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# Advancing avian road ecology research through systematic review

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ABSTRACT

Linear Transport Infrastructure (LTI) often has important impacts on wildlife and landscape processes. Two reviews provided early insight and nuance into LTI impacts on birdlife but were published when road ecology experiments were still being developed. Four factors were identified to impact birds near roads: habitat quality, species-specific traits, traffic noise, and infrastructure. Although early work identified traffic noise as the main selective force, recent studies lend more support to habitat quality and infrastructure. However, this literature was deemed to possess low inferential strength given inconsistent data collection, inadequate management of confounding variables, limited inclusion of vehicle-free environments, short-term experimental timeframes, and use of methodologies susceptible to bias. A new experimental framework for better evaluation of the impact of roads on birdlife is proposed. This would facilitate the construction of species and/or community profiles useful in the design, construction, and management of transport networks.

## 1. Rationale

**Road ecology** is a relatively recent hybrid field that brings together insights from a range of disciplines (van der Ree et al. 2015). This important field received limited attention from land-use planners and resource managers who tended to focus narrowly on the roadbed and its immediate footprint, whereas ecologists mainly focussed on impacts on larger animals (Forman and Deblinger 2000; Forman et al., 2002; Wilson et al., 2007; Kociolek et al. 2015). However, the field has matured rapidly with a significant expansion of wildlife crossing structures (e.g., ecoducts, underpasses, land bridges, etc.) designed to mitigate the negative impacts of roads. Indeed, these are essential for sustainable transport planning and management (Forman et al., 2002).

Two important reviews have formed the basis of our understanding of the negative and positive influences of **linear transport infrastructure** (LTI) on smaller animals, specifically birds (Kociolek et al., 2011; Morelli et al., 2014). These were, however, published around a decade ago when road ecology experimental approaches were still being developed (Roedenbeck et al. 2007; Fahrig and Rytwinski, 2009; Benítez-López et al., 2010). While these papers have contributed significantly to our understanding of the LTI impact on birds, more recent research has offered greater insight and nuance into road impacts on birds within the 'road effect zone' (see Johnson et al. 2017). Therefore, an up-to-date review and synthesis of the latest research are necessary to establish how the field has responded and evolved in recent years.

To explore the latest avian road ecology research, the present study will apply a systematic quantitative literature review, modified to incorporate the De Vos and El-Geneidy (2022) review framework. This will be used to synthesise and articulate the current state-of-

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the-art, in the context of its limitations and biases, which will provide useful direction to future research needs. Additionally, a new conceptual model suitable for future road ecology experiments will be developed to promote the application of uniform and consistent study designs that will improve the inferential strength of the field. This will be guided by the question: 'What does recent avian road ecology research tell us of the direct impacts of roads on bird populations, and how certain are we of the evidence?'.

## 2. Background

LTI (highways, paved roads, unsealed roads, and railways) are integral to the transport network, enabling the movement of people and the safe distribution of goods and services. However, LTI fragments and degrades the landscape well beyond the physical features of the surfaces (the 'road effect zone') (Forman and Deblinger, 2000; van der Ree et al., 2015). The associated changes and disturbances may also result in significant consequences to wildlife within these affected landscapes, especially where these intersect natural areas (Reijnen and Foppen, 2006; Jones and Pickvance, 2013; Pell and Jones, 2015). Indeed, habitat fragmentation and degradation, in general, are recognised as the greatest threats to species survival worldwide with LTI being a major contributor (Ford et al., 2000; Benítez-López et al., 2010; Evans, 2014; Selva et al., 2015; Da Silva et al., 2017).

Two systematic reviews, Kociolek et al. (2011) and Morelli et al. (2014), provided a comprehensive foundation for avian road ecology research over the last decade. These highlighted several factors that influence bird's nearby roads:

- **road traffic** – populations may be directly impacted by vehicle-wildlife collisions, or indirectly impacted through the generation of traffic noise and pollution;
- **roadside plantings and management** – regimens directly influence the occupation of road environments by birds (e.g., foraging and nesting). Similarly, management techniques may indirectly impact local populations (e.g., poisoning, fire, etc.);
- **physical barriers** – fencing, traffic barriers, ditches, and embankments may impede wildlife movement between habitat patches;
- **artificial light** – streetlamps may extend day-time foraging, disrupt bird migration patterns, and attract nocturnal birds; and,
- **road infrastructure** – powerlines, electrical wires, fencing, traffic barriers, etc., may provide areas for perching and foraging.

Additionally, several mitigation measures to address road impacts and promote planning and conservation were proposed: **vehicle-wildlife collisions** could be reduced through temporal adjustments to traffic flows to reduce traffic volumes; **traffic noise** may be lessened by the adoption of new tyre and asphalt designs to reduce noise generation; impacts of **artificial light** on foraging, migration and breeding patterns may be reduced through the installation of green lights; and, **road verges** can be better maintained to enhance their value as ecological corridors (Kociolek et al., 2011; Morelli et al., 2014).

Like Fahrig and Rytwinski (2009), both Kociolek et al. (2011) and Morelli et al. (2014) suggested that vehicle-caused mortality and traffic noise represented the greatest threat to population persistence and recommended this as a priority for mitigation. Although

