

Some of the interspecific 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. We therefore incorporate measures of two traits – body mass and the importance of aural vs. visual cues in detection of each species – in our data analysis.

METHODS

To analyse relationships between road exposure and detectability in bird surveys, we 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. 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. A graphical overview of the methods used for this study is given in Fig. S1.1.

Data collection and preparation

Bird counts

We obtained bird counts from the BTO/RSPB/JNCC Breeding Bird Survey (BBS), for which the full methods 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 (Fig. 1). Squares are allocated to surveyors using a stratified-random protocol and surveyors are only recruited if able to identify all British bird species by sight and sound, meaning BBS data are not

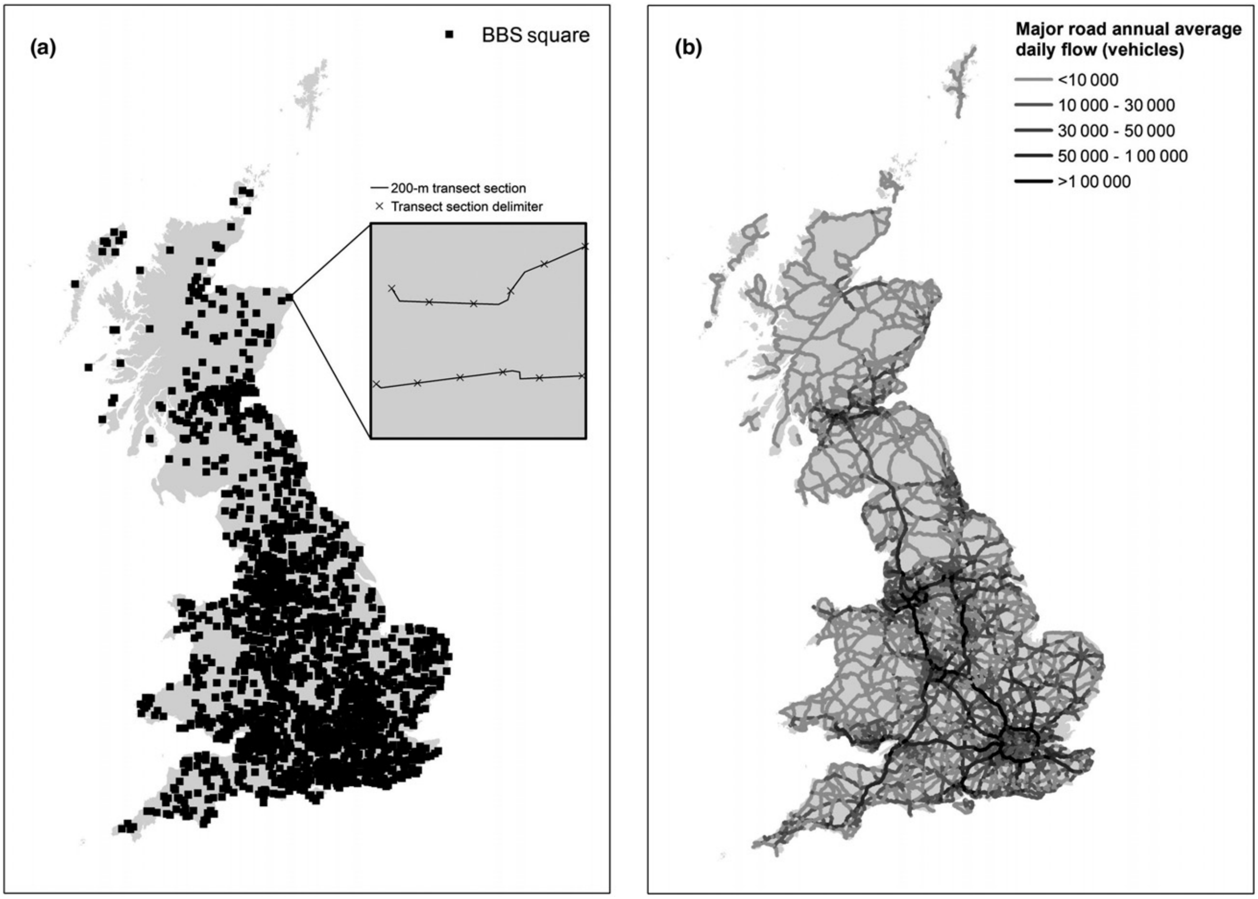


Figure 1. (a) Locations of BBS squares used in this study with an inset example of the layout of a BBS square, crossed by two 1-km transects. (b) A map of major roads in Britain with their traffic volumes.

significantly affected by surveyor experience (Eglington *et al.* 2010). During the surveys, the surveyors note all birds they see or hear, along with the estimated perpendicular distance of each bird detected from the transect line (recorded as one of four categories: 0–25 m; 25–100 m; >100 m; flying). They also record the dominant habitat type in each transect section as one of nine broad classes: woodland; scrubland; semi-natural grassland and marsh; heathland and bogs; farmland; human sites; water bodies (freshwater); coastal; inland rock.

For this analysis we extracted observations from transects in squares that were surveyed each year from 2012 to 2014 inclusive, in England, Scotland and Wales. We chose a period of 3 years to increase the sample size of counts and to average out the effect of annual population fluctuations due to, for example, weather changes. We considered 3 years to be sufficiently short for long-term trends in abundance not to influence the analysis. We removed observations from transect sections that did not have habitat or specific route data recorded (i.e. the highest resolution information about their location was the square they were in). This left 19 909 transect sections, from 2034 1-km BBS squares (Fig. 1). We then extracted observations of birds in the distance bands 0–25 m and 25–100 m as only these have set lower and upper distance limits. Within each species, we removed counts from habitat types with < 20 observations in total. As a level of pseudoreplication was expected, for each species we calculated the correlation between counts at transect sections in 2012 and 2013, and in 2013 and 2014. If the mean of these two correlation coefficients was ≥ 0.6, a cut-off considered to be sufficiently conservative, we used only data from 2013 for that

