

# Influence of traffic mortality on forest bird abundance

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**Abstract** Lower abundance of forest birds near high traffic roads is usually attributed to traffic noise, but the potential role of traffic mortality has not been adequately tested. We tested for the effect of traffic mortality independent of traffic noise, by sampling forest birds at sites with similar traffic volume (and noise levels), that varied in the likelihood of traffic collisions. Collision rates should be higher at forest sites next to roads where there is forest directly across the road, since forest birds are more likely to attempt to cross a small forest gap than a large one. We predicted that if traffic collisions play a significant role in the road effect on birds then in sites where there is a higher risk of traffic collision (small gap sites), there should be a stronger decline through the season in the number of forest birds close to roads, than in sites where there is a lower risk of collision (large gap sites). We compared relative abundance of forest birds, at four distances from high traffic roads, at 10 sites where the birds were more likely to cross the road (small-gap sites, with forest on the other side) versus at 10 sites where they were less likely to cross the road (large-gap sites with open field on the other side). Our prediction was supported; the slope of the relationship between abundance and distance from the road (the negative road effect) became stronger as the season progressed at the small-gap sites but not at the large-gap sites. Our results support the notion that traffic mortality is an important component of the negative road effect, and that mitigation of road effects on birds should include mitigation for traffic mortality.

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## Introduction

We are only beginning to understand the ecological consequences of the 100 million km road network spanning the world's terrestrial ecosystems (CIA 2008). The effects of roads are diverse and complex (Forman et al. 2003), resulting in a range of impacts on wildlife populations, most of them negative (Trombulak and Frissell 2000; Fahrig and Rytwinski 2009; Benítez-López et al. 2010; Rytwinski and Fahrig 2012). Among the studies documenting impacts of roads on wildlife, many have shown that birds are less abundant near high traffic roads than low traffic roads (Van Der Zande et al. 1980; Reijnen et al. 1995, 1996; Brotons and Herrando 2001; Fuller et al. 2001; Forman et al. 2002; Kuitunen et al. 2003; Rheindt 2003; Peris and Pescador 2004; Pocock and Lawrence 2005; Summers et al. 2011; Polak et al. 2013). Hereafter, we refer to the phenomenon of reduced animal abundance near high traffic roads as the “negative road effect”. Although many studies have reported negative road effects on wildlife, the underlying mechanism(s) (e.g., behavioural avoidance, mortality) remains unknown or assumed in many cases (Forman et al. 2003; Roedenbeck et al. 2007; Fahrig and Rytwinski 2009). To design effective mitigation measures we need to understand the main cause(s) of the road effects.

In past studies, the negative road effect on birds has usually been attributed to traffic noise. Birds rely on sound to attract mates, defend territories (Nowicki and Searcy 2004) and avoid predation (Klump and Shalter 1984). Therefore, it seems a reasonable assumption that disruption of vocal communication by traffic noise would lead to a negative road effect on birds (Reijnen and Foppen 2006). This is supported by studies showing that anthropogenic noise can affect bird reproduction, behaviour and abundance. For example, Ovenbirds (*Seiurus aurocapilla*) near noise-emitting natural gas compressor stations showed reduced pairing success (Habib et al. 2006). The density of certain bird species, as well as bird species richness, also appears to be reduced near noisy compressor stations (Bayne et al. 2008; Francis et al. 2009). In addition, a study on chaffinches (*Fringilla coelebs*) demonstrated that they increased their visual surveillance activity when exposed to background noise generated at frequencies intended to reduce their ability to use auditory cues (Quinn et al. 2006).

Despite evidence for negative effects of anthropogenic noise on birds, it is premature to conclude that the effect of roads on bird abundance is driven mainly by noise, because, as suggested by Summers et al. (2011), in past studies noise effects were confounded with other road-related impacts that co-vary with traffic volume and thus with traffic noise. One such impact is road mortality. Bird-vehicle collisions are common (e.g., Erritzoe et al. 2003; Orłowski 2008; Eberhardt 2009). For example, wildlife-vehicle collisions are estimated to kill 653,000 birds annually in the Netherlands (as cited in Erritzoe et al. 2003), 10–60 million annually in England (as cited in Bishop and Brogan 2013), 80 million annually in the USA (Erickson et al. 2005), and in Canada, 13.8 million birds are killed on paved roads during the breeding season (Bishop and Brogan 2013).

Furthermore, some studies have suggested that the traffic mortality on birds can affect local bird populations. For example, both pied flycatchers (*Ficedula hypoleuca*) and great tits (*Parus major*) nestlings were found to be less likely to fledge from nest boxes close to

roads than nestlings in nest boxes farther away from roads (Kuitunen et al. 2003; Holm and Laursen 2011), the authors suggesting the most likely explanation is traffic-related mortality of the parents. An analysis of gray jay (*Perisoreus canadensis*) survivorship near and far from a major highway in Ontario found jays inhabiting territories adjacent to the highway had lower survival rates than those on territories away from the road; dead jays were common along the road (Norris et al. 2013). Further south, Florida scrub-jays (*Aphelocoma coerulescens*) living next to a two-lane highway were found to have mortality rates nearly twice as high as those living away from the road, and in territories next to roads, more scrub-jays were killed than yearlings produced (Mumme et al. 2000). Taken together, these studies suggest that traffic mortality could contribute to or could even be a major driver of observed negative road effects on birds.

To determine whether a given mechanism has an effect, it must be evaluated while controlling for other potential confounding mechanisms. Two recent studies attempting to isolate the effect of traffic noise on birds from other possible causes of road effects revealed mixed results. In eastern Ontario, Canada, Summers et al. (2011) conducted breeding bird point-count surveys along transects perpendicular to 10 high traffic roads, recording traffic noise at each bird survey location. Though both traffic noise and bird species richness were negatively correlated with distance from the road, species richness was not related to variation in traffic noise after controlling for the effect of distance from the roads. Summers et al. (2011) speculated that some mechanism related to traffic volume, other than noise, such as traffic mortality, may be the main mechanism causing the observed decline in bird richness with proximity to the roads. More recently, McClure et al. (2013) propagated traffic noise through speakers, to create a “phantom road” in a road-less area during autumn at a migration stopover site in Idaho, USA. They found that bird abundance was lower at the phantom road than at control plots. McClure et al. (2013) thus provide evidence that in a non-noisy landscape, some bird species respond negatively to the addition of noise; however, many birds still choose to nest close to busy roadways and, at such sites, Summers et al. (2011) found that traffic noise did not explain declines in bird abundance with proximity to the high traffic roads.