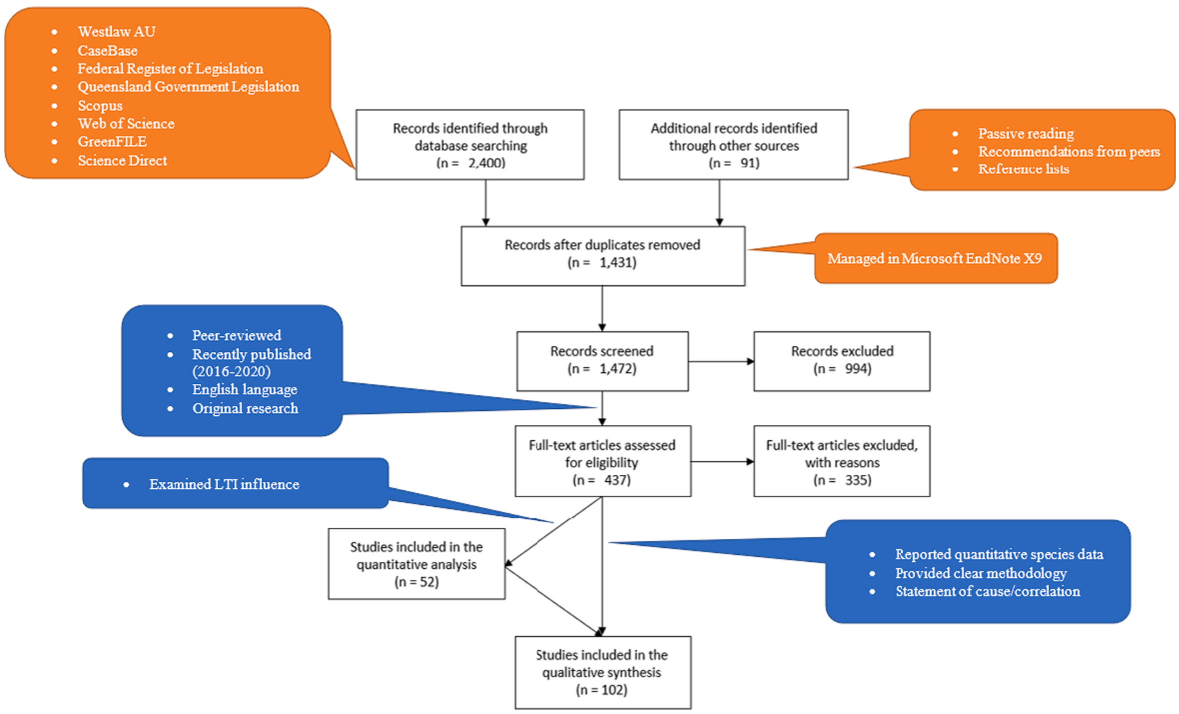


**Fig. 1.** Preferred Reporting Items for Systematic Review and Meta-Analysis (Prisma-P) flow-chart.

these reviews provided great insight into the field at this time, their conclusions were founded on studies regarded to be of low inferential strength and susceptible to the generalities of assumed knowledge (Roedenbeck et al. 2007; Fahrig and Rytwinski, 2009; Benítez-López et al., 2010).

First, while bird richness and abundance do increase with distance from the road, several LTI elements suspected to influence this (e.g., traffic noise, habitat quality, light intensity, etc.) also change over the same space and are therefore confounded (Orlowski, 2008; Rytwinski and Fahrig, 2012; Read et al., 2015; Betleja et al., 2020). Few studies have accounted for this (see Ewers and Didham, 2006; Fahrig and Rytwinski, 2009; Tremblay and St. Clair, 2009; Summers et al., 2011).

Second, limited research suggests birds may be deterred by gaps (e.g., unsealed roads, forest clearings, plantations, rivers, etc.) within otherwise suitable habitat, rather than solely road infrastructure (A. Desrochers and Hannon, 1997; St Clair, 2003; Lees and Peres, 2009; Summers et al., 2011). Yet very few studies have included non-vehicle gap comparisons in their design (but see Kociolek et al. 2011). Third, it is difficult to argue that LTI has positive impacts when the few species that do benefit, typically raptors, scavengers, and generalists, ultimately exacerbate the **road effect zone** for most other species, small birds in particular (Desrochers and Hannon, 1997; Ford et al. 2000; Orlowski, 2008; Lees and Peres, 2009; Montague-Drake et al., 2011; Johnson et al., 2017).

## 3. Methods

A Systematic Quantitative Literature Review (SQLR) was performed following the Pickering and Byrne (2014) model and PRISMA-P guideline (Moher et al., 2009). This was further modified to incorporate the De Vos and El-Geneidy (2022) review framework to ensure new contributions to the field are clearly articulated. This needs to be by way of: A) a conceptual model; B) future research needs; and or, C) policy implications. The former two comprise the primary focus of this review.

An exhaustive search of the literature was carried out between February 2020 and February 2021. A search period of Jan 2016 – Feb 2021 ensured only the most recent information was captured. Research before this period has already been comprehensively addressed in four previous works (Fahrig and Rytwinski, 2009; Kociolek et al., 2011; Rytwinski and Fahrig, 2012; van der Ree et al., 2015).

English-language, peer-reviewed research articles were obtained through a search of eight journal databases (see Fig. 1). Examination of peer-reviewed literature, as opposed to grey literature, ensured appropriate scientific rigour. Grey literature was not examined as it was assumed that any relevant information would be indirectly captured within peer-reviewed publications, including those published in non-English languages. See supplementary material for keyword strings used in database searches.

## 4. Results

A total of 102 avian road ecology articles were reviewed from the original collection of 1,431 articles. Approximately one-third (34.3%) of these were published across nine (9) journals. Papers originated from a considerable geographic spread. Three quarters (74.5%) of all studies were conducted in the Northern Hemisphere (Europe, North America, Asia, and the Middle East). Southern Hemisphere studies (Africa, South America, and Oceania) remained grossly understudied (<20%). A small number of articles (4.9%) did not specify a particular region of interest.

A total of 52 articles directly assessed the influence of road and/or roadless gaps on birds and were examined further in this review.

### 4.1. Experimental design

In terms of **spatial scale**, 46 papers studied road gaps. Most (78.3%) examined multiple roads within their design, while the remainder (21.7%) examined only a single road. Roadless gaps (i.e., powerlines, firebreaks, rivers, etc.) were featured in a few studies (n = 8). In the case of the latter, two articles included roadless gaps as a comparator to roads, while six examined roadless gaps in isolation. Road influence was assessed at both edge (near the road) and interior (far road) sites in 69.2% of studies. *Rural* landscapes appeared more prominently within the literature compared to *urban/suburban* landscapes (n = 47 and n = 5 respectively). Habitat types most frequently examined were *forest* (i.e., deciduous, coniferous, evergreen, etc.), *woodland*, and *grassland* (n = 18, 14 and 7 respectively).

In terms of **temporal scale**, three-quarters of all studies reviewed were short-term (≤2-years) (n = 39), with very few studies performed over longer periods: 2–5 years (n = 9) and ≥ 6-years (n = 4).

In terms of **methods employed**, most studies (84.6%) involved *field experiments* (n = 44). Of these, species data were obtained most frequently from the use of *point-count survey* methods (n = 35), followed by *observation* (n = 7), *audio recording/playback* (n = 5), *before after control investigation* (n = 3), and *radiotelemetry* (n = 3).

In terms of **data collection**, gap characteristics were reported in 48 articles (92.1%). Within these, *traffic volume* and *traffic noise* were most frequently reported (n = 23 and 21 respectively), followed by *size* (length/width) (n = 14), *surface type* (paved/unpaved) (n = 13), *lane no.* (n = 11), *designation* (highway/arterial/local) (n = 7), *density* (n = 7), *type* (major/minor) (n = 6), and *traffic speed* (n = 6). Four (4) articles did not supply information on gap characteristics.