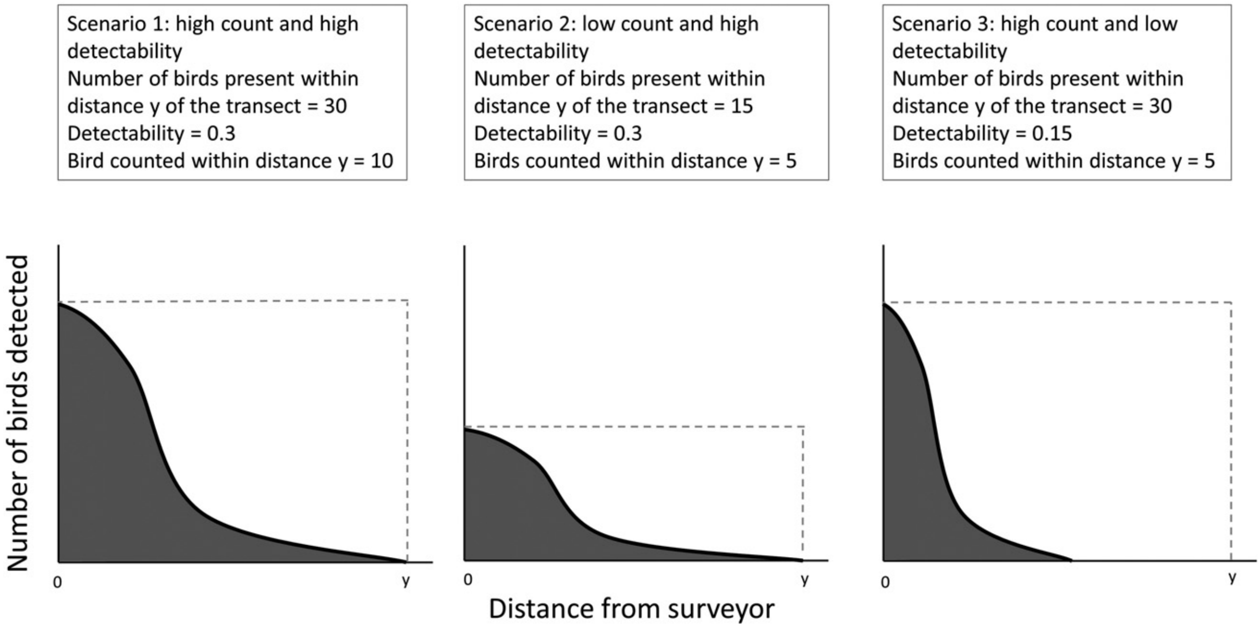


Figure 2. Graphical representation of bird count vs. detectability. Distance sampling assumes that detectability = 1 along the transect line (where the distance from the surveyor = 0) and declines with increasing distance. The actual bird abundance is represented by the area enclosed within the dashed lines. Within this, the shaded area represents birds counted and 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, we are able to quantify the associations between road exposure and detectability, independent of those between roads and bird abundance.

species, otherwise data from all 3 years were used. Following this, we extracted counts of species with > 1000 observations, as preliminary analyses indicated this to be a minimum threshold requirement for model convergence. This resulted in a final dataset of 63 bird species (given in Table S4.1), each with a list of observations containing the following information: year (2012, 2013 or 2014); survey visit (early or late); transect section ID (a combination of BBS square ID and transect section number 1–10); distance category (0–25 m or 25–100 m); and dominant habitat class (one of nine classes).

Road exposure

We 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, we 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 3641 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). We 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.

We 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 motorized 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 1300 vehicles, respectively (DfT 2015). Whereas AADF estimates are available for all major roads, only data for a very limited sample of minor roads are collected, so we incorporated traffic volume for major roads only. Where major road traffic data were missing, we used interpolation to estimate the AADF. We then combined the major road shapefile with the traffic data and identified and corrected any errors resulting from misalignment of the two (Figure S2.2; S2.3). Further detail of this process is given in Supplementary Section S2. The result was a digital map of Great Britain with every major road and its traffic volume (Fig. 1).

To estimate a measure of exposure of each 200-m BBS transect section to both major and minor roads, we used kernel density estimation (KDE). We 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. Foppen & Reijnen 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 (equations available in Supplementary Section S3). For minor roads, the locations of roads within a 5-km radius were used without any weighting. We 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 optimize k for each species and road type we ran multiple iterations of the distance sampling model (described below), using different values of k. For each species, and road type, we chose two initial values – identified in preliminary analyses as being above and below the plausible values, which we used to estimate road exposure at the midpoint of every 200-m BBS transect section. We 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) (Figure S3.3). Full KDE methods are given in Supplementary Section S3.

Data analysis

Fitting the distance sampling models

To quantify the associations between road exposure and detectability, we fitted distance sampling models (using the R package 'mrds'; Laake *et al.* 2017) to the count data for each species, using raw counts 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. We 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:

