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Are the negative effects of roads on breeding birds caused by traffic noise?

Patricia D. Summers, Glenn M. Cunnington and Lenore Fahrig*

Geomatics and Landscape Ecology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, ON K1S 5B6, Canada

Summary

1. The effects of roads on wildlife populations are widespread and well documented. Many studies have shown that bird abundance, occurrence and species richness are reduced near roads, with the largest reductions where traffic levels are high. Negative correlations have been reported between bird richness/abundance and traffic noise but the possible causes of road effects are inter-correlated. It is important to disentangle the different effects so that appropriate mitigation measures can be implemented.

2. We tested the hypothesis that traffic noise is a key negative effect by testing three predictions: (i) bird richness/abundance should reach a maximum at the same distance from roads that traffic noise reaches a minimum; (ii) the effect of traffic noise on bird richness/abundance should be stronger than the effect of distance from the road on bird richness/abundance; and (iii) sites with more traffic noise at a given distance from the road should show lower bird richness/abundance than sites with less traffic noise at the same distance.

3. We collected breeding bird occurrence and traffic noise data along twenty 600-m transects perpendicular to roads at 10 high-traffic road sites.

4. Traffic noise decreased and bird species richness increased with increasing distance from the roads. However, none of the predictions derived from the traffic noise hypothesis was supported.

5. *Synthesis and applications*. Our results suggest that traffic noise is not the main cause of the negative relationship between bird species richness/abundance and proximity to roads. Instead, traffic mortality may be the main mechanism causing this relationship. We suggest that mitigation of road impacts on birds should focus mainly on reducing mortality rather than reducing traffic noise. In particular, engineering road surfaces, tyres and vehicle engines to reduce noise would not mitigate road effects; instead, structures to keep birds away from roads or force them to fly above the traffic would be more effective.

Key-words: breeding birds, ecological trap, edge effect, habitat quality, road disturbance, road effect zone, road mitigation, road mortality, sink habitat, traffic mortality

Introduction

The effects of roads on wildlife populations are widespread and well documented (Fahrig & Rytwinski 2009). In the case of birds, many studies have shown that abundance, occurrence and species richness of breeding birds is reduced near roads, with larger reductions near high-traffic roads than near lower-traffic roads (van der Zande, ter Keurs & van der Weijden 1980; Reijnen *et al.* 1995; Reijnen, Foppen & Meeuwsen 1996; Kuitunen, Rossi & Stenroos 1998; Brotons & Herrando 2001; Fuller *et al.* 2001; Burton *et al.* 2002; Forman, Reineking & Hersperger 2002; Rheindt 2003; Ingelfinger & Anderson 2004; Peris & Pescador 2004; Pocock & Lawrence 2005; Palomino & Carrascal 2007; Delgado García, Arevalo & Fernandez-Palacios 2008; Griffith, Sauer & Royle 2010). Most of the studies to date have either argued or assumed that the main cause of the responses of breeding birds to high-traffic roads is disturbance by traffic noise. The essential argument is that, as noise declines with distance from the road and with decreasing traffic, and as bird abundance declines with proximity to the road and with increasing traffic, the decline in birds with proximity to the road and traffic are probably because of traffic noise. In other words, the negative correlation between bird richness/abundance and traffic noise with increasing distance from roads has been taken as evidence that traffic noise actually causes the effect of roads on bird richness/abundance.

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*Correspondence author. E-mail: lenore_fahrig@carleton.ca

The suggestion that the negative effects of roads on birds are because of traffic noise does seem reasonable for several reasons (Barber, Crooks & Fristrup 2010). First, traffic noise could interfere with the acoustic communication on which birds depend for establishment and maintenance of territories and for intra-pair and adult–young communication (Rheindt 2003). Slabbekoorn & Ripmeester (2008) argue that although some birds are known to adjust their songs in the presence of noise (Wood & Yezerinac 2006; Parris & Schneider 2009; Francis, Ortega & Cruz 2010), other species may lack this ability making them 'unsuitable' for life in a noisy environment. Secondly, anthropogenic noise could distract individuals, making them more vulnerable to predation, as suggested by Yim-Hol Chan *et al.* (2010). Alternatively, noise could cause an increase in anti-predator vigilance, which could indirectly affect bird reproductive rate by reducing foraging time (Quinn *et al.* 2006). Finally, birds could avoid using noisy areas altogether (Schaub, Ostwald & Siemers 2008).