**Environment characteristics** within the road effect zone were reported in 45 articles (86.5%). Within these, *vegetation composition* and *vegetation cover* were most frequently reported (n = 30 and 21 respectively). Other information reported included: *vegetation height* (n = 15), *stem size* (n = 7), *stem density* (n = 6), *roadkill* (carrion availability) (n = 2), *dust deposition* (n = 1), and *light intensity* (n = 1). Seven (7) articles did not supply information on environmental characteristics.

Most articles investigated impacts across multiple species (n = 41), while ten focussed on a single species. Species taxonomic information was supplied in only 67.3% (n = 35) of articles: passerines received greater research focus (n = 27) compared to non-passerines (n = 8). Similarly, species dispersal modes were only supplied in 50% of articles (n = 26): *resident* (n = 20), *migrant* (n = 14), and *nomadic* (i.e., partial migrant) (n = 2).

The most supplied population-level data for birds in the road effect zone were *abundance/richness* (n = 35) and *behaviour* (e.g., foraging, vigilance, dispersal, etc.) (n = 14). Other data periodically supplied included: *breeding* (e.g., territory size, pairing success, etc.) (n = 6), *mortality* (e.g., roadkill, predation, etc.) (n = 5), and *communication* (e.g., call frequency) (n = 4). Three (3) studies did not supply population-level data.

### 4.2. Standardised approach

There was no evidence to indicate the existence of a documented standardised approach to the conduct of avian road ecology experiments. However, a pattern did emerge from the reviewed literature. This is summarised in Table 1.

### 4.3. Road impacts

Impacts on bird communities were either negative near the road (n = 19) or mixed (i.e., negative for some, positive for some) (n = 19). Eight studies observed some species and/or communities to be unaffected by the road network. Six studies observed positive impacts.

Only four characteristics were identified in the reviewed literature to directly influence bird communities: *habitat quality* (n = 19), *species-specific traits* (n = 13), *traffic noise* (n = 12) and *infrastructure* (n = 8). Traffic volume, vehicle-wildlife collisions, seasonal changes and/or pollution were not observed to result in population-level impacts in the reviewed literature. An overview of the four identified characteristics will now be provided.

#### 4.3.1. Habitat quality

Several studies indicated vegetation strongly influenced species richness and abundance in urban (Rao and Koli, 2017; Heggie-Gracie et al., 2020; Leveau and Leveau, 2020) and rural (Grinde et al., 2017) environments. Khanaposhtani et al. (2019) observed increased interior species richness and abundance with distance from the highway, and this coincided with increased vegetation structure. Hall et al. (2016) observed woodland bird communities were influenced by site configuration, with more species present at cross-sections, particularly where larger trees (>30 cm diameter) were present. Similarly, van der Horst et al. (2019), in their study observed low tawny owl (*Strix aluco*) abundance, a negative population trend, and high variation in site occupancy adjacent to high-traffic volume roads compared to interior forest sites. These were consistent with observations by Johnson et al. (2017), where forest structure and composition, in particular the understory, were visibly reduced near the roadside. This coincided with reduced bird richness and abundance along the roadside, compared to interior forest locations (Johnson et al., 2017).

Khamcha et al. (2018a) observed four out of six predator species experienced reduced relative abundance near the forest edge adjacent to the highway. In addition, nest predation rates of the top three predators were greatest at interior forest sites (Khamcha et al., 2018a). This coincided with greater density and complexity of different forest strata at interior sites compared to edge sites (simpler, with more vegetation near ground level), and may have provided a more suitable habitat in which to forage (Khamcha et al., 2018b). Reduced activity of several species of vulture near roads has also been reported (Hill et al., 2018). The absence of predator activity, in addition to a dense shrub layer and other human infrastructure, nearer to the forest edge may have, in turn, enhanced nest

**Table 1**
Current experiment approach to avian road impact studies, based on recent literature.

| Site Assessment | Data Collection | | |
|---|---|---|---|
| | Frequent | Infrequent | Rare |
| Road gap surveys | • Traffic volume – Annual Average Daily Flow (AADF)<br>• Traffic noise – decibels (dB) | • Size – length/width<br>• Surface type – paved/unpaved No. lanes | • Roadkill – carrion availability) |
| Habitat surveys | • Forest composition (i.e., habitat description)<br>• Vegetation cover (%) | • Vegetation height (m) | • Stem size – diameter breast height (dbh)<br>• Stem density (stems/ha)<br>• Dust<br>• Light intensity |
| Bird point-count surveys | • Abundance/richness | • Behavioural patterns (foraging, dispersal, vigilance, etc.) | • Breeding (territory size, pairing success, etc.)<br>• Nest survival (hatchling success, fledgling survival, etc.)<br>• Mortality (road-killed birds, predation, etc.)<br>• Communication (call frequency, etc.) |
| Data analysis | Distance from the road (m) – grouped by individual species or life history guilds | | |

success and post-fledgling survival documented in several species (Rao and Koli, 2017; Angkaew et al., 2019; Silva et al., 2019; Somsiri et al., 2019).

Vegetation between habitat fragments, along road margins, for example, positively influenced functional connectivity within urbanised landscapes (Matsuba et al., 2016; van Strien and Grêt-Regamey, 2016; Chong et al., 2019; Belanger et al., 2020). Cox et al. (2016) examined the influence of different urban features on urban bird movements, specifically the structural (presence/absence of connections) and functional (frequency of connections) connectivity between feeder stations, within three urban networks: low, medium and high landscape fragmentation (Cox et al., 2016). Importantly, vegetation cover increased both structural and functional connectivity, even in landscapes bisected by roads (Cox et al., 2016). Leveau and Leveau (2020) also reported street a significant association between street design and species diversity in Argentina. Specifically, chicanes supported greater taxonomic and functional species diversity compared to streets (Leveau and Leveau, 2020). Heggie-Gracie et al. (2020) observed reduced species richness and abundance in Auckland, which was correlated with increased levels of built cover and reduced vegetation cover. Similarly, Rao and Koli (2017) reported that three nesting tree attributes (girth at breast height, canopy cover, and tree height) were positively correlated with nesting species richness in an urban area.

#### *4.3.2. Species-specific traits*

Roads did not impact all species to the same degree. Indeed, population-level responses towards LTI may be determined by species' ecological and life-history traits, and therefore is highly species-specific. Ladin et al. (2018) reported that juveniles of two closely related species – wood thrush (*Hylocichla mustelina*) and grey catbird (*Dumetella carolinensis*) – responded differently to an urbanised landscape. Specifically, the wood thrush displayed a greater preference for landscapes with greater forest cover, whereas the grey catbird preferred more developed landscapes (e.g., roads) (Ladin et al., 2018). In addition, smaller-sized resident birds were reportedly more susceptible to the impacts of fragmentation compared to larger-bodied species (Cuervo and Moller, 2020). Similarly, the richness and abundance of insectivorous and grassland species were observed to increase with distance from a major road in Brazil (Da Silva et al., 2017). Similar observations were made in an earlier study (Johnson et al., 2017), where roadside abundance and richness, as well as road crossing likelihood, of smaller birds, were greatly reduced compared to larger birds.