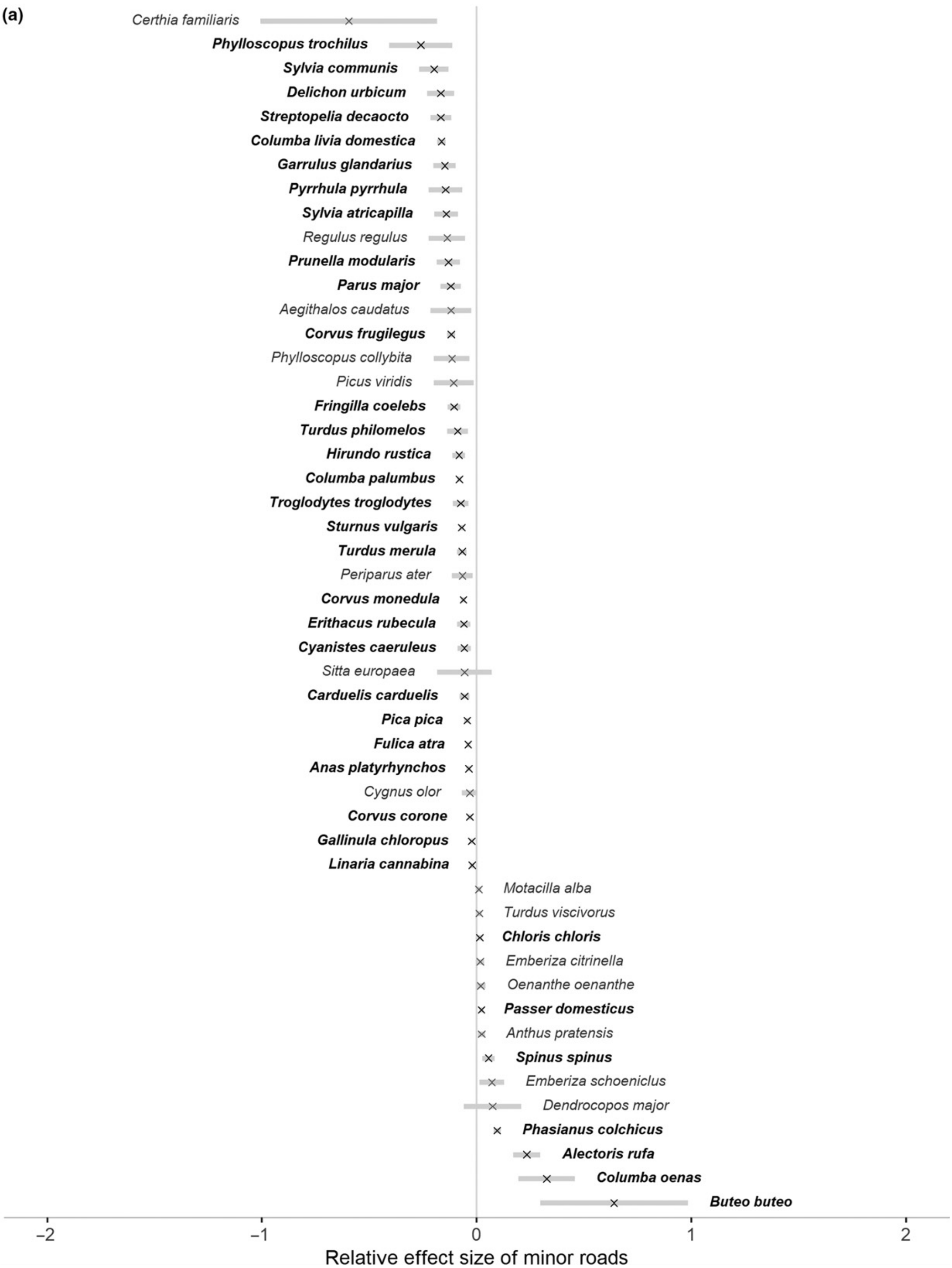
$$g(d; o') = \exp(-(d^2/2o\prime^2))$$

where g = detectability at distance d and for standard deviation o'; $o' = \exp(\beta_0 + \sum \beta c \zeta c))$; β_0 = intercept; βc = coefficient; ζc = 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 associations between detectability and each covariate to be estimated.

From the model results, we 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, we applied a Bonferroni correction, dividing the chosen critical alpha level (0.05) by the number of species that achieved model convergence (n = 51). We then calculated confidence limits using the t-value from the Student's t-distribution that corresponded to

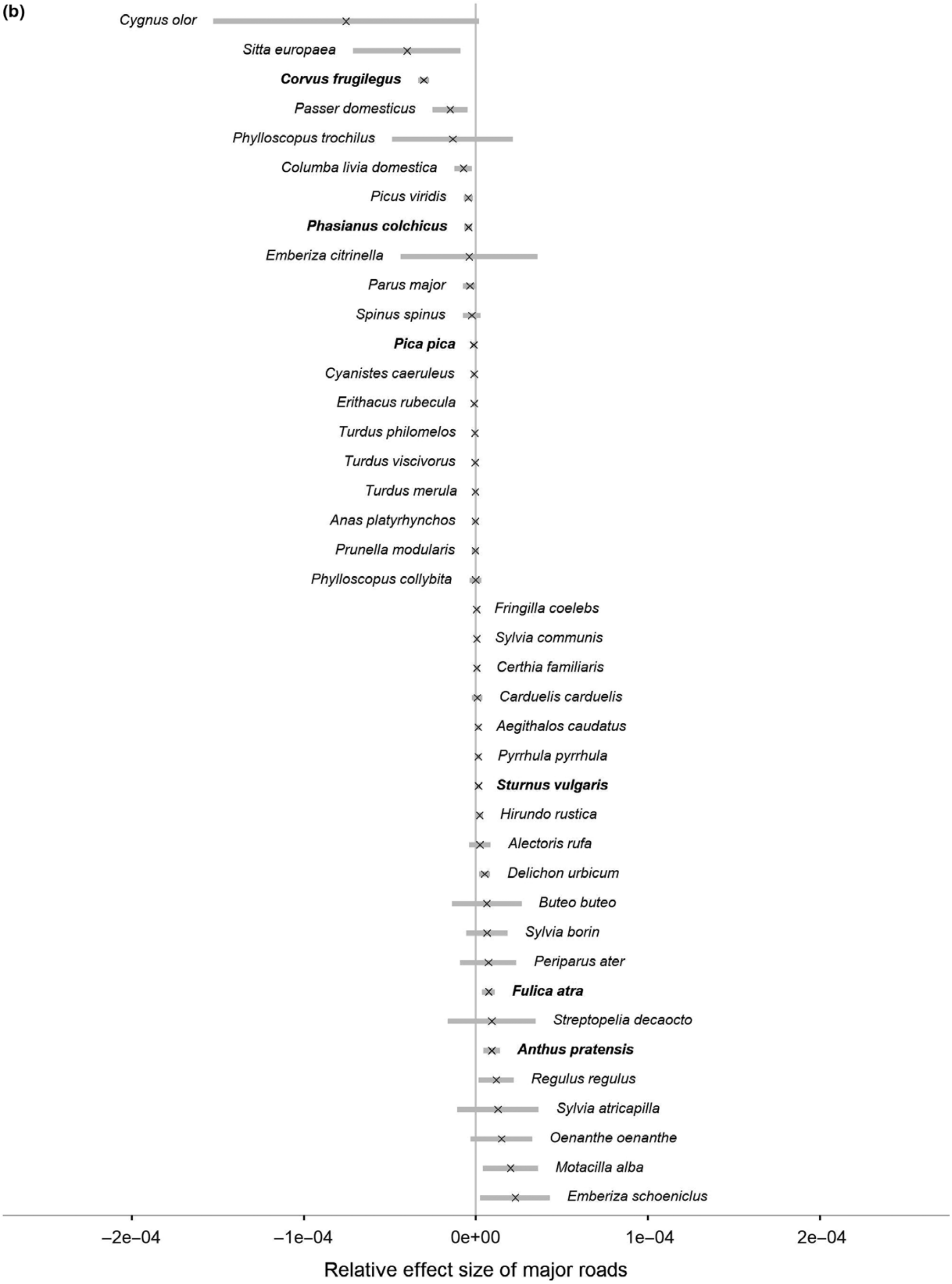
Figure 3. Association between detectability and (a) minor and (b) major road exposure for each species. For ease of comparison, the effect size for each species has been divided by the log of its optimum identified value of k_{minor} or k_{major} to show the relative effect size. This combines the magnitude of the effect with the spatial area over which the effect occurs. Species with significant effects (calculated using a Bonferroni correction) are highlighted in bold type and confidence intervals (calculated using a critical alpha of 0.05) 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.