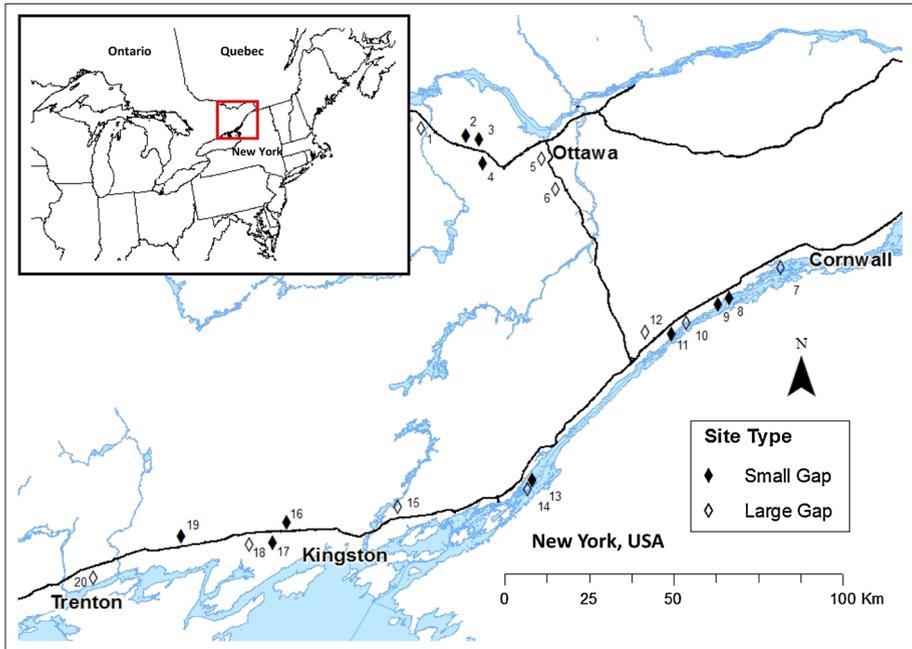
The purpose of this study was to determine whether road mortality is an important driver of bird declines in proximity to high-traffic roads, independent of any traffic noise effects. To do this, we sought to compare the road effect on forest birds in forest sites with similar traffic noise levels but with differing probabilities that birds would be killed crossing the road. We identified two site types for which road mortality should vary even though traffic volume does not. We inferred the mortality difference based on the assumption that forest birds are more likely to cross small forest gaps than they are to cross large forest gaps. When forest is directly across the road from a forest site, the road effectively creates a small gap, as compared to the case where there is an open area, e.g., a crop field across the road. Forest birds should be more likely to attempt to cross the road (and therefore have a greater risk of being killed by traffic) in the former situation than in the latter. A lower probability of forest birds crossing larger gaps has been documented using territorial call playbacks (Rail et al. 2011), mobbing call playbacks (Bélisle and Desrochers 2002; St. Clair 2003), simple observation (Grubb and Doherty 2011) and radio tracking (Norris and Stutchbury 2001; Fraser and Stutchbury 2004; Evans et al. 2008). In addition, road kill studies have suggested that collisions are more frequent where roads cut through forests (Erritzoe et al. 2003). Along a four-lane highway, Clevenger et al. (2003) found more dead birds where the road was separated by a forested median than where the highway had no median at all, a result they attributed to forested medians reducing the size of forest gap perceived by birds. Therefore, our two site types were forest sites next to high

traffic roads (a) where the road represented a small gap in the forest (hereafter “small-gap sites”) and (b) where there was no forest immediately across the road (hereafter “large-gap sites”). Road mortality should be higher in the former than the latter.

We predicted that, if mortality is a significant component of decline in forest birds with proximity to roads, then the negative road effect should become stronger over the breeding season at small-gap sites than at large-gap sites. The effects of traffic mortality should accumulate throughout the breeding season, especially at small-gap sites, assuming a dead bird’s territory remains empty for at least part of the season. Higher mortality at small-gap sites should lead to lower bird abundance at locations closest to the road, in small-gap sites than in large-gap sites, due to the accumulation of empty territories. In addition, the slope of the relationship between bird abundance and distance from the road should become stronger (increasingly positive, as birds become less abundant close to the road) throughout the breeding season, and this effect should be stronger at small-gap sites than at large-gap sites. Thus, if mortality is an important contributor to the negative road effect on birds, both a greater decrease in abundance closest to the road as well as a stronger increase in the negative road effect through the breeding season should occur at small-gap sites relative to large-gap sites, even if traffic volume (and traffic noise) is the same at the two site types.

## Materials and methods

Throughout the 2012 breeding season from the end of May to early July, we surveyed for birds along transects perpendicular to the road in forest sites next to high traffic roads.

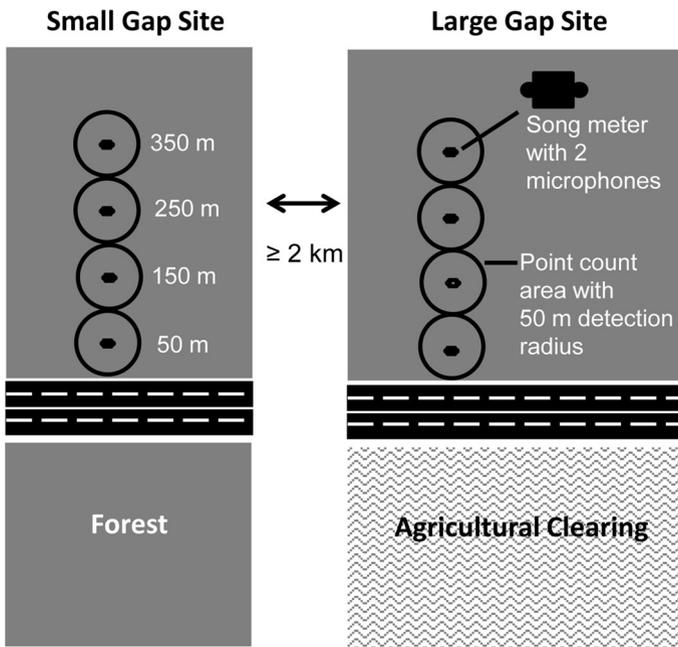


**Fig. 1** Distribution of the 20 forest sites adjacent to high traffic four-lane highways (10 small-gap sites and 10 large-gap sites) sampled across southern and eastern Ontario, Canada, with *inset* highlighting location of study area within eastern North America

These forest sites were selected such that the adjacent highway either represented (1) a small-gap in the forest (small-gap sites), or (2) had no forest immediately on the other side of it (large-gap sites). Simultaneous to the bird surveys, we collected audio recordings to test for potential issues with bird detectability and potential differences in traffic noise levels between site types. To document habitat structure, we also conducted vegetation surveys at the point count sites.

### Site selection

We selected 20 forest sites adjacent to high traffic four-lane highways in southern and eastern Ontario (Fig. 1). Ten of the sites were selected as small-gap sites, where there was forest immediately across the road from the forest patch, i.e., the road created a small-gap in the forest (75–110 m), and the other 10 sites were selected as large-gap sites, where there was no forest immediately across the road, but instead a large agricultural clearing such that the distance from the road-side perimeter of the sample site to the nearest forest patch (>1 ha in size) on the other side of the road ranged from 175 to 1,000 m (Figs. 2, 3; see Appendix 1). All forest sites were greater than 2 km apart to ensure spatial independence, based on reported home range estimates of birds in our study area (range: 0–10.4 ha; which translates to ~0–400 m straight line distances). All highways exceeded 10,000 annual average daily traffic (AADT) (Ministry of Transportation 2010). Sites were also selected to minimize differences in AADT [small-gap sites: mean = 23 880 ± 2 793.7 AADT (SE); large-gap sites: mean = 26 770 ± 2 851.6 AADT (SE)]. The difference in traffic volume between site types was not statistically significant ( $t = 0.69$ ,



**Fig. 2** Illustration of study design for each of the two types of sites surveyed. Point counts were carried out where Song Meters were located



**Fig. 3** Example aerial images of **a** a small-gap site and **b** a large-gap site. Circles represent 50-m radius detection areas within which point counts were conducted at points 50, 150, 250, and 350 m from the road-side edge of the forest

$df = 18, p = 0.50$ ). All forest patches were mixed woods, i.e., contained coniferous and deciduous trees.