Despite these possible mechanisms, a correlation between bird species richness/abundance and traffic noise does not necessarily imply a causal relationship. There are other possible mechanisms that are correlated with traffic noise, which could contribute to or could even be the main factor causing the negative effects of roads on birds. First, as noted by Delgado García, Arevalo & Fernandez-Palacios (2007), some of the studies of road effects on birds were designed such that the effects of distance from the road and distance from habitat edge are confounded, which means that apparent road effects could be partly or even mainly because of habitat edge effects on birds. Secondly, road traffic could disturb birds through vehicle lights and motion rather than (or in addition to) traffic noise; Pocock & Lawrence (2005) found that both noise and light penetration occurred to about the same distance in a tropical forest. Thirdly, roads could reduce bird abundance through toxic effects of car exhaust, either directly on the birds or indirectly by killing insects thus reducing food availability for the birds. Finally, the cause of the negative road effects on bird richness/abundance could be direct mortality because of collisions with traffic. Bird mortality along roads can be substantial; for example, in our region of eastern Ontario, Canada, Eberhardt (2009) found 212 road-killed birds along a 34-km stretch of a two-lane highway during a single field season. All of these alternative mechanisms are correlated with traffic amount, which is correlated with traffic noise. Therefore, correlations between bird richness/abundance and traffic noise could actually be caused by any or a combination of these alternative mechanisms.

From a management perspective, it is important to understand the main cause of the negative relationship between bird richness/abundance and roads, because the mitigation measures most appropriate for reducing road effects on birds depend on the cause(s) of the effects. As all mitigations are costly, it is important to ensure that the mitigation chosen will actually reduce the impact of concern. For example, if the road effect is mainly because of traffic noise, appropriate mitigation would include noise barriers and/or road surfaces, vehicle engines, and tyres that are engineered to reduce traffic noise. Alternatively, if the road effects are mainly because of traffic mortality, structures should be installed that keep birds away from roads or force them to fly above the traffic level when they cross roads.

The purpose of this study was to test the hypothesis that the negative effect of high-traffic roads on bird richness/abundance is mainly attributed to traffic noise. To do this, we first note, again, that negative correlations between traffic noise and bird abundance do not support the traffic noise hypothesis because traffic noise is correlated with the other possible causes of road effects on breeding birds discussed previously, i.e., other traffic disturbances and traffic mortality. We tested three predictions derived specifically from the noise hypothesis. While support of any one of these predictions in itself would not offer strong support of the noise hypothesis, we reasoned that, if several different predictions derived from the same hypothesis were supported, we would be more confident in concluding that traffic noise is the main cause of the negative relationship between bird richness/abundance and roads. The first prediction was that, if the effect of roads on birds is mainly because of traffic noise, bird richness/abundance should reach its maximum at the same distance from the road at which traffic noise reaches its minimum. Secondly, if traffic noise is largely responsible for the effect of roads on breeding bird richness/abundance, the effect of traffic noise should be stronger than the effect of distance from the road (even though distance and traffic noise are correlated). The argument behind this second prediction is that the effect of the direct putative cause (traffic noise) should be stronger than the effect of a secondary variable (distance from the road) that is only correlated with the direct putative cause. Thirdly, if traffic noise is largely responsible for the road effects on bird richness/abundance, then sites with more traffic noise at a given distance from the road should show lower bird richness/abundance than sites with less traffic noise at the same distance from the road. This third prediction effectively controls for the relationship between distance from the road and traffic noise.

Materials and methods

We conducted bird point-count surveys in forest patches that were in close proximity to high-traffic roads in eastern Ontario, Canada. To test and control for a possible confounding of forest edge and road effects, we conducted point-count surveys along transects both in the forest patches and along the edges of the patches perpendicular to the road (Fig. 1). We measured traffic noise at each bird survey location during each point count. Sample plots of spectral characteristics are shown in Fig. 2.