Many smaller species were heavily reliant on dense understory and mid-story vegetation layers for resources (i.e., food, shelter, and nesting sites) (Johnson et al., 2017). Small birds also typically possessed wider and more rounded wings suitable for manoeuvring amongst dense vegetation and capturing insects. Larger species, however, typically possessed long and narrow wings for longer and more direct flight (Keast 1996 in Johnson et al., 2017). Smaller species may be less capable of dispersing and foraging in areas with sparse understory. Smaller species were also more prone to exclusion through interspecific interactions, such as predation and competition. Larger predatory and aggressive species were frequently reported to colonise roadside habitats (Johnson et al., 2017; Joseph et al., 2017; Hill et al., 2018; Hennigar et al., 2019), and have been associated with reduced smaller bird presence.

Several studies also detected strong declines in small bird richness and abundance in the presence of larger and more aggressive species (Ford et al. 2000; Hall et al., 2016). Indeed, Davitt et al. (2018) have reported short-term recovery of a small bird community after the removal of noisy miners (*Manorina melanocephala*), albeit only temporary. Reductions in abundance and richness may have been further enhanced through the increased presence of brood parasites along edges (Bernath-Plaisted et al., 2017), although this was not considered to have a significant impact on Australian bird communities (Ford et al., 2000).

Lituma and Buehler (2016) reported that both detection probability and abundance of eight grassland bird species adjacent to low-traffic volume roads were most influenced by landcover covariates, but did not differ with distance from the road. Similarly, van der Horst et al. (2019) also reported comparable tawny owl abundance, population trend, and site occupancy between interior forest sites and areas adjacent to secondary, low-traffic volume roads. This observation led them to suggest that secondary roads did not influence habitat quality, as much as main roads (van der Horst et al., 2019). Vegetation has been shown to correlate positively with the spatial distribution of several forest species in forest fragments (Mahmoudi et al., 2016; Hofmeister et al., 2017; Mokross et al., 2018; Rutt et al., 2019). This appeared consistent with earlier observations by Johnson et al. (2017), in which smaller roads (i.e., two-lane carriageways) had no noticeable impact on species richness and abundance in adjacent forest sites, nor crossing frequency over roads.

#### *4.3.3. Traffic noise*

*4.3.3.1. Impacts on richness and abundance.* Numerous studies highlighted the various impacts of anthropogenic noise pollution on bird populations near roads. This phenomenon was widespread and reported for many species globally (Brumm et al., 2017). The potential consequences of traffic noise on the surrounding landscape were demonstrated by a recent study in which land-take (structural fragmentation) and noise effect zones (functional fragmentation) caused by a road network were modelled and compared (Madadi et al., 2017). Nearly half (45.2%) of the landscape studied fell within the noise effect zone, and thus was functionally fragmented, and extended beyond the area impacted by the physical properties of the road land-take zone (19.4%) (Madadi et al., 2017). Similarly, large parts of Cyprus, including several conservation areas, were reportedly exposed to intense traffic noise (Konstantopoulos et al., 2020).

Most of the reviewed studies also reported reduced species density and breeding in proximity to roads. Traffic noise exposure has coincided with reduced species richness and abundance near roads. Rashidi et al. (2019) observed that bird richness and abundance at a forest site adjacent to a major highway in Iran increased with increasing distance from the highway. This coincided strongly with the sound average, equivalent sound level ($LeQ_{30}$), produced by the highway over 30 min (Rashidi et al., 2019). Khanaposhtani et al. (2019) observed increased richness and abundance of forest interior species with distance from two major highways in Canada. This was attributed partly to the intrusion of traffic noise pollution into the surrounding landscape (Khanaposhtani et al., 2019). Bird richness and abundance have also declined significantly through traffic noise playbacks in quiet (i.e., non-road) environments (McClure et al., 2013; Ware et al., 2015; Senzaki et al., 2020).

Laboratory experiments that examined single species response to simulated vehicle traffic noise have highlighted individuals' preferences for quiet environments. In a study by Liu et al. (2020), captive-bred zebra finches (*Taeniopygia guttata*) were exposed to high amplitude ('near'; 5–15 m) and moderate amplitude ('far'; 200–400 m) traffic noise playbacks, with individuals allowed to move freely between 'quiet' and 'noisy' aviaries. Individuals spent significantly more time in 'quiet' aviaries when exposed to high amplitude traffic noise, whereas no such spatial preference was observed under moderate amplitude conditions. This was in line with earlier observations of this species (Evans et al., 2018).

While there was considerable documentation of the adverse impacts of traffic noise, several studies appeared to rely upon the analysis of bird call frequency, in particular minimum frequency, to support the acoustic masking effect of traffic noise (Kleist et al., 2016; Luther et al., 2016; Derryberry et al., 2017; Schepers and Proppe, 2017; Yip et al., 2017; Narango and Rodewald, 2018; Tolentino et al., 2018; Walters et al., 2019; Courter et al., 2020). Smaller species were more susceptible to anthropogenic noise influence, with a greater proportion of these species displaying increased dominant frequencies when confronted with anthropogenic noise (Roca et al., 2016). However, Brumm et al. (2017) raised concerns over the potential bias that resulted from visual extraction ('eyeballing') of frequency measurements from spectrograms. This was experimentally demonstrated to result in false positives, with the potential for effect sizes larger than those in many published studies (Brumm et al., 2017).

Additionally, several studies presented evidence of inconsistent outcomes concerning traffic noise, or at least the degree of impact. Although often perceived by many to be a key contributor to reduced species richness and abundance near roads, Heggie-Gracie et al. (2020) reported neighbouring human density to exert a greater influence on declined richness and abundance than noise near habitat fragment edges. Similarly, Lituma and Buehler (2016) reported traffic noise to be less influential than landcover covariates on the abundance or detection probability of eight species of grassland species, at least for low-traffic roads. In their study, Long et al. (2017a, b) experimentally tested the influence of anthropogenic noise on golden-cheeked warbler (*Setophaga chrysoparia*) at their breeding sites over nine years. Mean territory distance from the road, territory density, pairing and fledgling success, and vocalisations were also unaffected by highway construction and traffic noise; this included playback of noise within 'quiet' areas (Long et al., 2017a,b). This was further reinforced through a follow-up investigation by the same authors, in which breeding birds continued to display no adverse response to anthropogenic noise post-construction (Long et al., 2017a,b).