#### Point count surveys

To ensure similar traffic levels during bird surveys, they were only performed on weekday mornings. Due to the time it took to access each site, only one site could be surveyed per day, so each site was surveyed only once during the breeding season between 30 May and 5 July 2012. To avoid confounding date of survey with geographic location, sites were surveyed in a random order, with the stipulation that we alternated surveys of small-gap and large-gap sites through the season, to avoid confounding date of survey with site type. The first author (J. Jack) performed all point counts for this study, thus avoiding variation among sites due to observer effects (Bibby et al. 2000). Point counts were positioned along a transect perpendicular to the road at 50, 150, 250, and 350 m from the road-side edge of the forest (Fig. 2). To avoid confounding time of point count with distance from the road, the order of point counts ran either from 50 to 350 m or from 350 to 50 m. Half of the small-gap sites were randomly selected to start at 350 m and the rest of the small-gap surveys started at 50 m. Each large-gap site survey was always performed in the same direction as the small-gap survey preceding it. We started the first point count 30 min before sunrise and each point count was for 10 min. All birds seen or heard were recorded (i.e., forest bird abundance = total number of individuals of any species seen or heard). To maximize detectability, point counts were not conducted during rainy or windy conditions ( $>4$  on the Beaufort scale). To avoid an effect of traffic noise on bird detectability, we only included birds heard within 50 m of the observer during the point count (see results for mixed woods forest in Pacifici et al. 2008).

## Audio recordings

The day before each point count survey, four automated digital recorders (SM2 and SM2 + Song Meters; Wildlife Acoustics Inc., Maynard, MA, USA) were set up at each point count location where birds were to be counted and programmed to simultaneously record sound on the morning of the survey from 4:30 to 9:00 am. The Song Meters were set to record using a 2 Hz high pass filter, a combined gain stage of 48 dB, and a sampling rate of 48 kHz. Each Song Meter was equipped with two omni-directional SMX-II microphones (with a sensitivity of  $-36 \pm 4$  dB), aimed parallel to the road in opposing directions (Fig. 2). The Song Meters were attached to small trees, 1.5 m above the ground. On three occasions, recordings were affected by wind, rain, or a traffic accident. For these three cases, replacement recordings were made for the full recording period of 4:30 to 9:00 am on weekdays in July and August.

Audio recordings were taken to: (1) verify bird identifications made during the point counts; (2) test (and correct if necessary) for effects of traffic noise on bird detectability; and (3) verify that traffic noise at the sites was not confounded with either site type (small-gap vs. large-gap sites) or date of survey.

To verify bird identifications made during the field surveys, recordings were checked by listening to the segments taken during the point count surveys.

To determine whether there was an effect of traffic noise on bird detectability, we documented birds singing during traffic-free periods recorded at a randomly selected subsample of the study sites (five small-gap and five large-gap sites) and tested whether the relationships with the in-person point count at those same locations was affected by the amount of traffic noise. We reasoned that if traffic noise had affected the observer's ability to detect birds, the difference between the birds documented from the traffic-free recordings and the birds documented during the in-person point counts would increase with traffic noise during the in-person point counts. To generate our traffic-free estimates of bird abundance, we used sections of each recording that had no traffic from the first 2 h of the morning i.e., the period with the lowest traffic and the most frequent birdsong (4:30–6:30 am). From these traffic-free segments, we stitched together randomly selected segments longer than 6 s into a 4 min audio file for each point count location. This was done for recordings at all four point count locations of the 10 sites, yielding a sample size of 40 points for analysis. We then identified all birds recorded singing during these traffic-free audio files. By listening to stereo recordings through headphones, it was possible to estimate the number of different individuals of the same species singing at each point based on a combination of cues including: timing of songs and overlap among individuals, the apparent direction to each bird, the loudness of each song, and differences in song quality/song type among individuals. To measure the traffic noise that occurred during the in-person point count, we calculated an index of traffic noise, as described in next paragraph, but using only the 10 min period of time during which each in-person point count occurred.

To verify that traffic noise at the sites was not confounded with either site type (small-gap vs. large-gap sites) or date of survey, we calculated an index of traffic noise using the sound recordings taken from 4:30 to 9:00 am at each site. First, we excluded from all recordings periods of noise generated by the observers as they approached and left each point count location. The shortest observer-free recording was 3.7 h. We then calculated our traffic noise index for every site using the last 3.7 h of observer-free audio recordings taken before 9:00 am. This ensured that the loudest period of traffic noise in the morning was included. To calculate the index of traffic noise, we measured the average power, in unweighted dB, of each second of sound across 0.3–2 kHz using Raven pro 1.4 (Cornell

Lab of Ornithology, Ithaca, NY, USA). We excluded sounds above this range because traffic noise tends to be loudest below 2 kHz (Warren et al. 2006), while sounds above this frequency are strongly influenced by birdsong which is predominantly above 2 kHz (Slabbekoorn and Ripmeester 2008). We excluded sounds below 0.3 kHz because they were affected by wind and recorder vibrations below 0.3 kHz, which may have varied among sites. Summers et al. (2011) found a high correlation between traffic noise across the full spectrum noise and noise in this frequency band (0.3–2 kHz), indicating that this index is a good relative index of total traffic noise.

To correct for differences in sensitivity among microphones, we used an Extech 407766 sound calibrator (Extech Instruments Corp., a subsidiary of FLIR Systems, Nashua, NH, USA), to measure the sensitivity of each microphone, and used the measurements to adjust the noise level measurements. In conducting these comparisons, we discovered that two Song Meters had issues with unreliable microphones, i.e., at least one of the two microphones on the Song Meter failed to produce a consistent measure in average power (dB) of the noise produced by the sound calibrator. For one Song Meter, both microphones were unreliable, therefore, for measuring traffic noise, we excluded data from this Song Meter (resulting in five missing data points—see Appendix 1). For the other Song Meter, one of the two microphones was unreliable; therefore, we only used the average power calculated from the functioning microphone.