SITE SELECTION

We selected 10 forest patches next to high-traffic roads, having a distinct forest edge running perpendicular to the road, where the forest edge bordered agricultural land, either arable crops or pasture. The length of the forest edge running perpendicular to the road was at least 600 m, except for one site where it was 500 m. High-traffic roads were classified as four-lane highways with > 10 000 average annual daily traffic volumes (AADT), as this is the traffic volume above

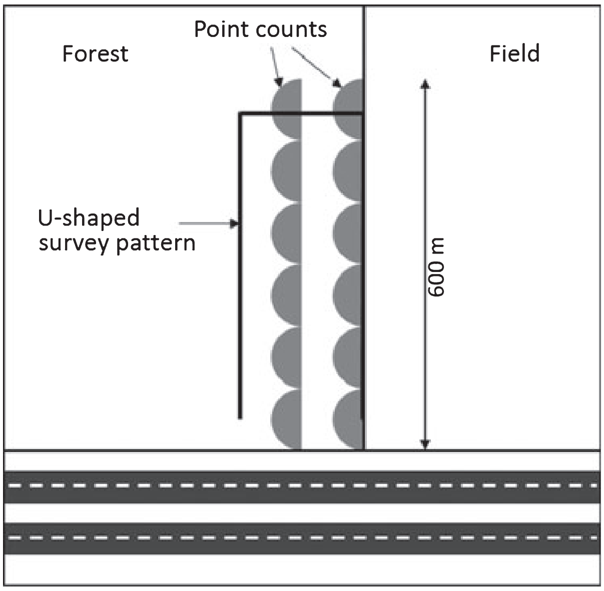

Fig. 1. Illustration of the layout of breeding bird point-count surveys at each of 10 high-traffic sites. Point counts were half-circles of 50-m radius.

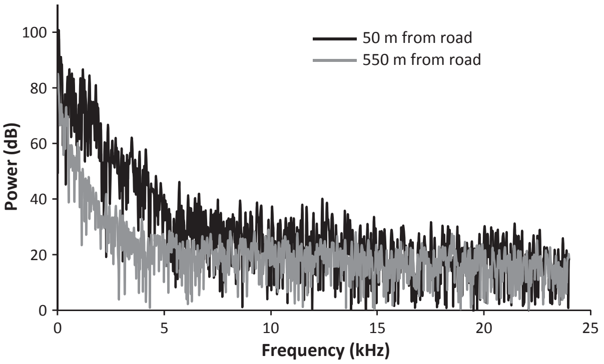

Fig. 2. Spectral characteristics of traffic noise extracted from sample recordings at one site, at the point-count nearest a road (50 m: black lines) and farthest from a road (550 m: grey lines).

which effects of roads on birds are regularly found (Forman, Reineking & Hersperger 2002). The range in AADT across sites was 13 700–87 100 vehicles per day. All forest patches were mixed woods (i.e. containing deciduous and coniferous trees).

BIRD SURVEYS

Each site was surveyed on two separate visits between 12 May and 18 July 2008. To ensure similar diurnal traffic patterns, surveys were only conducted during weekdays, when the morning traffic pattern is determined largely by commuter travel to work. The 10 sites were surveyed in a random order, one site per day, using the same order for both series of visits. All point-count locations at a site were surveyed twice on the same day, the first beginning 30 min before sunrise and the second during rush hour and ending before 9:00. Therefore, each point was surveyed a total of four times, on two visits with two counts per visit.

At each site, we conducted point counts along two separate parallel transects that ran perpendicular to the road (Fig. 1). One transect ran along the forest edge and the other ran into the forest 100 m from the edge transect. The centre of the first point count for both transects was 50 m from the forest edge adjacent to the road, and point counts were then conducted every 100 m along the transects. The starting transect (edge or forest) was randomly chosen on the first visit to the site, with the two transects run in a U-shape (i.e. in opposite directions; Fig. 1). Both the early morning and the rush hour surveys were run in the same direction around the U-shape within each visit, but on the second visit the U-shape was run in the opposite direction to the direction taken on the first visit. This procedure was designed to avoid any possible bias of time of day in our surveys. For example, each survey point next to a road was sampled once at the beginning of the early morning survey period, at the end of the early morning period, at the beginning of the rush hour survey period and at the end of the rush hour survey period. Surveys were not conducted in rainy or windy (> 20 km h^{-1}) conditions. Bird surveys were 5-min, 50-m radius point counts where all birds seen or heard were recorded (Bibby *et al.* 2000), except for birds that flew through the point-count area. To avoid double-counting of birds, we only recorded birds in half of each 50-m radius circle (Fig. 1). For the edge transects, we recorded birds only in the forested half of the circle. For the forest transects, we recorded birds only in the half of the circle farthest from the edge transect, thus avoiding double-counting of birds in the two transects. In limiting our detection radius to 50 m, we aimed to avoid the effects of traffic noise on bird detection: in an experimental study, Pacifici, Simons & Pollock (2008) found essentially no effect of low-frequency background noise on bird detections within 50 m of observers in mixed wood forest, although we note that their experiment did not mimic noise levels across the full range of frequencies seen at high-traffic roads. All point counts were recorded with an audio recorder (see below), and the recordings were later checked for any species missed during the field surveys.