(a)


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

(continued)

Figure 3. *(continued)*



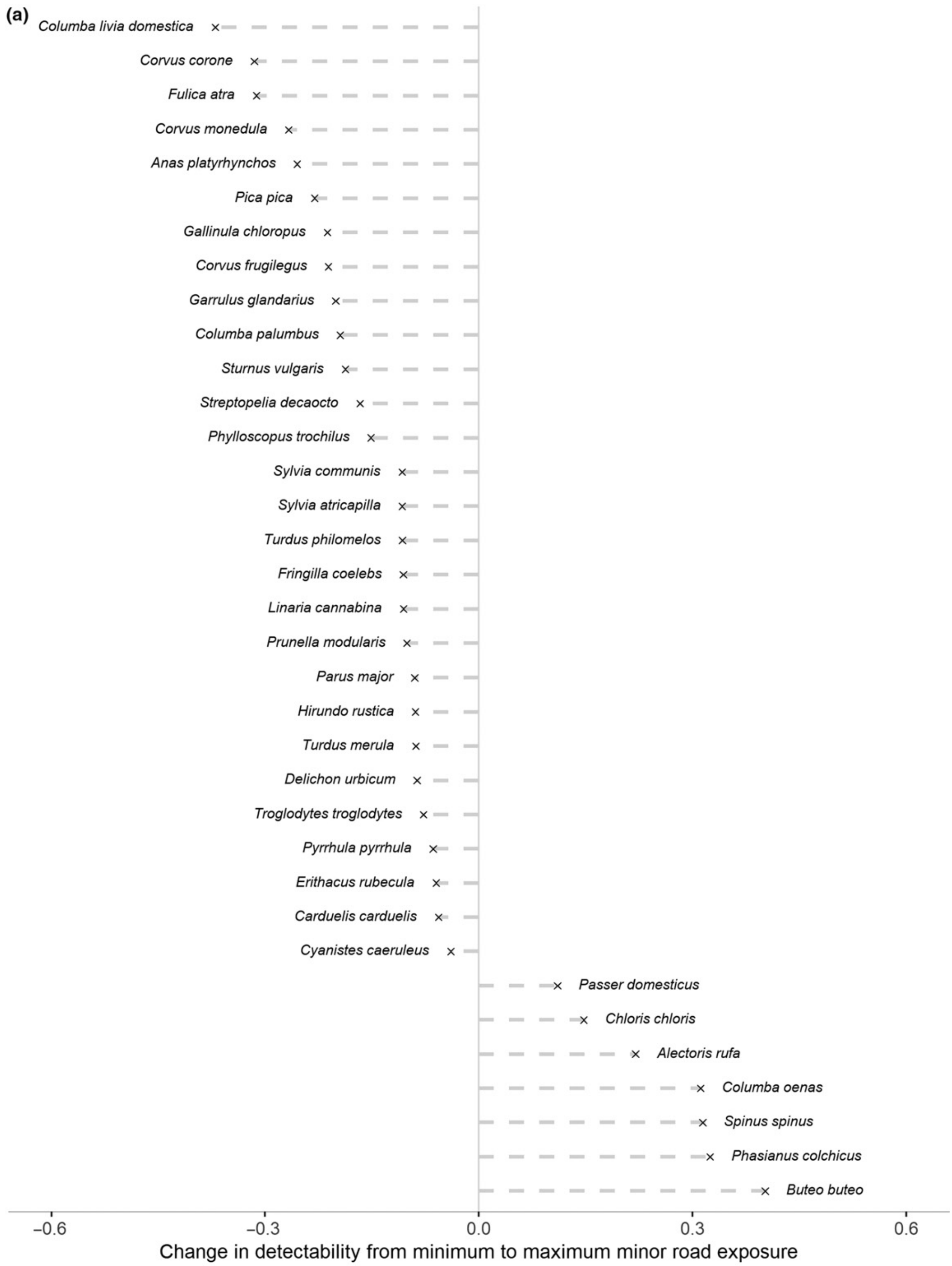
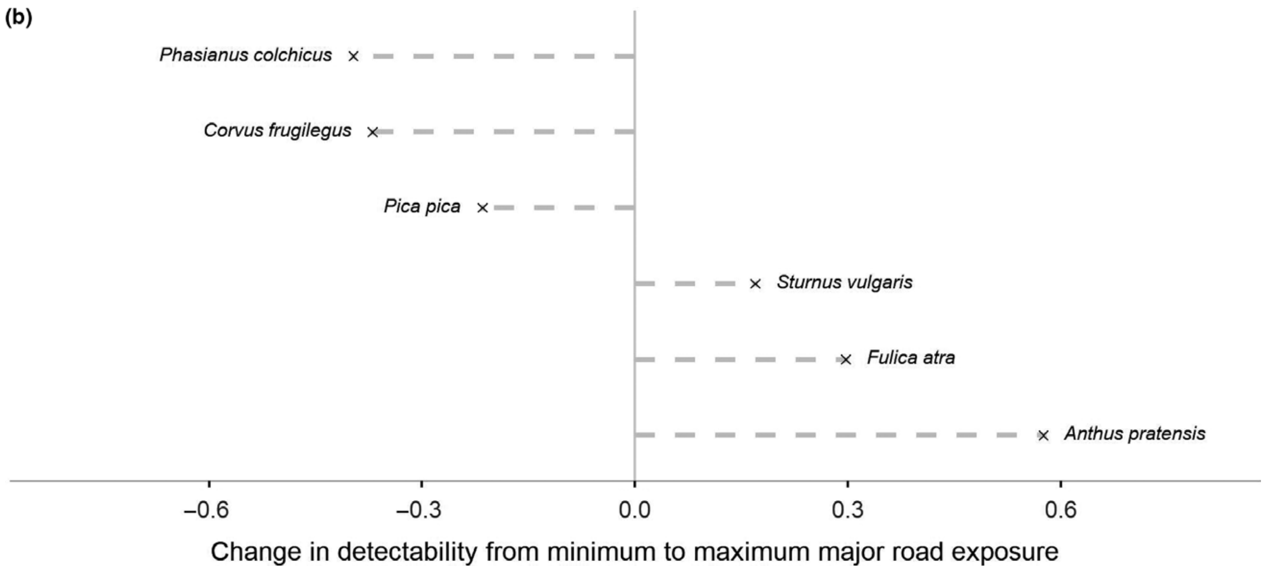


Figure 4. Change in detectability between (a) minimum and maximum minor road exposure values, and (b) minimum and maximum major road exposure values, recorded for each species. Only species for which associations between minor or major road exposure and detectability were found to be significant are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

Figure 4. *(continued)*



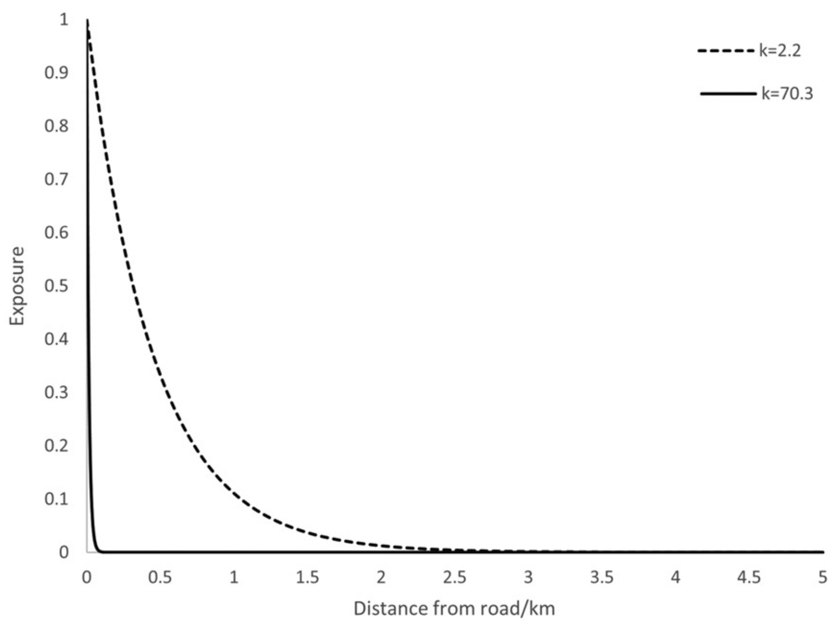


Figure 5. Relationship between distance from road and road exposure with *k* values of 2.2 and 70.3.

the adjusted alpha as: upper confidence limit = E + se*t-value; lower confidence limit = E − se*t-value. We accepted significance if these limits did not span zero.