#### Local site characteristics

We carried out vegetation surveys at each point count location between mid-July and mid-August 2012. Within the 50-m radius of each point count, we randomly located and surveyed a 100-m<sup>2</sup> circular plot, divided into quadrants defined by the cardinal directions. To survey trees, we used the point centre quarter method (Cottam and Curtis 1956). Within each quadrant, we determined the distance to the nearest tree (tree dispersion), and that tree's diameter at breast height. Within the four quadrants, we recorded the total number of shrubs, and estimated the average shrub height and average ground vegetation height. Woody plants with a stem <3 cm in diameter were classified as shrubs while non-woody plants were classified as ground cover. We also took measurements of canopy and ground cover at the centre and edge of the circular plot in each cardinal direction, by looking up (for canopy vegetation) and down (for ground vegetation) through an ocular tube (tissue roll with cross hairs). If vegetation crossed the field of view where the crosshairs intersected, we recorded a positive observation (Grushecky and Fajvan 1999). We then summed these observations and divided by five to generate coarse measures of percent cover of canopy and ground vegetation.

#### Statistical analyses

All raw data used in our analyses can be found in Jack (2013) but a summary is provided in Appendix 1.

#### *Potential confounding variables*

Given that birds were aurally detected, it was necessary to first investigate whether traffic noise influenced the observer's ability to detect breeding birds. To determine whether bird detectability declined with increasing traffic noise, we conducted a mixed effects linear

model using the difference in bird abundance between the measurements from the traffic-free recordings and the measurements from the in-person point counts as the response variable, traffic noise (measured as average power, dB) during the in-person point counts and distance from the road as continuous fixed effects and site (an id variable for each of the 20 locations as a random effect to reflect the fact that the four point count locations at each site were not independent of each other) as predictors. If traffic noise decreased the observer's ability to detect birds, we would expect to find that the difference between bird abundances estimated from the traffic-free recordings and the in-person point counts would be positively related to traffic noise.

Although we tried to control for potentially confounding variables during site selection, there were still some variables potentially affecting bird abundance that we were unable to completely control for. Therefore, to test the similarity of local site characteristics between the two site types, we ran linear mixed models with each of our vegetation measurements as a response variable: canopy cover (%; arcsine transformed), ground cover (%; arcsine transformed), ground cover height (cm; log transformed), number of shrubs (log transformed), shrub height (m; log transformed), average tree dispersion (m; inverse transformed), and average diameter of trees (cm; inverse transformed). For all of the models, site type (small-gap vs. large-gap), distance from the road (continuous) and their interaction were fixed effects and site (an id variable) as a random effect.

To test whether our results could be confounded by variation among sites or over time in traffic noise, we tested whether traffic noise varied with site type (small-gap vs. large-gap), or date of survey (Julian date), using a mixed effects linear model with the site's traffic noise (measured over 3.7 h) as the response variable, site as a random effect and distance from the road, site type, and date of survey as fixed effects. Note, 14 of 80 traffic recordings were excluded from the analysis; five traffic recordings due to the problems with unreliable microphones and an additional nine recordings due to wind, rain, or a traffic accident that prevented traffic noise estimates to be taken on the morning of the actual bird survey as explained above (see [Appendix 1](#)).

### *Tests of the traffic mortality hypothesis*

To test our prediction that the negative road effect would become stronger over time at small-gap sites than at large-gap sites, we conducted two analyses. First, we examined bird abundance measured at the point closest to the road (50 m from the road) at the two site types, expecting that the difference in abundance between small-gap and large-gap sites would be strongest close to the road. We conducted a generalized linear model using a Poisson distribution with bird abundance 50 m from the road at each site as the response variable, and site type (small-gap vs. large-gap), date of survey (Julian date) and their interaction as predictors. If mortality is an important component of the road effect on birds, then higher mortality at small-gap sites should lead to lower bird abundances at locations closest to the road, in small-gap sites than in large-gap sites, due to the accumulation of empty territories. Second, we examined the road effect (the slope of bird abundance vs. distance from the road) at each site, expecting the negative road effect to intensify (reflected in increasingly positive slope value measurements) throughout the breeding season more strongly at the small-gap sites than at the large-gap sites. To do this, we ran a regression with road effect (the slope) as the response, and site type, date of survey and their interaction as predictors. If mortality is an important contributor to the negative road effect on birds, we would expect to find a stronger increase in the negative road effect through the breeding season, and this effect should be stronger at small-gap sites than at

large-gap sites. To investigate this, we also conducted separate regressions of the road effect on date of survey for small-gap and large-gap sites.

We did not perform analysis on individual species due to low sample sizes. We performed analyses using R v 3.0.1 (R Development Core Team 2013). Mixed effects models were run in R using the nlme package (version 3.1-110; Pinheiro et al. 2013). Results are presented as means  $\pm$  standard errors (S.E.).

## Results

Altogether, we detected 45 bird species and found, on average, 11 species per forest site. There was rarely more than one individual of each species within the 50 m point count radius. As a result, bird abundance was highly correlated with species richness ( $r = 0.87$ ,  $p < 0.001$ ; Appendix 1). On average we observed five individual birds and four bird species during each point count (range = 1–12 individuals; 1–8 species).

There was no evidence of an effect of traffic noise on bird detectability in the data ( $\beta = 0.0329 \pm 0.0873$ ,  $F_{1, 27} = 0.292$ ,  $p = 0.594$ ; see Appendix 2), nor an effect of distance from the road ( $\beta = -0.0003 \pm 0.0047$ ,  $F_{1, 27} = 0.004$ ,  $p = 0.951$ ), indicating traffic noise did not interfere with the observer's ability to detect breeding birds. The local site characteristics that we measured were not significantly different between site types, with the exception of the average tree dispersion, which was 1 m greater at the large gap sites than small-gap sites ( $F_{1, 18} = 6.645$ ,  $p = 0.019$ ; Table 1). Mean traffic noise at the small-gap and large-gap sites were nearly identical ( $89.3 \pm 1.04$  and  $88.4 \pm 1.09$  dB respectively), and there was no significant difference between site types ( $F_{1, 14} = 0.058$ ,  $p = 0.813$ ; Table 1). As expected, traffic noise decreased with distance from the road ( $\beta = -0.0360 \pm 0.0030$ ,  $F_{1, 48} = 146.557$ ,  $p < 0.0001$ ; Table 1). Traffic noise had a weak non-significant negative relationship with date of survey ( $\beta = -0.1252 \pm 0.0898$ ,  $F_{1, 14} = 2.309$ ,  $p = 0.151$ ; see Appendix 3). This made our tests of the traffic mortality hypothesis conservative, as we predicted an increasing road effect with date of survey at the small-gap sites.

The first test of the traffic mortality hypothesis, using the abundance data collected 50 m from the roads, weakly supported our prediction. Bird abundance close to the road was lower at the small-gap sites surveyed later in the season, and this was not the case for the large-gap sites (Fig. 4); however the effect was not statistically significant (interaction between site type and date of survey:  $z = -1.8$ ,  $p = 0.068$ ). There was also no significant difference in bird abundance between small-gap ( $4.2 \pm 0.70$ ) and large-gap ( $4.4 \pm 0.66$ ) sites ( $z = 1.8$ ,  $p = 0.071$ ).