TRAFFIC NOISE

We recorded the duration of each point count using a Zoom H4 recorder (Samson) with stereo unidirectional electret condenser microphone at a sampling rate of 48 kHz, placed on a tripod 1 m from the ground. A box (*c.* 15 × 15 × 10 cm) of flexible Styrofoam covered in 'fun fur' was fitted tightly over the recorder and microphones to create dead air space to reduce wind noise on the recordings. Using RAVEN PRO 1.3 (Cornell Lab of Ornithology, Ithaca, New York, USA), we extracted the average power (dB) of the noise between 0·3 and 2 kHz over the full 5-min recording, as an index of traffic noise. Most loud traffic noise is below 2 kHz (Warren *et al.* 2006). We did not include noise below 0·3 kHz in our index, to eliminate variation because of wind and recorder vibration noises, which we could not reliably eliminate from the recordings. Most bird song occurs above 2 kHz, and we were not able to reliably eliminate these from the recordings. Therefore, our index of traffic noise (between 0·3 and 2 kHz) was intended as a relative index of total traffic noise, on the assumption that the correlation (across point counts) between traffic noise below and above 2 kHz should be high. We tested this assumption by finding the first reliably bird-call-free 20-s segment of each rush hour recording and calculating the correlation between power in the range 0·3–2 kHz (our traffic noise index) and power in the range > 2 kHz. The correlation was 0·8 ($P << 0{\cdot}00001$, $n = 196$), indicating that our index was a good relative index of total traffic noise. Note we only used the rush hour recordings for this test because it was often not possible to find reliably bird-call-free 20-s segments in the early morning recordings. Average traffic noise level for a point-count location was then calculated from the four recordings at that location.

ANALYSES

All raw data used in our analyses can be found in Summers (2009). Bird response variables were species richness (the total number of species from the four point counts at each point-count location) and species occurrence (presence at least once or absence of a species at each point-count location). We did not use abundance (either total abundance or abundances of individual species) because, given the size of the point-count areas (half of a 50 m radius circle), we only rarely found more than one singing individual of the same species in a single point-count area. Therefore, species richness was effectively equivalent to total bird abundance (across species) in our data. Note that we did conduct all analyses using abundance instead of species richness, and we obtained qualitatively identical results to the results reported below.

To determine whether the relationship between bird species richness and distance reached its maximum at the same distance from the road as the distance at which traffic noise reached its minimum, (prediction 1), we conducted polynomial regressions (with random intercept) of (i) traffic noise on distance from the road and (ii) bird species richness on distance from the road. We included site (as a random effect) and transect in these analyses. Site was entered to control for differences among sites – e.g. forest patch size, local vegetation, surrounding landscape composition – that could affect bird species richness and occurrence. To compare the relative effects of traffic noise and distance from the road (prediction 2) on bird species richness, we conducted a general linear models mixed effects analysis (with random intercept). We included quadratic terms for noise and distance, and we included site (n = 10; random effect) and transect (edge or forest) as categorical variables. We also conducted multi-model inference (all 15 possible combinations of noise, noise^2, distance, and distance^2), including dummy variables for transect and site in all models. We ranked the models using Akaike's Information Criterion (AIC) and compared relative effects using the model-weighted mean standardized coefficients. To test whether sites with more traffic noise at a given distance had lower bird species richness than sites with less traffic noise at the same distance (prediction 3), we conducted separate regressions of species richness on traffic noise, for each of the six point-count distances. We included transect as a categorical variable in these analyses. We also included forest patch size as a co-variate in these analyses, because of a marginally significant correlation across the 10 sites between forest patch size and traffic volume (r = 0·6, P = 0·06); note this was not necessary in the other analyses because site was included as a dummy variable. We confirmed that residuals of all analyses met the assumptions for parametric tests (normality and homoscedasticity). All analyses were conducted using SAS.