For species that showed significant associations between detectability and major or minor road exposure, we calculated the relative effect size to allow comparison between species. We achieved this by dividing the effect size by the log of the value of k_{major} or k_{minor} used for that species. This combines the magnitude of the effect with the spatial area over which the effect occurs.

To estimate the magnitude of the associations in real terms, for each species that showed a significant relationship between major or minor road exposure and detectability, we 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 the transects that species was detected. We 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. We did this for all combinations of habitat and survey visit recorded for that species. From these, we 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 understand further the interspecific patterns in the associations between road exposure and detectability, we compared the results with species-specific values for two traits in generalized estimating equations (GEEs), using the R package 'Zelig' (Choirat *et al.* 2018). We 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 vs. aural cues in the detection of each species. We calculated this as the proportion of individual birds first detected by sight as opposed to their song or call. We 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, we were able to account for any non-independence between species, resulting from phylogenetic relatedness. We 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.

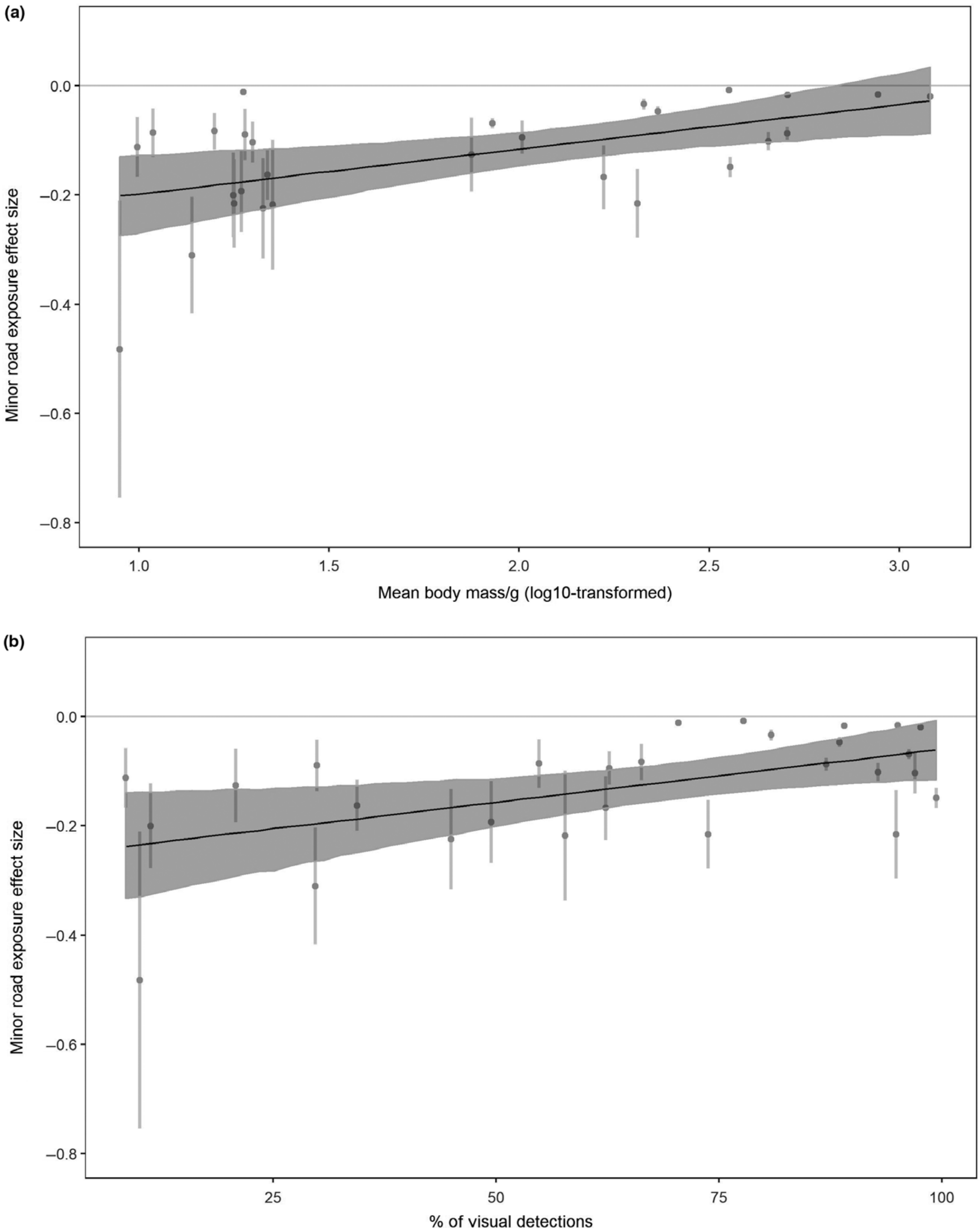
RESULTS

Road exposure

The models successfully converged for 51 of 63 species. Convergence probably failed for the other 12 species either because the sample size was too small or because there were not enough observations at either high or low levels of minor or major road exposure. Of the 51 successfully modelled species, 28 showed a significant negative relationship between minor road exposure and detectability, whereas seven showed a positive relationship (Fig. 3). Three showed a negative relationship between major road exposure and detectability and three a positive relationship (Fig. 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 S4.1–3.

For species that showed a significant association between minor road exposure and detectability, we calculated the change in detectability as minor road exposure increased from the lowest to highest values recorded across the transects that species was detected. 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 (Fig. 4; Table S4.2). We 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 (Fig. 4; Table S4.3).

For both minor and major road exposure, stronger associations were generally found to act over smaller distances and weaker associations over larger distances (Pearson's r of absolute effect of minor roads and $k_{\mathrm{minor}} = 0.62$ and of absolute effect of major roads and $k_{\mathrm{major}} = 0.98$). 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; Fig. 5; Supplementary Section S3 for further information) 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).