The second test of the traffic mortality hypothesis, based on the slope of abundance versus distance from the road, i.e., the negative road effect itself, supported our prediction. The interaction between site type and date of survey was statistically significant ( $F_{1, 16} = 6.271$ ,  $p = 0.023$ ); the negative road effect on bird abundance became stronger (as shown by more positive slope values) over the breeding season at small-gap sites ( $\beta = 0.0008 \pm 0.0001$ ,  $F_{1, 8} = 35.219$ ,  $p < 0.001$ ) but not at large-gaps sites ( $\beta = -0.0003 \pm 0.0004$ ,  $F_{1, 8} = 0.456$ ,  $p = 0.519$ ) (Fig. 5).

Since there was a significant difference in the average tree dispersion between site types, we included this variable and its interaction with site type in a multiple regression in the second analysis, to determine whether average tree dispersion confounded our results. The interaction between the average tree dispersion and site type was not statistically significant ( $F_{1, 14} = 0.034$ ,  $p = 0.857$ ), while the interaction between site type and date of

**Table 1** Mean and standard error (SE) for measurements of vegetation structure and traffic noise recorded at the two site types (small-gap and large gap), along with model results of fixed effects from testing whether either vegetation structure or traffic noise differed between site types or with distance from the road

Measurements	Mean ( $\pm$ SE)		Fixed effect	Model results		
	Small-gap	Large-gap		df	<i>F</i>	<i>p</i>
Canopy cover (%)	87.0 (3.83)	81.0 (3.65)	Site type	1.18	2.87	0.11
			Distance from road	1.58	0.48	0.49
Ground cover (%)	57.5 (4.00)	63.3 (4.91)	Site type	1.18	1.63	0.22
			Distance from road	1.58	0.002	0.97
Ground cover height (cm)	30.6 (3.27)	33.5 (2.48)	Site type	1.18	0.79	0.39
			Distance from road	1.58	0.0005	0.98
Number of shrubs	66.9 (6.27)	96.4 (15.30)	Site type	1.18	0.13	0.73
			Distance from road	1.58	0.07	0.79
Shrub height (m)	1.1 (0.06)	1.5 (0.28)	Site type	1.18	1.56	0.23
			Distance from road	1.58	2.23	0.14
Average tree dispersion (m)	2.1 (0.15)	3.1 (0.40)	Site type	1.18	6.65	0.02
			Distance from road	1.58	1.31	0.26
Average diameter of trees (cm)	22.9 (9.86)	15.8 (4.93)	Site type	1.18	0.84	0.37
			Distance from road	1.58	0.07	0.79
Traffic noise (dB) <sup>a</sup>	89.3 (1.04)	88.4 (1.09)	Site type	1.14	0.06	0.81
			Distance from road	1.48	146.56	<0.0001
			Date of survey	1.48	2.31	0.15

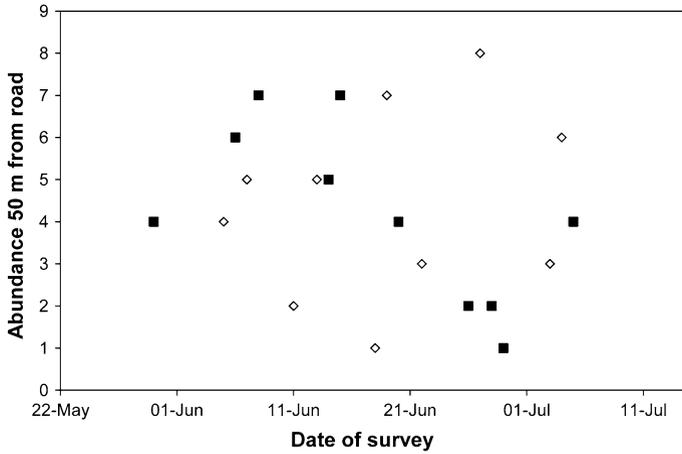
Model results are from linear mixed models with each measurement as a response, site type, distance from the road and their interaction (vegetation structure measurements only) as fixed effects, and site (a dummy variable for each of the 20 locations) as a random effect. Note, date of survey (as a fixed effect) was also included in the model for traffic noise. Means for traffic noise include recordings from the four distance from road categories at each site. Note, the interaction between site type and distance from the road was not statistically significant in any model ( $p > 0.05$ )

<sup>a</sup> Fourteen of 80 traffic recordings were excluded from the analysis due to wind, rain, or a traffic accident that prevented estimates to be taken on the morning of the actual bird survey and/or due to unreliable microphones

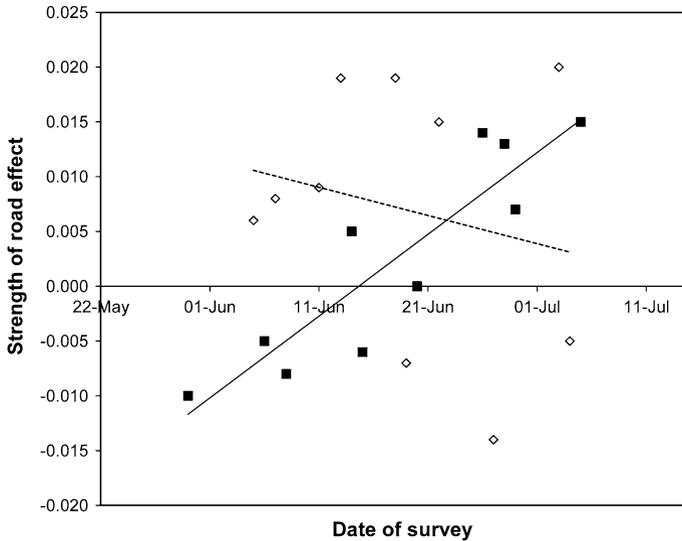
survey remained statistically significant ( $F_{1, 14} = 5.016$ ,  $p = 0.042$ ), and there was no significant relationship between the slope of abundance and the average tree dispersion ( $\beta = -0.0003 \pm 0.0003$ ,  $F_{1, 14} = 0.494$ ,  $p = 0.494$ ). Furthermore, there were no significant relationships between the slope and the average tree dispersion at small-gap sites ( $\beta = 0.0158 \pm 0.0113$ ,  $F_{1, 8} = 1.970$ ,  $p = 0.198$ ) or at large-gap sites ( $\beta = 0.0007 \pm 0.0030$ ,  $F_{1, 8} = 0.051$ ,  $p = 0.827$ ) in separate regressions. Thus, tree dispersion did not confound our results.

## Discussion

This study provides evidence that traffic mortality is an important component of the negative effect of roads on bird abundance. We predicted that, if mortality was important,



**Fig. 4** Bird abundance 50 m from the road at small-gap (*Black square*) and large-gap (*Lozenge*) sites versus date of survey. Bird abundance was lower at the small-gap sites surveyed later in the season, and this was not the case for the large-gap sites (interaction between date of survey and site type  $z = -1.8$ ,  $p = 0.068$ )



**Fig. 5** The strength of the negative road effect increased through the season at small-gap sites (*Black square*) ( $\beta = 0.0008 \pm 0.0001$ ,  $F_{1, 8} = 35.219$ ,  $p < 0.001$ ,  $R^2 = 0.82$ ), but not at large-gap sites (*Lozenge*) ( $\beta = -0.0003 \pm 0.0004$ ,  $F_{1, 8} = 0.456$ ,  $p = 0.519$ ,  $R^2 = 0.05$ ), where road effect is the slope of the relationship between bird abundance and distance from the road

the negative road effect would become stronger at small-gap sites than at large-gap sites through the breeding season, on the assumption that birds are more likely to be hit by vehicles at small-gap sites than at large-gap sites. This prediction was supported, particularly clearly in the second analysis in which the slope of the relationship between

abundance and distance from the road (the negative road effect) became stronger as the season progressed at the small-gap sites but not at the large-gap sites. Note, a post hoc analysis verified that the interaction effect between site type and date of survey in our second analysis was not due to a stronger increase in abundance far from the road in small-gap sites when examining bird abundance 350 m from the road at each site (interaction between site type and date of survey was not significant:  $z = 1.6$ ,  $p = 0.110$ ).