Results

Altogether, we observed 63 bird species, 54 along the edge transects and 54 along the forest transects. The mean number of species per point count on edge transects was 7·15 (range 2–12 species) and on forest transects was 8·29 (range 3–13 species). Traffic noise declined with distance from the roads in a curvilinear fashion (Table 1, Fig. 3, Spearman r = −0·61). Although the overall noise level was higher on edge transects than on forest transects, there was no significant difference between transect types (edge or forest) in the shape of the relationship between noise and distance (Table 1: interaction effects not significant); traffic noise reached a minimum at about 450 m from the roads (Fig. 3). Bird species richness increased with distance from the roads in a curvilinear fashion. Although overall bird species richness was higher on forest transects than on edge transects, there was no significant difference between transect types in the shape of the relationship between richness and distance (Table 2: interaction effects not significant); species richness reached a maximum at about

Table 1. ANOVA results from a mixed effects linear model of the effects of site (10 sites: random effect), transect type (edge versus forest; Fig. 1) and distance from the roads on traffic noise level (dB)

Source	d.f.	Type III sums of squares	F	P
Site	9	1148·8	31·4	< 0·0001
Transect (modelled without its interaction effects below)	1	55·3	13·62	< 0·0001
Distance	1	430·2	103·9	< 0·0001
Distance^2	1	163·4	39·5	< 0·0001
Transect × Distance	1	0·197	0·05	0·83
Transect × Distance^2	1	0·164	0·04	0·84

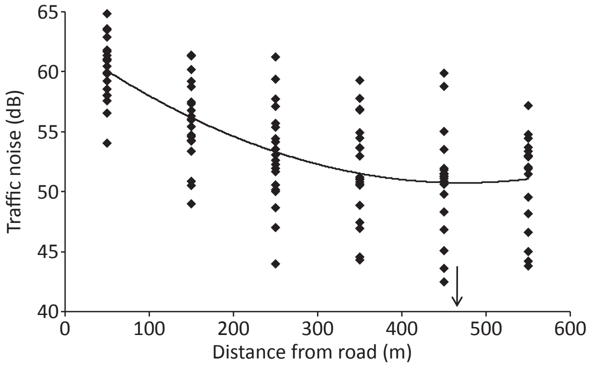

Fig. 3. Relationship between average recorded traffic noise (dB) at point-count locations and distance from the roads (see Table 1). Arrow indicates the distance from the roads at which traffic noise was at a minimum.

Table 2. ANOVA results from a mixed effects linear model of the effects of site (10 sites: random effect), transect type (edge versus forest; Fig. 1) and distance from the roads on bird species richness

Source	d.f.	Type III sums of squares	F	P
Site	9	291·0	9·04	< 0·0001
Transect (modelled without its interaction effects below)	1	35·01	9·79	0·0023
Distance	1	60·18	16·83	< 0·0001
Distance^2	1	41·63	11·64	0·001
Transect × Distance	1	1·19	0·33	0·57
Transect × Distance^2	1	0·97	0·27	0·61

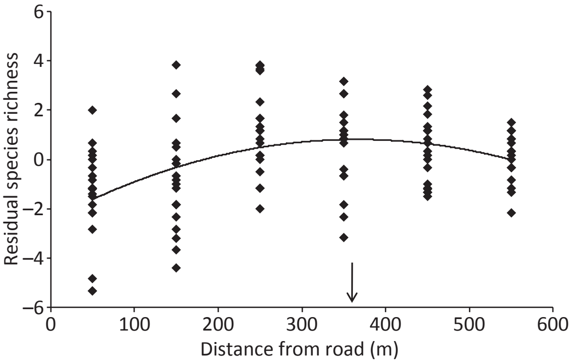

Fig. 4. Relationship between bird species richness at point-count locations and distance from the roads, after correcting for differences among sites (i.e. residuals; see Table 2). Arrow indicates the distance from the roads at which species richness was at a maximum.