Several grassland species also did not appear to be physically displaced when exposed to traffic noise in roadside environments (Martinez-Marivela et al., 2018; Daniel and Koper, 2019; Spiess et al., 2020), and traffic noise playbacks in quiet areas (Hawkins et al., 2020; Senzaki et al., 2020). At least one recent study reported that several passerine and non-passerine species were attracted to experimental traffic noise (Hennigar et al., 2019), a finding that contradicted those of previous studies. Several common species in urban landscapes were also reported to be able to still perceive predator calls under traffic noise conditions (Pettinga et al., 2016).

*4.3.3.2. Impacts on behaviour.* Under noisy conditions, as is often the case in roadside environments, individuals may become 'distracted' by the higher ambient noise, leading them to divert attention from foraging towards visual anti-predator behaviours. Zebra finches were observed to significantly reduce forage time and increase vigilance when exposed to high noise conditions (Evans et al. 2018). Similarly, Merrall and Evans (2020) found six passerine species reduced visit and feeding rates and increase vigilance at supplementary feeding stations after exposure to playbacks of anthropogenic noise. Grade and Sieving (2016) reported highway noise disrupted eavesdropping by northern cardinals (*Cardinalis cardinalis*) on playback alarm calls produced by tufted titmice (*Baeolophus bicolor*). Northern cardinals successfully elicited predator response behaviour in quiet areas, however, failed to do so in 'noisy' environments nearby highways (Grade and Sieving, 2016). Additionally, traffic noise was reported to influence nest-site selection in great tits (*Parus major*) and blue tits (*Cyanistes caeruleus*); individuals of both displayed preference for quiet nest boxes over nest boxes where traffic noise was played inside (Halfwerk et al., 2016).

Traffic noise may also 'mask' calls of conspecifics, in particular smaller-bodied passerines. This group (songbirds) are acoustically oriented and rely heavily on call vocalisations in communication, territory defence, and courtship (Grade and Sieving, 2016; Cooke et al., 2019; Cuervo and Moller, 2020; Hawkins et al., 2020; Senzaki et al., 2020). Kleist et al. (2016) observed conspecific territorial defence behaviour of spotted towhee (*Pipilo maculatus*) and chipping sparrow (*Spizella passerina*) to be impaired in areas nearby anthropogenic noise sources. Although all birds reacted to the playbacks, response latency was observed to correlate positively with background noise (Kleist et al., 2016). Red-backed fairy-wrens (*Malurus melanocephalus*) have also displayed significantly reduced social interactions with outside groups after exposure to traffic noise playbacks (Hawkins et al., 2020).

Several species displayed a high degree of flexibility in their ability to adjust the frequency of their calls in response to low-frequency anthropogenic noise, and thus minimise call overlap (Roca et al., 2016). Tolentino et al. (2018) reported that eight of nine studied tropical bird species used higher frequency vocalisations in forest fragments nearer to urban areas; these locations were characterised by higher ambient noise. Black-capped chickadees (*Poecile atricapillus*) were also reported to utilise higher frequencies in urban environments (Lazerte et al., 2016), and displayed considerable flexibility in duration and acoustical structure of predator alarm calls. Specifically, Courter et al. (2020) observed that birds exposed to traffic noise playback produced more introductory notes, more total notes, longer alarm calls, and alarm calls of lower peak frequencies. A similar trend was reported in other species (Villain et al., 2016; Derryberry et al., 2017; Walters et al., 2019). However, this also represented a challenge, as although the expansion of song minimum frequency may have increased signal detectability, signal attractiveness was compromised (Kleist et al., 2016; Luther et al., 2016). Indeed, several authors noted the importance of low-frequency calls in mate attraction (Kleist et al., 2016; Luther et al., 2016), whilst higher frequency calls were negatively correlated with poorer nestling condition (Narango and Rodewald, 2018), and perceived poorer male condition by females (Luther et al., 2016).

Species may also experience adverse noise-mediated physiological and psychological stress in response to high vehicle volume roads. Road proximity may accelerate developmental telomere shortening of nestling birds of several species (Meillère *et al.* in Casasole et al. 2017; Dorado-Correa et al., 2018; Injaian et al., 2019; Grunst et al., 2020a,b). Early and rapid telomere loss, particularly during the developmental and post-fledging stages, may result in genomic instability, disease, and reduced longevity, all of which have life-long implications for physiology, behaviour and fitness (Dorado-Correa et al., 2018; Grunst et al., 2020a,b). Kleist et al. (2017) also reported hypocorticism; reduced glucocorticoid signalling in response to a stressor, in three cavity-nesting species (*Sialia mexicana*, *Sialia currucoides* and *Myiarchus cinerascens*) living near an anthropogenic noise source. This is believed to be a natural and adaptive response that may prevent an organism, in the short term, from experiencing the full effects of allostatic overload (Kleist et al., 2017). However, prolonged and continuous exposure may have resulted in detrimental effects, such as reduced fitness in the form of lower hatching success and poorer nestling body condition (Mulholland et al., 2018; Flores et al., 2019; Walthers and Barber, 2019). Hypocorticism was also reported to occur in other species following exposure to an anthropogenic noise source (Injaian et al., 2018; Flores et al., 2019; Zollinger et al., 2019; Blickley et al., 2012b in Walthers and Barber, 2019).

Laboratory experiments have produced mixed results. For example, Angelier et al. (2016) found no effect of noise exposure on growth, body condition, or stress response of nestling house sparrow (*Passer domesticus*). Similarly, Walthers and Barber (2019) observed no effect of traffic noise mediated stress response in nestling common starling (*Sturnus vulgaris*). Crino *et al.* (in Walthers & Barber, 2020) also observed greater stress response in control than experimental groups of white-crowned sparrow (*Zonotrichia leucophrys*), a non-urban adapted species. This may suggest that, at the very least, some urban-adapted species display some degree of tolerance towards traffic noise.

#### 4.3.4. *Infrastructure*

According to Morelli et al. (2014), powerlines, signs and roadside vegetation may provide suitable nesting, refuge, and perching habitats for birds (Spiess et al., 2020). Both Rodgers and Koper (2017), and Nenninger and Koper (2018) observed a greater presence of vesper sparrow (*Pooecetes gramineus*), western meadowlark (*Sturnella neglecta*), and later savannah sparrow (*Passerculus sandwichensis*) near natural gas wells and associated roads. By comparison, the presence of Baird's sparrow (*Centronyx bairdii*) and Sprague's pipit (*Anthus spragueii*) was lower near these sites (Nenninger and Koper, 2018). It was suggested that such infrastructure acted as artificial shrubs and attracted species that used vegetation for perching whilst simultaneously repelling species that avoided shrubs (Rodgers and Koper, 2017).