Two potential shortcomings of our study are that we (1) did not have road mortality data, and (2) did not measure bird abundance at each study site multiple times over the breeding season. We discuss each of these in turn. First, though it would have been useful to conduct road kill surveys testing the assumption that birds are more likely to be hit by vehicles where there are small gaps in the forest than where there are large gaps in the forest, it was not possible to incorporate this component into the study. We could not perform such surveys because we could not obtain legal permission to stop a vehicle or to enter the high-traffic roadways on foot or other non-motorized means (e.g., bicycle; see Eberhardt 2009), due to the danger associated with high traffic volumes and speeds. We considered previous gap-crossing and road kill studies (e.g., Clevenger et al. 2003; Erritzoe et al. 2003; St. Clair 2003; Evans et al. 2008; Rail et al. 2011) to be sufficient support for our assumption that birds are more likely to attempt to cross roads at sites where the road represents a small-gap in the forest than at sites with no forest immediately across the road. We then focussed our tests on an associated population-level prediction arising from the mortality hypothesis. The second limitation of our study was that each site was surveyed only once during the breeding season because there was not enough time to survey multiple sites per day. Here we chose, rather, to study different sites at different times, to ensure a reasonable sample size of sites ( $n = 20$ ). Nonetheless, we were able to make sure that other variables were not confounded with date of survey, by alternating site type, geographic region and direction of survey. Despite this limitation, our results are particularly significant, considering that, we were only able to sample 20 sites and with only one survey date at each site. Even in our first analysis, using only the data from the point counts nearest the roads (50 m from the roads), the relationship was in the predicted direction (Fig. 4). The second analysis, using all the data, showed clearly that the negative road effect strengthened over the breeding season at small-gap sites but not at large-gap sites (Fig. 5), despite a slight decrease in traffic noise (and thus possibly traffic volume) over the breeding season (Appendix 3). Therefore, we suggest our results are robust and do support the notion that traffic mortality is an important component of the negative road effect, and that mortality should be considered in future studies on the effects of roads on birds.

Overall, our results are consistent with an effect of traffic mortality on bird abundance and would not be predicted by other potential mechanisms, especially traffic noise, that might cause negative effects of roads on bird populations. We selected sites such that traffic volume was similar between the small-gap and large-gap sites. This allowed us to vary traffic mortality (i.e., higher mortality in small-gap sites than large-gap sites) while controlling for other road effects that co-vary with traffic volume, including traffic noise, visual disturbances, and chemical pollution. To be confident that traffic noise did not bias our data, we verified that our ability to detect birds was not influenced by traffic noise (Appendix 2). We also verified that traffic noise was similar between site types (Table 1) and that it did not increase over the course of the breeding season (it actually decreased) (Appendix 3). Furthermore, a post hoc analysis verified that differences in traffic noise between sites did not explain difference in the strength of the road effect between sites i.e., the negative road effect did not strengthen (the slope of abundance vs. distance from the

road did not become more positive) with increasing traffic noise ( $\beta = -0.0012 \pm 0.0007$ ,  $F_{1, 18} = 3.340$ ,  $p = 0.080$ ; Appendix 4). Consequently, we suggest the differences we observed between small-gap and large-gap sites are consistent with an effect of traffic mortality, and cannot be explained by other road effects that co-vary with traffic volume.

Our results likely did not arise from habitat differences between site types. We carefully chose sites comparable in habitat structure (Table 1), within the constraints of site availability. While the average tree dispersion was 1 m greater at the large gap sites than small-gap sites (Table 1), including this variable and its interaction with site type in the multiple regression for the second analysis did not qualitatively change the results. The interaction between the average tree dispersion and site type was not statistically significant and there were no significant relationships between the slope and the average tree dispersion at small-gap sites or at large-gap sites, suggesting that differences in the average tree dispersion between site types did not confound our results. Given our study design, however, the large-gap sites were situated in landscapes with a higher ratio of agricultural land to forest than the landscapes surrounding the small-gap sites. If nest predators are more abundant along edges in landscapes with more forest, then nest predation, rather than road mortality, might explain the observed pattern of diminishing bird abundance near the edge at the small-gap sites. However, a review of studies on nest predators suggests the opposite pattern is true; that nest predators are actually more abundant in agricultural landscapes than in forest landscapes (see Chalfoun et al. 2002). Therefore it is unlikely that our results are confounded by effects of nest predation. The same can be said of any negative effects of agricultural practices (e.g., pesticide use) on forest birds, as these would be more prevalent in the landscapes surrounding the large-gap sites than the small-gap sites.

An interesting and unexpected pattern in the data is that the road effect was positive (indicated by negative slope values showing higher bird abundance closer to roads than farther away) at the small-gap sites surveyed early in the season (Fig. 5; Appendix 5). This may be explained by birds being attracted to roadside territories, due to higher primary productivity (denser vegetation) and associated insect abundance, similar to that observed in forest gaps. For example, two studies of regenerating clearcuts (Strelke and Dickson 1980; Hansson 1983) found forest bird densities to be higher at the forest/clearcut edge than in the forest interior. However, we acknowledge that this explanation is highly speculative, since studies comparing interior and edge habitats created by powerline corridors (Kroodsmma 1982; Small and Hunter 1989) and small roads (Rich et al. 1994) did not find higher bird densities at the forest edges. We hypothesize that this pattern is not found at the large-gap sites because the benefits of edge habitat may be outweighed by a higher perceived risk of predation, due to a greater abundance of predators, such as the American Crow (*Corvus brachyrhynchos*) (Bayne and Hobson 1997), near open agricultural areas.

Past studies of the negative road effect on birds often attributed the effect to traffic noise, dismissing the role of traffic mortality. For example, Reijnen and Foppen (2006) suggested that traffic mortality may not affect recruitment rates for bird populations because many of the road-killed birds found were juveniles (Erritzoe et al. 2003), an age class with a naturally high mortality rate. However, this argument depends on the assumption that mortality is compensatory, or in other words that other forms of mortality are reduced when traffic mortality is increased, an assumption that has yet to be tested. Though our study did not directly measure traffic mortality, it does indirectly add to the growing body of evidence that adult birds are being killed on roads, because it suggests a decreasing

number of singing adult birds close to the road throughout the breeding season at sites where risk of collision was high. This finding is corroborated by studies that reported the age of road-killed birds, showing that there were substantial numbers of adults killed and, in some cases, more adults killed than juveniles (Erritzoe et al. 2003). Studies examining decreased rates of fledging for birds in nests near roads (Kuitunen et al. 2003; Holm and Laursen 2011) further emphasize the implications of adults being killed. Loss of an adult bird not only has a direct effect on the population, it also means a reduction in nestling survival for that year. Thus, the contribution of traffic mortality merits further consideration when drawing inferences from past and future studies that examine the negative effects of roads on bird populations.