Table 3. ANOVA results from a mixed effects linear model of the effects of site (10 sites: random effect), transect type (edge versus forest; Fig. 1), traffic noise (mean dB) and distance from the roads on bird species richness

Source	d.f.	Type III SS	*F*	*P*
Site	9	257·4	8·03	< 0·0001
Transect	1	22·7	6·38	0·013
Noise	1	3·39	0·98	0·32
Noise^2	1	2·46	0·69	0·41
Distance	1	15·91	4·47	0·04
Distance^2	1	19·68	5·53	0·02

Table 4. Signs of coefficients for all 15 possible model combinations of traffic noise, distance from the roads and their quadratic terms on bird species richness. A blank entry indicates that the term was not included in the model. All models also included a dummy variable representing transect (edge versus forest) and four dummy variables representing the 10 sites. Models are ranked from best to worst according to model ΔAIC

Noise	Noise^2	Distance	Distance^2	ΔAIC	Model weight
		+	−	0	0·3817
	+	+	−	1·217	0·2077
+		+	−	1·357	0·1937
−	+	+	−	1·937	0·1449
		+		5·139	0·0292
−		+		7·122	0·0108
	−	+		7·125	0·0108
			+	8·733	0·0048
−	+	+		9·089	0·0041
	−			9·822	0·0028
−				9·874	0·0027
	−		+	10·011	0·0026
−			+	10·022	0·0025
+	−			11·785	0·0011
+	−		+	12·005	0·0010
Model-weighted mean standardized coefficients					
−0·596	0·732	2·987	−2·352		

AIC, Akaike's Information Criterion.

Table 5. ANOVA results from regressions of bird species richness on traffic noise, transect type (edge versus forest; Fig. 1; statistics for transect type not shown) and forest patch size (not statistically significant; statistics not shown) at different distances from the roads across 10 sites with two transects per site. Mean dB range is the range across transects in mean dB values at the given distance

Distance from road (m)	Mean dB range	Coefficient for noise	Error d.f.	*F*	*P*
50	54·08–64·85	0·26	17	2·04	0·24
150	49·03–61·40	0·24	17	0·28	0·39
250	44·03–61·25	0·12	17	0·21	0·55
350	44·35–59·30	0·05	17	0·49	0·77
450	42·53–59·90	−0·06	17	0·44	0·70
550	43·85–57·20	0·05	14	0·18	0·74

350 m from the roads (Fig. 4). The mean number of species at point counts closest to the roads was 26% lower than the mean number at point counts 350 m from the roads (6·20 versus 8·35 species on average, respectively).

The effect of distance from the roads on species richness was stronger than the effect of traffic noise (Tables 3 and 4). Adding traffic noise to a model that already contained distance from the roads did not improve the fit of the model. However, there was an improvement to the fit of the model when distance from the roads (in quadratic form) was added to a model that already contained traffic noise (Table 3). Therefore, the effect of distance from the roads on species richness was not explained by traffic noise. The multi-model inference analysis was consistent with this: the best model contained distance and distance^2, and the AIC for this model was 11·8 points lower than the AIC for the model containing noise and noise^2, and 9·9 points lower than the AIC for the model containing noise only (Table 4). The model containing only distance had an AIC value 4·7 points lower than the model containing only noise (Table 4). The model-weighted mean standardized coefficients for distance and distance^2 were over three times those for noise and noise^2, indicating a stronger relative effect of distance from the roads than noise on bird species richness. The variance inflation factors for distance and noise (when regressed on noise or distance (respectively) plus the dummy variables for transect and site) were 1·79 and 2·09, respectively, indicating that colinearity did not hinder interpretation of the results (O'Brien 2007). Despite the fact that bird species richness increased overall with distance from the roads, there were no significant relationships between traffic noise (across sites) and species richness at any of the six distances from the roads (Table 5).

Discussion

Our results are consistent with previous studies: species richness/abundance of birds increased with increasing distance from the roads. However, counter to our *a priori* expectations, our results did not support the traffic noise hypothesis as the main explanation for this pattern. None of the three predictions based on the traffic noise hypothesis was supported. First, while traffic noise reached a minimum at about 450 m from the roads, bird species richness reached a maximum at about 350 m from the roads. Secondly, the effect of distance from the roads on bird richness was stronger than the effect of traffic noise. Distance from the roads had an effect on richness after controlling for traffic noise, suggesting that the effect of distance from the roads on species richness is not explained by traffic noise. Finally, bird species richness was not related to traffic noise (across sites) when distance from the roads was controlled. While each of these results taken individually may not strongly refute the traffic noise hypothesis, taken together they do suggest that the traffic noise hypothesis should be revisited: it seems that traffic noise, while affecting the vital rates of some bird species (e.g. *Parus major*, Halfwerk *et al.* 2011), may nevertheless not be the dominant cause of the negative relationship between bird species richness/occurrence and proximity to roads.