(a)
Minor road exposure effect size
0.0
−0.2
−0.4
−0.6
−0.8
1.0
1.5
2.0
2.5
3.0
Mean body mass/g (log10-transformed)
(b)
Minor road exposure effect size
0.0
−0.2
−0.4
−0.6
−0.8
25
50
75
100
% of visual detections

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 S4.4.

Species traits

We examined whether species with certain characteristics had different magnitudes of negative associations between minor road exposure and detectability. We 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: $P = 0.002$; Fig. 6). The mean body mass and the proportion of birds detected visually for each species are given Table S4.5.

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, we 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%. Whereas 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, 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 Common 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, we 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 $k_{\text{minor}} = 1$, Eurasian Siskin has the lowest percentage of observations in the upper quartile of the exposure values recorded across all species, implying that there are very few data to support the detected relationship. Excluding Eurasian Siskin, the mean increase in detectability with minor road exposure fell to 55%.

Only six of 51 (12%) species showed significant associations between major road exposure and detectability, half of which were negative. It is likely that our analysis underestimated the associations with major road exposure due to there being a limited number of observations 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

Figure 6. The relationships between effect size and (a) log-transformed mean body mass and (b) percentage of visual detections, for species that showed a negative effect of minor road exposure on detectability. Grey dots indicate effect size estimates for each species, and the black lines represent the relationships between those effect sizes and each trait. Confidence intervals around each effect size estimate are shown by grey lines, and prediction intervals around the trait relationships (calculated using the simulation function 'sim' in the R package 'Zelig') are shown by the shaded grey bar.

surveying next to busy major roads. Of the six significant results for major roads, we consider the result for Meadow Pipit *Anthus pratensis* to be unreliable. Like Eurasian Siskin with minor roads, it had a very low proportion of observations in the upper quartile of major road exposure values recorded across all species (when exposure was calculated using $k_{\text{major}} = 1$ 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, the mean increase in detectability for both road types together fell to 52%.

We 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 relationship was present was small (i.e. the identified optimum value of k_{minor} or k_{major} was high). This is somewhat unexpected but could possibly be explained by changes in the dominant mechanisms by which road exposure affects detectability across different spatial scales.

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 quite highly correlated, 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 vs. 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. We were therefore only able to consider detectability of common bird species. In addition, due to the limited number of BBS squares near to major roads, our power of analysis for major roads was much less strong than for minor roads. We were also unable to incorporate interaction terms to test, for example, the impacts of different habitats on the relationship between road exposure and detectability. In addition, we were 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 we were unable to test. Nevertheless, our results demonstrate the potential importance of accounting for the relationships 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). Our 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 1 km 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.

We therefore suggest that future studies involving bird surveys in areas exposed to roads recognize, and correct for, the potential impacts of road exposure on detectability. As high-resolution traffic data are not readily available everywhere, and we found major road exposure weighted by traffic intensity at our analysed BBS transect sections to be strongly correlated with unweighted major road exposure (Pearson's r of 0.80, calculated using $k_{\text{major}} = 1$), the latter could be used as an approximation. Either way, we 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. We 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.

Currently, around half of the land area in Europe is within 1.5 km of transport infrastructure (Science for Environmental Policy 2017) and between 2010 and 2050 the global total road length is expected to increase by > 60% (Dulac 2013). For mitigation of road impacts to be properly planned and implemented, it is necessary for these impacts to be quantified accurately. As our findings suggest that roads might have significant effects on detectability, this effect should be accounted for in studies of road impacts on birds and possibly other taxa, too.

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REFERENCES

Arévalo, J.E. & Newhard, K. 2010. Traffic noise affects forest bird species in a protected tropical forest. *Revista de Biología Tropical* **59**: 969–980.

Bautista, L.M., Garcia, J.T., Calmaestra, R.G., Palacin, C., Martin, C.A., Morales, M.B., Bonal, R. & Vinuela, J. 2004. Effect of weekend road traffic on the use of space by raptors. *Conserv. Biol.* **18**: 726–732.

Benítez-López, A., Alkemade, R. & Verweij, P.A. 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. *Biol. Conserv.* **143**: 1307–1316.

Brotons, L. & Herrando, S. 2001. Reduced bird occurrence in pine forest fragments associated with road proximity in a Mediterranean agricultural area. *Landsc. Urban Plan.* **57**: 77–89.

Brumm, H. 2004. The impact of environmental noise on song amplitude in a territorial bird. *J. Anim. Ecol.* **73**: 434–440.

BTO. 2018. Methodology and survey design. https://www.bto.org/volunteer-surveys/bbs/research-conservation/methodology (accessed August 2018).

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L. & Thomas, L. 2004. *Advanced Distance Sampling: Estimating Abundance of Biological Populations*. Oxford: Oxford University Press.

Choirat, C., Honaker, J., Imai, K., King, G. & Lau, O. (2018). Zelig: Everyone's Statistical Software. Version 5.1.6.1. http://zeligproject.org/

Clark, W.D. & Karr, J.R. 1979. Effects of highways on Red-Winged Blackbird and Horned Lark populations. *Wilson Bull.* **91**: 143–145.

Clarke, R.T., Liley, D., Sharp, J.M. & Green, R.E. 2013. Building development and roads: implications for the distribution of stone curlews across the Brecks. *PLoS ONE* **8**: e72984.

Coffin, A.W. 2007. From roadkill to road ecology: a review of the ecological effects of roads. *J. Transp. Geogr.* **15**: 396–406.

Crino, O.L., Johnson, E.E., Blickley, J.L., Patricelli, G.L. & Breuner, C.W. 2013. Effects of experimentally elevated traffic noise on nestling White-crowned Sparrow stress physiology, immune function and life history. *J. Exp. Biol.* **216**: 2055–2062.

De Molenaar, J.G., Saunders, M.E. & Jonkers, D.A. 2006. Roadway lighting and grassland birds: local influence of road lighting on a black-tailed godwit population. In Rich, C. & Longcore, T. (eds) *Ecological Consequences of Artificial Night Lighting*. Washington, DC: Island Press.

Dean, W. & Milton, S. 2003. The importance of roads and road verges for raptors and crows in the Succulent- and Nama-Karoo, South Africa. *Ostrich* **74**: 181–186.

DeGregorio, B.A., Weatherhead, P.J. & Sperry, J.H. 2014. Power lines, roads, and avian nest survival: effects on predator identity and predation intensity. *Ecol. Evol.* **4**: 1589–1600.

Develey, P.F. & Stouffer, P.C. 2001. Effects of roads on movements by understory birds in mixed-species flocks in Central Amazonian Brazil. *Conserv. Biol.* **15**: 7.