Although there are some examples of bird populations adapting to road mortality, for most bird species, habitats next to roads are likely acting as population sinks. Over a 30-year study period, Brown and Bomberger Brown (2013) showed that cliff swallows (*Petrochelidon pyrrhonota*) nesting colonially on culverts and bridges were hit on the road less frequently, and the population increased over time. Over the same period the average wing length of the swallows had shortened, likely increasing their manoeuvrability in the face of oncoming cars. A study in western France found that birds sitting on roads and roadsides initiate flight sooner on roads with higher speed limits, which the authors interpreted as a learned behaviour (Legagneux and Ducatez 2013). Using data from 11 species of European birds, Husby and Husby (2014) found that on larger roads and at higher vehicle speeds, birds were more likely to fly away from the road than to cross it, and that species with a larger relative brain size flew away from the road more often than species with a small brain size. Husby and Husby (2014) suggest their results provide further support for the notion that behavioral adjustments to anthropogenic changes can be flexible and that the ability of different species to adjust to such changes may be determined in part by relative brain size. Though these findings might suggest that some species adapt rapidly to roads, not all bird species do. Many birds are clearly not avoiding road mortality, as documented by recent road kill studies (Eberhardt 2009; Guinard et al. 2012). Birds in Banff National Park were found to be more likely to cross highway gaps than they were to cross rivers creating gaps of similar width (St. Clair 2003), suggesting that those species have not identified the risks associated with crossing roads. Gray jays in Algonquin Park were found to establish territories in roadside and non-roadside habitat with equal preference, despite the lower survivorship on territories adjacent to roads (Norris et al. 2013). Similarly, overall mortality of Florida scrub jays was found to exceed the number of yearlings produced in roadside territories (Mumme et al. 2000), despite the superior foraging opportunities on those territories and the apparent ability of older birds to avoid vehicle collisions (Mumme et al. 2000; Morgan et al. 2010). In the case of this species, experience with roads and an ability to avoid collisions did not appear to be passed on from parents to their young (Mumme et al. 2000). These examples suggest that many birds that tolerate or are even attracted to habitats near roads are able to adequately identify or avoid the risks of vehicle collision. For these birds, roadside habitats may be acting as population sinks or, in some cases, ecological traps.

It would be erroneous to infer from this study that removing forest on one side of the road would benefit forest birds by reducing road mortality of birds residing on the forested side of the road. Habitat loss is generally acknowledged to be the most important cause of current species declines (Kerr and Deguise 2004). Therefore, it is highly unlikely that reductions in road mortality would outweigh population reductions due to lost habitat on the other side of the road. Put simply, low quality habitat is better

than no habitat. The only condition under which removing forest on one side of the road might produce a positive effect on a population would be if forest bisected by a road were an “attractive sink” (Battin 2004). However, this has not been demonstrated. Even if habitat bisected by a road were demonstrated to be an ecological trap for a species of conservation concern, the net effect on the population of removing habitat might still be negative.

## Conclusions

Our results support the prediction that where there is a higher risk of traffic collision, there is a stronger decrease in the number of forest birds close to roads over the course of the breeding season. These results imply that mitigation of road effects on birds should include mitigation for traffic mortality. The data suggest that mortality rates of forest birds are higher on roads that bisect forest than on roads where there is open land on the other side of the road. New roads, which tend to be built on undeveloped land due to the lower cost, may have particularly detrimental effects on birds as they are killed while attempting to cross the small gaps created by these roads. In such situations, road mitigation measures should include mitigation for mortality. Measures aimed only at mitigating traffic noise, such as quieter vehicles or road surfaces, might improve perceived habitat quality for birds without discouraging them from flying at traffic level. If such measures encouraged more birds to nest near roads, the measures themselves could unintentionally increase traffic mortality. Consequently, a failure to address traffic mortality as an important component of negative road effects could mean that vulnerable bird communities might not be protected by the mitigation measures put in place. However, mitigation for traffic noise and traffic mortality are not necessarily mutually exclusive. For example, sound barriers that also encourage birds to cross roads above the height of traffic could serve both purposes.

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## Appendix 1

See Table 2.

**Table 2** Summary table of site-specific information for both site types (small-gap vs. large-gap) arranged by date of survey

Date of survey	Site	AADT	Distance to forest >1 ha (m)	Direction of survey	Distance from road (m)											
					Bird abundance		Species richness		Traffic noise (dB)							
					350	250	150	50	350	250	150	50	350	250	150	50
<i>Large-gap sites</i>																
June 5	12	18,600	174	Away	7	7	10	4	6	6	7	4	86.3	90.4	92.6	96.4
June 7	10	17,100	290	Away	8	3	4	5	6	3	4	4	83.0	–	90.4	95.6
June 11	1	14,600	560	Toward	5	4	4	2	5	4	4	2	82.2	83.7	87.4	92.1
June 13	15	34,400	530	Toward	11	7	6	5	5	6	5	5	80.8	82.6	89.9	91.1
June 18	20	39,200	1,000	Toward	7	3	2	1	6	3	2	1	78.9	90.7	93.2	99.3
June 19 <sup>a</sup>	7	19,600	700	Away	4	5	3	7	4	5	3	4	81.7	86.6	–	97.9
June 22	6	23,800	630	Away	8	9	9	3	6	6	6	3	82.0	83.6	86.0	91.5
June 27	18	35,100	550	Away	6	4	12	8	3	4	8	6	92.2	94.8	94.7	97.7
July 3	14	30,200	220	Toward	9	6	4	3	7	5	3	3	82.3	77.4	77.6	93.2
July 4	5	35,100	895	Toward	4	5	4	6	4	4	4	6	81.5	83.2	89.4	102.0
<i>Small-gap sites</i>																
May 30	9	17,200	95	Away	1	3	4	4	1	3	3	4	89.4	90.9	92.0	95.5
June 6	11	17,000	100	Away	4	7	6	6	4	7	6	4	85.5	–	90.9	96.6
June 8	3	15,700	90	Toward	4	9	8	7	4	6	7	6	82.3	82.8	83.6	91.2
June 14	17	35,100	80	Toward	6	5	3	5	4	5	2	4	91.4	93.6	96.1	99.1
June 15	16	35,300	95	Toward	6	3	6	7	6	3	6	4	87.3	90.7	93.2	99.3
June 20	8	17,200	90	Away	4	5	5	4	3	3	5	4	83.4	86.7	89.5	94.7
June 26 <sup>a</sup>	4	20,400	85	Away	6	5	3	2	6	5	3	2	84.0	86.7	–	97.7