A possible confounding factor in our study and others on road effects on birds is that traffic noise may also affect the ability of the observer to detect birds, which could result in spurious apparent effects of roads on birds. To minimize this problem, we recorded only birds detected within 50 m of the observer. Experiments by Pacifici, Simons & Pollock (2008) demonstrated essentially no effect of low-frequency background noise on an observer's ability to detect singing birds within 50 m in mixed-wood forest, although we note that their experiment did not mimic noise levels across the full range of frequencies seen at high-traffic roads. In addition, to test for this potential effect in our data, we analyzed the relationship between bird richness/abundance and distance from the roads using the data from our early morning surveys only, when traffic noise was very low. Bird richness in early morning increased significantly with distance from the road, indicating that the negative effect of roads on birds is probably not a spurious result because of an inability of observers to detect birds in the presence of traffic noise. We also note that Griffith, Sauer & Royle (2010) interpreted a lack of relationship between bird song frequency and traffic volume in roadside surveys for the North American Breeding Bird Survey as evidence that traffic noise does not impede observers ability to detect birds.

Our conclusion that the negative effect of roads on bird species richness may not be mainly attributed to traffic noise should be tempered for several reasons. First, it is possible that our results are particular to our region. For example, several of the studies to date in which noise was inferred as the cause of the negative effect of roads on birds, including the now-classic studies by Reijnen *et al.* (1995) and Reijnen, Foppen & Meeuwsen (1996), were conducted in Europe. Differences among regions in the type of traffic, roadside habitats, type of paved surface and the bird community itself all may cause differences in the effects of traffic noise on birds. Therefore, traffic noise may be more strongly implicated in the effects of roads on birds in some regions than in others. Secondly, there is a great deal of variation in our data (Figs 3 and 4), which means our power to detect small effects of traffic noise is limited. Traffic noise is highly variable because it is strongly affected by environmental conditions such as wind speed and direction, and humidity. We attempted to reduce this variability by taking the average of four recordings at each point-count location. The fact that these averaged values of traffic noise declined with distance from the roads as expected (Fig. 3) gives us confidence that our noise values do have meaning. However, we acknowledge that the variance associated with these values does reduce the power of our tests. Similarly, our estimates of bird species richness have error associated with them. While we do not have an estimate of this error, we know that the bird richness values have meaning because they showed the expected positive relationship with distance from the roads (Fig. 4). We also note that our sampling effort was relatively high, with 468 point counts and traffic noise recorded during each point count. Thirdly, while our results suggest that traffic noise may not be the dominant cause of the negative relationship between proximity to roads and bird species richness, there is recent evidence that traffic noise can affect reproductive rate in birds. Halfwerk *et al.* (2011) showed that clutch size and fledgling mass in great tits *Parus major* are reduced in locations with high traffic noise. It is not known to what extent this pattern is applicable to other species or to what extent such reductions in reproductive rate can cause reduced abundances near roads. Surprisingly, *Parus major* was one of 6 (of 23) bird species for which Reijnen *et al.* (1995) and Reijnen & Foppen (1995) found no evidence for an effect of roads on population density. Finally, we acknowledge that each of our three tests on its own should be considered only a weak test of the noise hypothesis. For example, it is possible that species richness does not reach its maximum where noise reaches its minimum because negative edge effects from the back side of the forest patches may reduce species richness at the points most distant from the road. Despite these issues, we suggest that the fact that none of our three tests supported the noise hypothesis seriously brings into question the common assumption that noise is the main cause of the negative effects of roads on birds, at least in our region.