Roadside lighting may potentially extend foraging time and activities of both diurnal species (permitting foraging for longer periods each day), and nocturnal species (providing light to facilitate hunting of congregating prey items) (Hennigar et al., 2019). Highway edges can also impart several reproductive advantages through the suppressed abundance of some predatory species.

#### 4.3.5. *Other impacts*

Some circumstantial evidence for sources of additional impact was also observed in the reviewed literature (Santos et al., 2016; van der Horst et al., 2019). However, this was largely dependent on whether a species could be attracted to the road surface, and not merely the vegetation nearby (Helldin and Seiler, 2003; Husby, 2016, 2017). Few species respond positively to roads. As such, wildlife-vehicle collisions likely only exert a 'random sampling' effect on bird populations (Morelli et al., 2020).

### 4.4. *Risk of bias*

Study bias arising from confounding variables was identified in less than half of the articles reviewed (n = 24). Confounding variables were managed in less than one-third of the reviewed literature (n = 18).

Biases arising from the confounding variables of habitat/life history and traffic noise were acknowledged most frequently within the reviewed literature (Table 2) but were managed least well. Only 60% of studies were observed to implement appropriate experimental and/or statistical controls for these factors.

## 5. Discussion

The key finding of the present study was that birds continue to experience a largely negative association with transport infrastructure. Bird richness and abundance tend to be substantially reduced in roadside habitats due to the presence of less suitable habitat

**Table 2**
Confounding variables acknowledged and managed in the reviewed literature.

| Confounded Variables | No. studies identified in | No. studies controlled in |
|---|---|---|
| Habitat / Life history × Infrastructure | 5 | 4 |
| Habitat / Life history × Traffic volume | 6 | 5 |
| Habitat / Life history × Traffic noise | 20 | 12 |
| Light × Traffic noise | 2 | 2 |

Moreover, very few studies acknowledged and managed instances in which multiple confounding variables occurred (Table 3).

(i.e., edge effects), increased traffic noise, and ancillary infrastructure (e.g., powerlines, streetlights, exclusion fences, etc.). This result is partly consistent with previous reviews (Fahrig and Rytwinski, 2009; Kociolek et al. 2011; Kociolek et al., 2015; Cooke et al., 2020). However, unlike Kociolek et al. (2011) and Fahrig and Rytwinski (2009), who suggested vehicle-caused mortality and traffic noise represented the greatest threats to birds, recent literature appears to lend more support to changes in the physical environment (i.e., habitat quality), and species preferences towards these.

Vegetation cover correlates positively with species richness and community composition (Matsuba et al. 2016; Santos et al., 2016; Hofmeister et al., 2017; Chong et al., 2019; Heggie-Gracie et al., 2020). Habitat quality and structure are known to correlate positively with distance from the road (Husby, 2017; Khamcha et al., 2018a). Frequent compaction and chemical treatment of the roadside environment typically results in a vegetation community that is composed of exotic species that are drought and disturbance tolerant (Johnson et al., 2017). These communities are often structurally simpler than interior sites and thus less able to support similar levels of diversity (Johnson et al., 2017; Chong et al., 2019). Indeed, substantial reductions in small bird occurrence and behaviour, a group more heavily reliant on dense vegetation, have occurred following vegetation disturbance (Ford et al., 2000; Bowen et al., 2009; Tremblay and St. Clair, 2009; Benítez-López et al., 2010; Jones and Bond, 2010; Kutt and Martin, 2010; Thinh et al., 2012; Pell and Jones, 2015; Matsuba et al., 2016; Hofmeister et al., 2017; Johnson et al., 2017; Chong et al., 2019; Khanaposhtani et al., 2019; Rutt et al., 2020). This may be further exacerbated through the establishment of generalist, predatory and/or aggressive species (Ford et al., 2000; Lees and Peres, 2009; Benítez-López et al., 2010; Hall et al., 2016; Bernath-Plaisted et al., 2017; Joseph et al., 2017; Davitt et al., 2018; Hall et al., 2018; Nenninger and Koper, 2018; Daniel and Koper, 2019).

Additional sources of direct impact, such as traffic noise and light pollution, were identified to influence bird populations. However, substantial limitations were encountered in the reviewed literature which brings into question the inferential strength of these studies. These are discussed as follows.

#### *5.0.1. Inconsistent and variable data collection*

A significant problem was the lack of a standardised 'baseline' approach to assist and guide scientists when conducting road ecology research. Data collection especially was inconsistent and highly variable between papers, most notably concerning the type and quality of data obtained from field surveys. For example, while many authors collected quantitative data in road surveys – traffic volume (AADF) and traffic noise (dB), most focussed on the collection of qualitative data in habitat surveys – primarily forest composition (descriptions) and forest cover (%). Surprisingly, few studies within the reviewed literature acquired additional (quantitative) vegetation metrics (e.g., stem density, stem size, vegetation height, etc.) in habitat surveys (but see Kleist et al. 2017; Rao and Koli 2017; Khamcha et al., 2018b); Khamcha et al., 2018a; Nenninger and Koper 2018; Angkaew et al. 2019; Khanaposhtani et al. 2019; Rashidi, Chamani and Moshtaghi 2019). Measurement of these is crucial as wildlife may respond strongly to fine-scale changes in the road and roadside environments (Canal et al., 2019; Miranda et al., 2020).

#### *5.0.2. High risk of bias in study design*

Many of the aspects identified as influencing bird population dynamics within the 'road effect zone' were potentially biased due to confounding. Although multiple sources of bias were identified in the reviewed literature, relatively few studies appeared to acknowledge and manage these. Fewer still managed for the occurrence of multiple sources of bias. Species richness and abundance generally increased with increasing distance from the road corridor, and these typically correlated with reduced anthropogenic influence (e.g., traffic, noise, light, infrastructure, etc.) and improved habitat condition (Lituma and Buehler, 2016; L. Desrochers and Proulx, 2017; Hennigar et al., 2019; Heggie-Gracie et al., 2020; Liu et al., 2020; Merrall and Evans, 2020; Senzaki et al., 2020).

Confounding variables within field experiments are a common feature of road ecology studies but are extremely difficult to manage (Khamcha et al., 2018a; Merrall and Evans, 2020). In particular, road and vegetation properties require experimental variation within the study design to explore population-level road-related impacts on birds (Khamcha et al., 2018a). Although a range of approaches may be broadly applicable to control for confounding variables in these types of studies, only two were readily identifiable from the reviewed literature. Other highly effective approaches, that originate from other fields, may become available to these types of studies as this field develops.