DfT. 2012. Guidance on road classification and the primary route network. https://assets.publishing.service.gov.uk/government/uploads/system/uploads/attachment_data/file/315783/road-classification-guidance.pdf

DfT. 2015. Road traffic statistics. Table TRA0302: Motor vehicle flow by road class and region and country in Great Britain. https://www.gov.uk/government/statistical-data-sets/road-traffic-statistics-tra#traffic-volume-in-kilometres-tra02 (accessed January 2019)

DfT. 2016. Traffic counts. http://www.dft.gov.uk/traffic-counts/index.php (accessed January 2016).

DfT. 2017. Road traffic statistics. Table RDL0203: Road lengths (kilometres) by road type in Great Britain, 1914-2017. https://www.gov.uk/government/statistics/road-lengths-in-great-britain-2017 (accessed April 2019).

Dominoni, D., Quetting, M. & Partecke, J. 2013. Artificial light at night advances avian reproductive physiology. *Proc. R. Soc. B Biol. Sci.* **280**: 20123017.

Dulac, J. 2013. Global land transport infrastructure requirements: Estimating road and railway infrastructure capacity and costs to 2050.

Eglington, S.M., Davis, S.E., Joys, A.C., Chamberlain, D.E. & Noble, D.G. 2010. The effect of observer experience on English Breeding Bird Survey population trends. *Bird Study* **57**: 129–141.

Erritzoe, J., Mazgajski, T.D. & Rejt, Ł. 2003. Bird casualties on European roads—A review. *Acta Ornithol.* **38**: 77–93.

ESRI 2015. ArcGIS Desktop: Release 10.3.1. Redlands: Environmental Systems Research Institute.

ESRI 2017. ArcGIS Desktop: Release 10.5.1. Redlands: Environmental Systems Research Institute.

Fahrig, L. & Rytwinski, T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecol. Soc.* **14**: 21.

Farmer, R.G., Leonard, M.L., Flemming, J.E.M. & Anderson, S.C. 2014. Observer aging and long-term avian survey data quality. *Ecol. Evol.* **4**: 2563–2576.

Ferris, C.R. 1979. Effects of interstate 95 on breeding birds in Northern Maine. *J. Wildl. Manag.* **43**: 421.

Forman, R.T.T. & Alexander, L.E. 1998. Roads and their major ecological effects. *Annu. Rev. Ecol. Syst.* **29**: 207–231.

Habib, L., Bayne, E.M. & Boutin, S. 2007. Chronic industrial noise affects pairing success and age structure of ovenbirds *Seiurus aurocapilla*. *J. Appl. Ecol.* **44**: 176–184.

Halfwerk, W., Holleman, L.J.M., Lessells, Ck.M. & Slabbekoorn, H. 2011. Negative impact of traffic noise on avian reproductive success: traffic noise and avian reproductive success. *J. Appl. Ecol.* **48**: 210–219.

Harris, S.J., Massimino, D., Gillings, S., Eaton, M.A., Noble, D.G., Balmer, D.E., Procter, D., Pearce-Higgins, J.W. & Woodcock, P. 2018. The breeding bird survey 2017. *BTO Research Report 706*. Thetford: British Trust for Ornithology.

Helldin, J.O. & Seiler, A. 2003. *Effects of roads on the abundance of birds in Swedish forest and farmland*. Proceedings of the IENE conference on Habitat Fragmentation due to Transportation Infrastructure.

Hernandez, M. 1988. Road mortality of the Little Owl (*Athene noctua*) in Spain. *J. Raptor Res.* **22**: 81–84.

Johnston, A., Newson, S.E., Risely, K., Musgrove, A.J., Massimino, D., Baillie, S.R. & Pearce-Higgins, J.W. 2014. Species traits explain variation in detectability of UK birds. *Bird Study* **61**: 340–350.

Knight, R.L. & Kawashima, J.Y. 1993. Responses of Raven and Red-Tailed Hawk Populations to linear right-of-ways. *J. Wildl. Manag.* **57**: 266.

Kociolek, A.V., Clevenger, A.P., St. Clair, C.C. & Proppe, D.S. 2011. Effects of road networks on bird populations. *Conserv. Biol.* **25**: 241–249.

Koper, N., Leston, L., Baker, T.M., Curry, C. & Rosa, P. 2016. Effects of ambient noise on detectability and localization of avian songs and tones by observers in grasslands. *Ecol. Evol.* **6**: 245–255.

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

Lambertucci, S.A., Speziale, K.L., Rogers, T.E. & Morales, J.M. 2009. How do roads affect the habitat use of an assemblage of scavenging raptors? *Biodivers. Conserv.* **18**: 2063–2074.

Laursen, K. 1981. Birds on roadside verges and the effect of mowing on frequency and distribution. *Biol. Cons.* **20**: 59–68.

Laurance, S.G.W., Stouffer, P.C. & Laurance, W.F. 2004. Effects of road clearings on movement patterns of understory rainforest birds in Central Amazonia. *Conserv. Biol.* **18**: 1099–1109.

Leonard, M.L. & Horn, A.G. 2005. Ambient noise and the design of begging signals. *Proc. R. Soc. B Biol. Sci.* **272**: 651–656.

Liker, A., Papp, Z., Bókony, V. & Lendvai, Á.Z. 2008. Lean birds in the city: body size and condition of House Sparrows along the urbanization gradient. *J. Anim. Ecol.* **77**: 789–795.

Lohr, B., Wright, T.F. & Dooling, R.J. 2003. Detection and discrimination of natural calls in masking noise by birds: estimating the active space of a signal. *Anim. Behav.* **65**: 763–777.

Marques, F.F.C. & Buckland, S.T. 2003. Incorporating covariates into standard line transect analyses. *Biometrics* **59**: 924–935.

McClure, C.J.W., Ware, H.E., Carlisle, J., Kaltenecker, G. & Barber, J.R. 2013. An experimental investigation into the effects of traffic noise on distributions of birds: avoiding the phantom road. *Proc. R. Soc. B Biol. Sci.* **280**: 20132290.

McClure, C.J.W., Ware, H.E., Carlisle, J.D. & Barber, J.R. 2017. Noise from a phantom road experiment alters the age structure of a community of migrating birds. *Anim. Conserv.* **20**: 164–172.

Meunier, F.D., Verheyden, C. & Jouventin, P. 1999. Bird communities of highway verges: Influence of adjacent habitat and roadside management. *Acta Oecol.* **20**: 1–13.

Meunier, F.D., Verheyden, C. & Jouventin, P. 2000. Use of roadsides by diurnal raptors in agricultural landscapes. *Biol. Conserv.* **92**: 291–298.

Mineau, P. & Brownlee, L.J. 2005. Road salts and birds: an assessment of the risk with particular emphasis on winter finch mortality. *Wildl. Soc. Bull.* **33**: 835–841.

Morelli, F., Beim, M., Jerzak, L., Jones, D. & Tryjanowski, P. 2014. Can roads, railways and related structures have positive effects on birds? – A review. *Transportation Research Part D: Transport and Environment* **30**: 21–31.