If traffic noise is not the main cause of the negative effects of roads on birds, what is the most likely explanation? We can rule out edge effects because we observed an effect of distance from the roads on bird richness/abundance after controlling for the effect of transect type (edge versus forest). The effects of other disturbances such as lights, vehicle motion and pollution are all possible explanations but we are not aware of data available to evaluate them directly. In contrast, there is evidence for road mortality effects on birds and we therefore suggest that road mortality should be viewed as the most likely 'alternate hypothesis' at this time. In farmland in SW Poland, Orłowski (2008) estimated a road mortality rate of 9 birds killed per km of road per year; in 56 survey days of 48·8 km of roads, they found 862 dead birds (49 species), and a much higher kill rate on high-traffic road segments than low-traffic road segments. Presumably, birds with territories near roads are those most commonly killed. In addition, Orłowski (2005) estimated that the annual number of barn swallows *Hirundo rustica* killed on roads in Poland is 180,000, which is 'much more than its entire breeding populations in some western European countries' (Orłowski 2008). A study on breeding success in pied flycatchers *Ficedula hypoleuca* near roads (Kuitunen *et al.* 2003) is also consistent with the mortality hypothesis. While proximity to the road had no effect on laying date, clutch size or brood size (all of which would have been consistent with road disturbance effects), nests closer to the road were more likely to fail at the chick stage; the number of broods lost completely was significantly higher near the roads than farther away from the roads. The most likely explanation for this is road mortality of the parents (Kuitunen *et al.* 2003). Similarly, Mumme *et al.* (2000) found that annual mortality of breeding adult and fledgling Florida scrub jays *Aphelocoma coerulescens* on roadside territories was significantly higher than the mortality rate on non-roadside territories and that this mortality was because of roadkill. In fact, breeder mortality greatly exceeded the production of yearlings on roadside territories, so roadsides were sink habitats for this species. We note that even if territories emptied by road mortality are filled by unpaired 'floater' males, there would still be a delay between the death of a bird and its replacement (Stewart & Aldrich 1951; Brown 1969), which would result in reduced average bird counts near roads. In addition, the replacement bird may not produce offspring if the replacement occurs too late in the season. For species with high breeding site fidelity, this could result in between-year persistence of lower abundances in roadside territories.

Even given the plausibility of the road mortality hypothesis, the lack of support for the traffic noise hypothesis seems surprising, particularly considering the importance of vocal communication for birds. However, it is possible that birds adjust their songs when necessary to compensate for traffic noise, thus avoiding its potential effects on their ability to communicate. For example, Parris & Schneider (2009) compared the song frequencies (kHz) of two bird species at sites varying widely in traffic noise. They found that the lower singing grey shrike-thrush *Colluricincla harmonica* sang at higher frequencies at high-traffic sites than at low-traffic sites. In contrast, the higher singing grey fantail *Rhipidura albiscapa* did not change its song frequency in response to traffic, presumably because its song was already well above the frequency of traffic noise. Similarly, Wood & Yezerinac (2006) found a positive relationship between the minimum frequency of male song and the amplitude of urban noise (mainly traffic) in song sparrows *Melospiza melodia* and that male sparrows shifted more energy into the higher frequency (4–9 kHz) portions of their songs in noisy areas. Francis, Ortega & Cruz (2010) found that the ash-throated flycatcher *Myiarchus cinerascens* vocalized at higher frequencies in noisier locations. Therefore, while our results suggest that traffic noise may not be the main cause of the negative effects of roads on bird richness/abundance, there is evidence that road noise affects the singing behaviour of some birds.

It is important to note that our finding that the negative effects of roads on bird species richness and occurrence may not be mainly attributed to traffic noise does not rule out the possibility that other anthropogenic noises have large effects on bird abundance. Studies of noise associated with oil and gas extraction do indicate impacts on birds (Bayne, Habib & Boutin 2008; Francis, Ortega & Cruz 2009, 2010). There are at least two possible explanations for the apparently higher impact of this type of noise than of traffic noise on birds. First, while the frequency of most traffic noise is lower than the frequencies of most bird songs, there appears to be more high frequency noise associated with oil and gas extraction (Francis, Ortega & Cruz 2009, 2010), which may interfere more with bird communication. Secondly, noise associated with oil and gas extraction appears to be generally louder than traffic noise; Bayne, Habib & Boutin (2008) mention noise levels of up to 105 dB at compressor stations, whereas the busiest freeway in our region, containing heavy truck traffic, has noise levels of about 76 dB (Cunnington & Fahrig 2010).

APPLIED SIGNIFICANCE

Our results support the findings of other studies that bird abundances and species richness are depressed near roads. However, our results cast into question the common assumption that this negative effect of roads on birds is mainly because of traffic noise. These results have implications for mitigation of road impacts on birds. In particular, they suggest that some engineering solutions for reducing traffic noise disturbance on humans – e.g. tyres, engines, and pavements engineered to reduce noise – may not mitigate the impacts of roads on birds. If the traffic mortality hypothesis is correct, mitigation of road effects on birds will require measures to keep birds from being killed by vehicles. Short of removing roads and/or reducing traffic volumes, such measures would consist of installing structures that force birds to fly above the level of traffic when they cross roads.

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