The first approach was the use of generalised linear mixed models (GLMMs) ranked by Akaike Information Criterion (AIC) scores. Using the data provided, this method identifies and ranks the most parsimonious explanation among competing models (e.g., noise, vegetation, traffic, etc.), without over-fitting or under-fitting them (Jaeger et al., 2011). This approach, however, requires the collection and input of quantitative data. As discussed above, relatively few papers identified in the present study collected quantitative data from all fields, particularly concerning vegetation (but see Kleist et al. 2017; Nenninger and Koper 2018; and Khanaposhtani et al. 2019).

The second approach was the use of 'phantom road' experiments. These represent the best means through which to manage confounding variables, particularly vegetation and noise, within studies that examine road influence (McClure et al., 2017; Liu et al., 2020; Senzaki et al., 2020). This is achieved through the exposure of a bird community at a remote location (i.e., 'road-less' area) to traffic noise broadcast from a series of loudspeakers, thereby replicating the sound of roads without other confounding road aspects (McClure et al., 2017; Senzaki et al., 2020). However, 'phantom road' experiments evaluated in this review only examined impacts on migrant birds at a stopover site (McClure et al., 2013; Ware et al., 2015; McClure et al., 2017). Migrant birds are known to visualise the landscape differently from resident species (Evans et al., 2017). For example, migrants prioritise landscapes for their foraging value over their habitat value as these species are less able to utilise and compete for resources in these landscapes compared to residents

(Paton et al., 2019). Results obtained from these studies may be further confounded by other biotic factors, such as species-species interactions (or lack thereof). For example, the absence of vocalisations from conspecific species at a site, either through call masking or species absence, may prevent the aggregation of more individuals, a phenomenon observed in Schepers and Proppe (2017). Site occupancy, or lack thereof, by acoustically oriented species may have a cascade effect on the occupancy of other acoustically and non-acoustically oriented species, through top-down interactions for example (Liu et al., 2020; Senzaki et al., 2020). Indeed, the use of song playback near roads has been used to attract many species, including those that are noise-sensitive, to roadside (Schepers and Proppe, 2017) and urban (Shimazaki et al., 2016; Shimazaki et al., 2017) environments.

#### *5.0.3. Limited longitudinal, multi-year/season studies*

Very few studies have used ***before after control impact*** (BACI) or ***before during after control impact*** (BDACI). The relative importance (and absence) of these studies within the field have long been recognised (Roedenbeck et al. 2007; Benítez-López et al., 2010). Only three studies that employed BACI/BDCI study designs were published in 2016–2020. The first, by Long et al. (2017a,b), examined the influence of highway construction and traffic noise on a critically endangered passerine golden-cheeked warbler (*Setophaga chrysoparia*) in urban Texas over five years. Traffic noise playback experiments were included in this to evaluate acute behavioural responses to highway construction noises (Long et al., 2017a,b). Breeding activity and behaviour were unaffected by highway construction noise and traffic noise. A follow-up study within a rural area further concluded no negative impacts on the species' breeding activity and behaviour (Long et al., 2017a,b). In the third study, Husby (2017) examined the relationship between traffic density and numbers of birds and crossover flight heights on roads in Iceland, Norway and the United States over three years, before and after they were opened to vehicle traffic. Bird abundance was significantly reduced at higher traffic densities, and crossover flight height increased significantly after roads were opened to vehicle traffic (Husby, 2017).

An earlier study is worthy of special mention here. Torres et al. (2011) investigated potential impacts on a population of great bustard (*Otis tarda*) from motorway construction and operation on a population over 12 years. The study species were observed to avoid habitats near a highway (<750 m) during construction and were generally intolerant of highway operation postconstruction (fewer individuals within 1,300 m).

#### *5.0.4. Limited evaluation of non-vehicle gaps*

Most studies within the reviewed literature examined species dispersal and behaviour post-disturbance in environments adjacent to established road infrastructure. Few appeared to examine the influence of other non-vehicle gaps, both natural (e.g., forest clearings) and anthropogenic (e.g., powerline easements and fire breaks). Only ten studies (~11%) examined non-vehicle gaps in their experiment design, the majority of which investigated the impact of traffic noise in quiet environments (Ware et al., 2015; Kleist et al., 2017; McClure et al., 2017; Munro et al., 2018). Unpaved and low-traffic roads are known to be detrimental to species' habits and movements in protected areas (Mammides et al., 2016). Previous research has indicated that birds may be more deterred by gaps between suitable habitats, such as physical gaps in vegetation and altered vegetation structure/cover, rather than road infrastructure, even if it represents the shortest route to their destination (Desrochers and Hannon, 1997; St Clair, 2003; Summers et al., 2011). Interestingly, this has remained largely unexplored within recent literature (but see Shimazaki et al. (2016) who reported species aversion to large gaps in wood cover when moving through an urbanised landscape).

Accurate and reliable quantification of bird movement in roadless environments, however, may be difficult given the considerable expanse of the road network and its pervasive influence on 'natural' landscapes. A recent analysis of the European landscape identified that approximately 50% of the continent was within 1.5 km of the transportation network, and thus potentially susceptible to its infrastructure (Torres et al., 2016). Similarly, Riitters and Wickham (in Torres et al. 2016) reported that 50% of all landscapes in North America are less than 0.38 km from the nearest road. Helldin (2019) also reported a high proportion (63%) of Natura 2000 areas – EU natural areas designated for bird conservation – to be within the road effect zone (1 km), and therefore unlikely to achieve their full conservation potential. Coincidentally, these are also the regions where research interest has been most active. The relative absence of suitable 'natural' landscapes as controls for comparison may limit the ability of scientists to measure the magnitude of road impacts on wildlife in these regions (Torres et al., 2016). Research effort should therefore be redirected to 'natural' landscapes outside of these regions where it may still be possible to obtain data from relatively undisturbed landscapes.

#### *5.0.5. Use of methodologies susceptible to bias*

Several of the papers examined in the present study relied heavily on the acoustic masking effect of traffic noise, evidenced by analysis of bird minimum song frequencies via visual inspection of spectrograms (Kleist et al., 2016; Luther et al., 2016; Derryberry et al., 2017; Schepers and Proppe, 2017; Yip et al., 2017; Narango and Rodewald, 2018; Tolentino et al., 2018; Walters et al., 2019; Courter et al., 2020). According to Brumm et al. (2017), several studies have, however, relied on visual inspection ('eyeballing') to observe changes in species' minimum song frequencies. There is concern over the accuracy and reliability of this approach ('eyeballing'), which has been experimentally shown to frequently result in false positives (Brumm et al. 2017).