**Table 2** continued

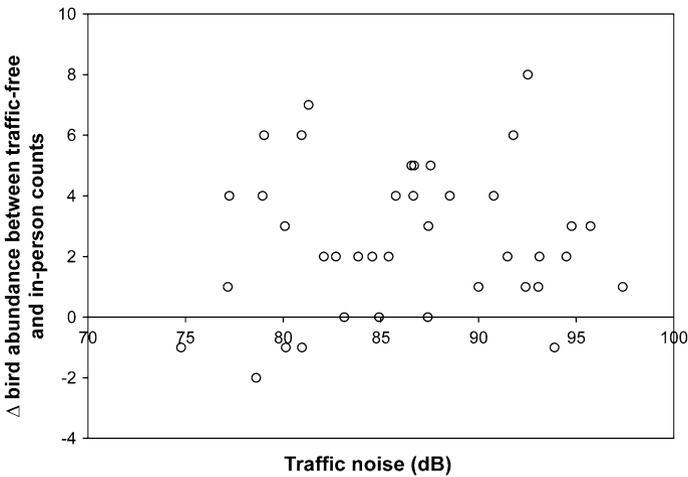
Date of survey	Site	AADT	Distance to forest >1 ha (m)	Direction of survey	Distance from road (m)											
					350	250	150	50	350	250	150	50	350	250	150	50
June 28	19	35,000	75	Away	5	7	3	2	4	6	2	2	85.1	88.2	92.0	91.7
June 29 <sup>a</sup>	13	30,200	110	Toward	3	4	3	1	3	3	3	1	78.4	84.6	–	98.7
July 5	2	15,700	80	Toward	8	7	4	4	5	5	4	4	75.3	78.0	82.1	90.0

Information includes traffic volume [Average annual daily traffic (AADT), obtained from Ministry of Transportation (2010)], distance to the closest patch of forest >1 ha across the road, direction of survey relative to road, bird abundance, species richness and morning traffic noise (average power) documented at all four distances from the road

<sup>a</sup> On three occasions, recordings were affected by either wind, rain, or a traffic accident. For these three cases, site estimates of traffic noise were derived from full-morning recordings (4:30–9:00 am) made on July 31 (site 7), August 2 (site 13) and August 16 (site 4). All missing estimates of traffic noise (i.e., five instances) were due to one Song Meter that had unreliable microphones; therefore these estimates were not included in analyses

**Appendix 2**

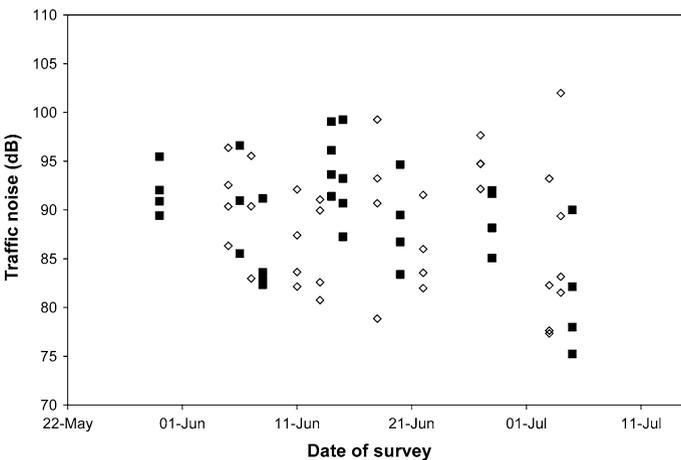
See Fig. 6.



**Fig. 6** Differences in bird abundance measured from traffic-free recordings (unlimited radius) and in-person point counts (50-m radius) vs. traffic noise (measured as average power) during the 10-min in-person point counts. Note traffic noise for one of the 40 locations could not be used due to an unreliable microphone

**Appendix 3**

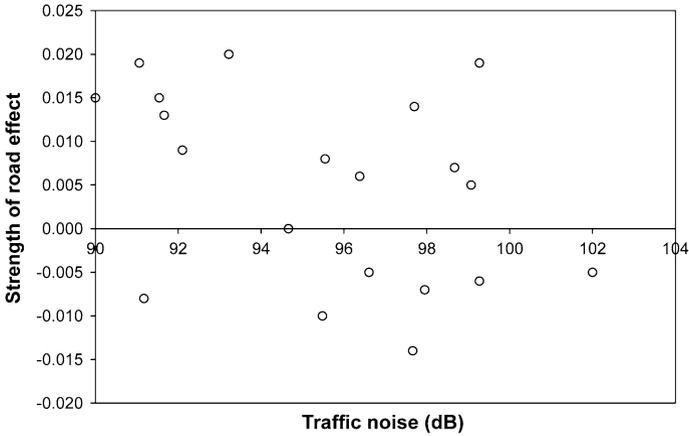
See Fig. 7.



**Fig. 7** Traffic noise (measured in average power) recorded throughout the morning of each bird survey at all four distances from the road at small-gap (*Black square*) and large-gap (*Lozenge*) sites versus data of survey. Traffic noise measurements are missing from point count locations 250 m from the road at the two sites surveyed on June 6 and 7 due to unreliable microphones, and from three sites where the morning’s recordings were not completed on the date of survey due to the recordings being affected by wind, rain, or a traffic accident (see Appendix 1)

## Appendix 4

See Fig. 8.



**Fig. 8** The negative road effect did not strengthen with increasing traffic noise ( $\beta = -0.0012 \pm 0.0007$ ,  $F_{1, 18} = 3.340$ ,  $p = 0.080$ ,  $R^2 = 0.16$ ), where road effect is the slope of the relationship between bird abundance and distance from the road and traffic noise was mean power in dB 50 m from the road

## Appendix 5

See Table 3.

**Table 3** Parameter estimates [regression coefficient ( $\beta$ ) with standard errors (SE)] and  $R^2$  values from simple linear regressions of bird abundance on distance from the road at each site

Site	Date of survey	Linear regression analysis		
		$\beta$	SE	$R^2$
<i>Large-gap sites</i>				
12	05-Jun	0.006	0.013	0.100
10	07-Jun	0.008	0.010	0.229
1	11-Jun	0.009	0.003	0.853
15	13-Jun	0.019	0.005	0.870
20	18-Jun	0.019	0.005	0.870
7	19-Jun	-0.007	0.008	0.280
6	22-Jun	0.015	0.012	0.455
18	27-Jun	-0.014	0.016	0.280
14	03-Jul	0.020	0.003	0.952
5	04-Jul	-0.005	0.004	0.455

**Table 3** continued

Site	Date of survey	Linear regression analysis		
		$\beta$	SE	R <sup>2</sup>
<i>Small-gap sites</i>				
9	30-May	−0.010	0.003	0.833
11	06-Jun	−0.005	0.006	0.263
3	08-Jun	−0.008	0.010	0.229
17	14-Jun	0.005	0.006	0.263
16	15-Jun	−0.006	0.008	0.200
8	20-Jun	0.000	0.003	0.000
4	26-Jun	0.014	0.001	0.980
19	28-Jun	0.013	0.008	0.573
13	29-Jun	0.007	0.005	0.516
2	05-Jul	0.015	0.004	0.882

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