Nemeth, E., Pieretti, N., Zollinger, S.A., Geberzahn, N., Partecke, J., Miranda, A.C. & Brumm, H. 2013. Bird song and anthropogenic noise: vocal constraints may explain why birds sing higher-frequency songs in cities. *Proc. R. Soc. B Biol. Sci.* **280**: 20122798.

Newson, S.E., Evans, K.L., Noble, D.G., Greenwood, J.J.D. & Gaston, K.J. 2008. Use of distance sampling to improve estimates of national population sizes for common and widespread breeding birds in the UK. *J. Appl. Ecol.* **45**: 1330–1338.

Ortega, C.P. 2012. Chapter 2: effects of noise pollution on birds: a brief review of our knowledge. *Ornithol. Monogr.* **74**: 6–22.

Ortega, C.P. & Francis, C.D. 2012. Chapter 7: effects of gas-well-compressor noise on the ability to detect birds during surveys in northwest New Mexico. *Ornithol. Monogr.* **74**: 78–90.

Pacifici, K., Simons, T.R. & Pollock, K.H. 2008. Effects of vegetation and background noise on the detection process in auditory avian point-count surveys. *Auk* **125**: 600–607.

Palomino, D. & Carrascal, L.M. 2007. Threshold distances to nearby cities and roads influence the bird community of a mosaic landscape. *Biol. Cons.* **140**: 100–109.

Parris, K.M. & Schneider, A. 2009. Impacts of traffic noise and traffic volume on birds of roadside habitats. *Ecol. Soc.* **14**.

Peris, S. & Pescador, M. 2004. Effects of traffic noise on passerine populations in Mediterranean wooded pastures. *Appl. Acoust.* **65**: 357–366.

R Core Team 2018. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Reijnen, R. & Foppen, R. 1994. The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for Willow Warblers (Phylloscopus trochilus) breeding close to a highway. *J. Appl. Ecol.* **31**: 85–94.

Reijnen, R., Foppen, R., Braak, C.T. & Thissen, J. 1995. The effects of car traffic on breeding bird populations in Woodland. III. Reduction of density in relation to the proximity of main roads. *J. Appl. Ecol.* **32**: 187.

Reijnen, R., Foppen, R. & Meeuwsen, H. 1996. The effects of traffic on the density of breeding birds in Dutch agricultural grasslands. *Biol. Conserv.* **75**: 255–260.

Reijnen, R. & Foppen, R. 2006. In Davenport, J. & Davenport, J.L. (eds) *The Ecology of Transportation: Managing Mobility for the Environment*, Environmental Pollution, vol. 10: 255–274. Dordrecht: Springer.

Rheindt, F.E. 2003. The impact of roads on birds: does song frequency play a role in determining susceptibility to noise pollution? *J. Ornithol.* **144**: 295–306.

Rich, A.C., Dobkin, D.S. & Niles, L.J. 1994. Defining forest fragmentation by corridor width: the influence of narrow forest-dividing corridors on forest-nesting birds in southern New Jersey. *Conserv. Biol.* **8**: 1109–1121.

Risely, K., Massimino, D., Newson, S.E., Eaton, M.A., Musgrove, A.J., Noble, D.G., Procter, D. & Baillie, S.R. 2013. The breeding bird survey 2012. *BTO Research Report 645*. Thetford: British Trust for Ornithology.

Robinson, R.A. 2005. *BirdFacts: Profiles of Birds Occurring in Britain & Ireland*. Thetford: British Trust for Ornithology. http://www.bto.org/birdfacts (accessed 24 July 2019).

Ryan, M.J. & Brenowitz, E.A. 1985. The role of body size, phylogeny, and ambient noise in the evolution of bird song. *Am. Nat.* **126**: 87–100.

Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. 2002. Ecological and evolutionary traps. *Trends Ecol. Evol.* **17**: 474–480.

Science for Environmental Policy. 2017. Half of the land area in Europe is within 1.5 kilometres of transport infrastructure with large-scale impact on wildlife. *Eur. Comm. DG Environ. News Alert* **2**.

Silva, C.C., Lourenço, R., Godinho, S., Gomes, E., Sabino-Marques, H., Medinas, D., Neves, V., Silva, C., Rabaça, J.E. & Mira, A. 2012. Major roads have a negative impact on the Tawny Owl *Strix aluco* and the Little Owl *Athene noctua* populations. *Acta Ornithol.* **47**: 47–54.

Slabbekoorn, H. & Peet, M. 2003. Birds sing at a higher pitch in urban noise. *Nature* **424**: 267.

Slabbekoorn, H. & Ripmeester, E.A.P. 2008. Birdsong and anthropogenic noise: implications and applications for conservation. *Mol. Ecol.* **17**: 72–83.

Tremblay, M.A. & Clair, C.C.S. 2009. Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. *J. Appl. Ecol.* **46**: 1314–1322.

Van de Laar, F. 2007. Green light to birds: investigation into the effect of bird-friendly lighting. https://www.waddenzee.nl/fileadmin/content/Dossiers/Energie/pdf/green_light_to_birdsNAM.pdf

Ware, H.E., McClure, C.J.W., Carlisle, J.D. & Barber, J.R. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. *Proc. Natl Acad. Sci. USA* **112**: 12105–12109.

Whitford, P.C. 1985. *Bird Behavior in Response to the Warmth of Blacktop Roads*: 73. Madison, WI: Wisconsin Academy of Sciences, Arts and Letters.

Wiley, R.H. 1991. Associations of song properties with habitats for territorial oscine birds of Eastern North America. *Am. Nat.* **138**: 973–993.

Yamac, E. & Kirazli, C. 2012. Road effect on the breeding success and nest characteristics of the Eurasian Magpie (*Pica pica*). *Ekoloji* **21**: 1–10.

Yip, D.A., Bayne, E.M., Sólymos, P., Campbell, J. & Proppe, D. 2017. Sound attenuation in forest and roadside environments: implications for avian point-count surveys. *Condor* **119**: 73–84.

Yosef, R. 2009. Highways as flyways: time and energy optimization in migratory Levant Sparrowhawk. *J. Arid Environ.* **73**: 139–141.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1.1. A graphical overview of the methods used in this study.

Figure S2.1. Major road traffic count points and section junctions.

Figure S2.2. Preparation of major roads.

Figure S2.3. Editing of major roads.

Figure S3.1. Placement of kernel points

Figure S3.2. Kernel density analysis.

Figure S3.3. Optimization of the kernel density estimation parameters k_{major} and k_{minor}.

Table S4.1. Effect sizes of minor and major road exposure, and identified optimum K_{minor} and K_{major} values, for each species.

Table S4.2. Change in detectability from minimum to maximum minor road exposure.

Table S4.3. Change in detectability from minimum to maximum major road exposure.

Table S4.4. Results for survey date and habitat covariates

Table S4.5. Species trait data.