Additionally, a substantial proportion of studies (~65.9%) relied on point-count survey (PCS) methodologies to estimate species richness and abundance. PCS is a widely used quantitative survey method where a single observer, stationed at a single point within a given area, records the number of birds detected over a standardised period (Loyn, 1986; Ralph et al., 1995; Bibby et al., 2000; Kulaga and Budka, 2019). Data derived from this technique can be used to measure biodiversity (i.e., species richness and abundance) (Loyn, 1986). Importantly, the procedure is highly flexible and can be modified to suit a range of experiments, species and conditions, and several methods have been derived and deployed (Bibby et al., 2000; BirdLife, 2021). There may, however, be several observer errors associated with this approach, including inaccurate bird position and distance measurements, species temporal and spatial detection probability, and observer influence on bird behaviour (Castro et al., 2019; Kulaga and Budka, 2019). In addition to these, a range of other logistical (i.e., difficult terrain, equipment transport, weather) and/or financial (i.e., fuel for transport, accommodation, hiring of field staff) challenges may also be encountered in the application of PCS (Hao et al., 2020).

The use of radiotelemetry was observed in very few studies in the available literature. This approach may broadly be used to track habits and movements of individual species (Perrow et al., 2006; Griffin et al., 2020; Young et al., 2020, 2021), and may have some application in the assessment of LTI influence (see Cox et al. 2016; Ladin et al. 2018; Angkaew et al. 2019). However, this approach is highly intrusive and obtrusive on birds and populations, and is primarily restricted to surveys of individual species. The inappropriate capture and handling of individuals, as well as general observer presence, can elicit substantial behavioural and/or biological responses that may bias experimental data (Perrow et al., 2006; Cid et al., 2013; Bombaci and Pejchar, 2018). Generally, other preferred methods are recommended for broader-scale surveillance of bird communities (Eyre et al., 2018; BirdLife, 2021).

Soundscape mapping (acoustic monitoring) is a new and valid approach that may be used to rapidly obtain and assess measures of biodiversity (Machado et al., 2017; Pankratz et al. 2017; Munro et al. 2018; Ducrettet et al., 2020; Hao et al., 2020). Similar to PCS, this method involves species/individual count data gathered from a single point in a pre-defined area but, using instead an autonomous recording unit (ARU) (Darras et al., 2019; Ericson et al., 2020; Stewart et al., 2020). However, relatively few studies using the acoustic monitoring approach were published during the period specified for the present review (2016–2020 inclusive). This may be due to the substantial upfront and ongoing costs, risk of equipment theft/damage/failure, and requirement for data storage (Stewart et al., 2020). Moreover, trained observers are required to listen to recordings and code each for weather, quality, and species, which can be a tedious process (Khanaposhtani et al., 2019; Ericson et al., 2020; Hao et al., 2020).

## 6. Implications and future directions

Whist this systematic quantitative literature review has identified habitat quality, species-specific traits, traffic noise, and infrastructure as key factors influencing bird populations near roads, it has also identified underlying problems in the methodologies employed in contemporary road ecology studies that appreciably limit the certainty of this evidence. Specifically, this study identified inconsistent data collection (e.g., quantitative road data vs qualitative habitat quality data), inadequate management of confounding variables (e.g., traffic noise and vegetation), limited inclusion of vehicle-free ('roadless') environments, short-term experimental timeframes (typically $<$ 2-years) and use of methodologies that were susceptible to bias (e.g., minimum song frequency, radiotelemetry and point-count surveys).

The essence of road ecology is the bringing together of disparate fields and new methodologies, techniques and approaches continue to emerge. Whilst previous studies have suggested targeted measures to address specific issues, the present review has identified a suite of key improvements that could be adopted and incorporated into road ecology studies. We propose a uniform, standardised framework for measuring the population-level impacts of roads on birds (Table 4). This framework includes: 1) gap assessments that measure traffic volume, technophony and ambient background noise; 2) habitat surveys that target forest composition and vegetation cover, density and height; 3) bird surveys (point-count and acoustic) that capture species richness and abundance; 4) a survey protocol to ensure relevant data is captured over consistent spatial and temporal scales (distance from the gap, vehicle vs. non-vehicle gap, $\geq$36-months), and; 5) statistical analyses that mitigate the risk of bias due to confounding variables (GLMM using AIC scores). The framework is broadly applicable to the study of road impacts on other wildlife and can be modified to include additional information, such as vehicle mortality, road crossing and breeding count data. Given time, this would facilitate the construction of species and/or community profiles, information that will be of considerable value to urban and regional planners, and road ecologists.

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**Table 3**
- Confounding variables acknowledged and managed relative to the reported source of population-level impact(s).

| Reported source of population-level impact(s) | No. studies | Confounding variables identified (no. studies) | | | Bias controlled (no. studies) | | |
|---|---|---|---|---|---|---|---|
| | | 1 pair | 2 pairs | 3 + pairs | 1 pair | 2 pairs | 3 + pairs |
| Habitat quality | 19 | 5 | – | 1 | 5 | – | – |
| Species-specific traits | 13 | 4 | 1 | – | 3 | – | – |
| Traffic noise | 12 | 8 | – | 2 | 5 | – | 2 |
| Infrastructure | 8 | 3 | 1 | – | 3 | – | – |

**Table 4**
–The suggested framework for measuring the impacts of roads on birds (and other wildlife).

| Site Assessment | Data collection | |
|---|---|---|
| | LTI gap | Non-LTI gap (comparison) |
| Gap assessment | • Traffic volume (AADF) | • Ambient background noise (dB) |
| | • Technophony (dB) | • Audio playback (traffic noise) |
| Habitat survey | • Forest composition (habitat description) | • Forest composition (habitat description) |
| | Within-strata vegetation cover (%) | • Within-strata vegetation cover (%) |
| | • Within-strata canopy height (m) | • Within-strata canopy height (m) |
| | Within-strata vegetation density (stems/ha) | • Within-strata vegetation density (stems/ha) |
| Bird point-count surveys | • Species abundance and richness | • Species abundance and richness |
| Acoustic monitoring surveys | • Species richness | • Species richness |
| Statistical analysis | • GLMM using AIC scores | |
| | • Distance from the road (m) – grouped by individual species or life history guilds | |
| Survey protocol | • Distance from gap: 0 m, 100 m, 200 m… | |
| | • Minimum period: 36-months | |
| Landscape description | • Land-type, terrain profile, connectivity to adjacent reserves/natural areas | |
| LTI description | • Type (road/highway/railway/), age, speed limit, surface type (concrete/asphalt/gravel/dirt), other infrastructure present | |

## Author contributions

Conceived the SQLR: CJ, DJ, TM. Performed the SQLR: CJ. Analysed the data: CJ. Contributed materials/critique/analysis tools: CJ, DJ, TM, MB. Wrote, formatted, and edited the paper: CJ, DJ, TM, MB.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.trd.2022.103375.

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