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Research article

Artificial lighting reduces the effectiveness of wildlife-crossing structures for insectivorous bats

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ABSTRACT

In an attempt to improve cost-effectiveness, it has become increasingly popular to adapt wildlife crossing structures to enable people to also use them for safe passage across roads. However, the required needs of humans and wildlife may conflict, resulting in a structure that does not actually provide the perceived improvement in cost-effectiveness, but instead a reduction in conservation benefits. For example, lighting within crossing structures for human safety at night may reduce use of the structure by nocturnal wildlife, thus contributing to barrier and mortality effects of roads rather than mitigating them.

In this study, we experimentally evaluated the impact of artificial light at night on the rate of use of wildlife crossing structures, specifically underpasses, by ten insectivorous bat species groups in south-eastern Australia. We monitored bat activity before, during and after artificially lighting the underpasses. We found that bats tended to avoided lit underpasses, and only one species consistently showed attraction to the light. Artificial light at night in underpasses hypothetically increases the vulnerability of bats to road-mortality or to the barrier effect of roads. The most likely outcomes of lighting underpasses were 1. an increase in crossing rate above the freeway and a decrease under the underpasses, or 2. a reduction in crossing rate both above freeways and under the underpasses, when structures were lit. Our results corroborate those of studies on terrestrial mammals, and thus we recommend that underpasses intended to facilitate the movement of wildlife across roads should not be lit.

1. Introduction

Roads are one of the most pervasive threats to the persistence of wildlife in many parts of the world (Forman and Alexander, 1998; Forman et al., 2003; van der Ree et al., 2011). Wildlife crossing structures are a common solution to addressing the mortality and barrier effects of roads and traffic by facilitating the safe movement of individuals, and their genes, across roads, while reducing exposure to the road and traffic (Soanes et al., 2013, 2018; Sawaya et al., 2014; Smith et al., 2015). To justify the significant construction and maintenance costs, additional uses for these structures have been proposed and implemented, such as providing a safe passage for people while bicycling, walking, horse riding, etc. (Smith et al., 2015; van der Ree and van der Grift, 2015). A dilemma arises when the needs of each user, humans and wildlife, compete. For example, incorporating artificial light at night (ALAN) throughout the structures may be considered essential for human safety (Baumgartner et al., 2011), but may also have adverse effects on nocturnal wildlife (Longcore and Rich, 2004). ALAN in underpasses (i.e. crossing structures that go under the road) has reduced the rate of crossings by Columbia black-tailed deer (*Odocoileus hemionus columbianus*), deer mice (*Peromyscus maniculatus*), and opossum (*Didelphis virginiana*; Bliss-Ketchum et al., 2016). If managers are to install underpasses that are useful for humans as well as wildlife, a better understanding of the trade-offs between human co-use and the effectiveness for wildlife is required (van der Ree and van der Grift, 2015).

Large roads can have numerous negative impacts on insectivorous bats (hereafter referred to as "bats"). Some bat species are susceptible to high rates of road mortality (Lesiński et al., 2011; Medinas et al., 2013),

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while others avoid approaching and crossing roads (Medinas et al., 2019) due to the gap created in the canopy (Bennett and Zurcher, 2013; Hale et al., 2015), the presence of vehicles (Zurcher et al., 2010), and/or traffic noise (Schaub et al., 2008; Siemers and Schaub, 2011). Crossing structures, such as purpose-built wildlife underpasses, may reduce these impacts and maintain the connectivity of bats in the landscape, as bats can roost under and commute through culvert and bridge underpasses (Abbott et al., 2012; Bhardwaj et al., 2017).

The impact of ALAN on the use of underpasses by bats is currently understudied (see Spoelstra et al., 2018 for exception), however the behaviour of bats around ALAN in other landscapes is insightful. For example, some species are sensitive to light at night and avoid lit landscapes (Stone et al., 2009; Threlfall et al., 2012; Rowse et al., 2016), while others show an attraction to light and exploit lit areas due to the rich food resources they provide (Threlfall et al., 2012; Rowse et al., 2016; Schoeman, 2016). Light pollution in urban landscapes has also been associated with reduced movement by bats (Laforge et al., 2019). In general, larger, faster-flying species of bats tend to be more tolerant of lighting, and in some cases may even exploit stationary lights as a resource for foraging. In contrast, smaller, slower-flying species of bats are less commonly found around lights, and more commonly are associated with light-sensitivity (Jung and Threlfall, 2016; Rowse et al., 2016; Laforge et al., 2019). Therefore, ALAN in underpasses may have contrasting effects on bats, such as improving rates of use of crossing structure, exacerbate road impacts such as road-mortality and barrier effects, or having no effect at all. Understanding this relationship, and the potential influence ALAN has on the use of underpasses by bats is essential in order to design the most effective crossing structures and reduce the impacts of roads on bats.

The aim of this study was to investigate how bats respond to ALAN within underpasses. We experimentally evaluated the changes in the number of bat passes (i.e. sequences of echolocation calls) of nine species and one species group of bats in south-eastern Australia at bridge and culvert underpasses when the structures were lit and not lit. By simultaneously monitoring lit and unlit structures, through a before-during-after control-impact experiment, we were able to evaluate the response of bats to lighting (i.e. attraction, avoidance, or no response; Fig. 1), while controlling for other confounding impacts of roads (e.g. vehicle presence, change in vegetation structure). We expected lighting to change the rate that bats cross through underpasses, and that species would show the same response to lighting in bridges and in culverts. We provide inference of the ecological consequences of lighting underpasses on bats based on changes in the number of bat passes and provide recommendations on lighting regimes in underpasses.

2. Methods and materials

2.1. Study area

We conducted this study along the Calder Freeway in Victoria, Australia, approximately 100–130 km to the north west of Melbourne. We studied a 40 km section of this highway, which was upgraded to a four-lane freeway between 2003 and 2009. The freeway has two lanes in each direction (each carriageway approximately 12 m wide, separated by a grassy median approximately 5–20 m in width), a maximum speed limit of 110 km/h and an average daily traffic volume ranging from 5500 to 9100 vehicles/day (average 6720 vehicles/day; VicRoads, 2015). Wildlife crossing structures, underpass bridges and culverts, were installed as part of the freeway upgrade. Bridges are large, open-span underpasses that varied in width (10–90 m), height (3.3–15 m), and length (entire width of double carriageway; 30–54 m) and had a natural floor of grassy vegetation and shrubs throughout them. Culverts are 3 m wide by 3 m high box culverts with a concrete floor, and were 24–67 m long (span of double carriageway). The landscape surrounding the freeway is a mosaic of cleared farmland, small towns and patches of heathy dry forest, with some grassy woodlands and box ironbark forest

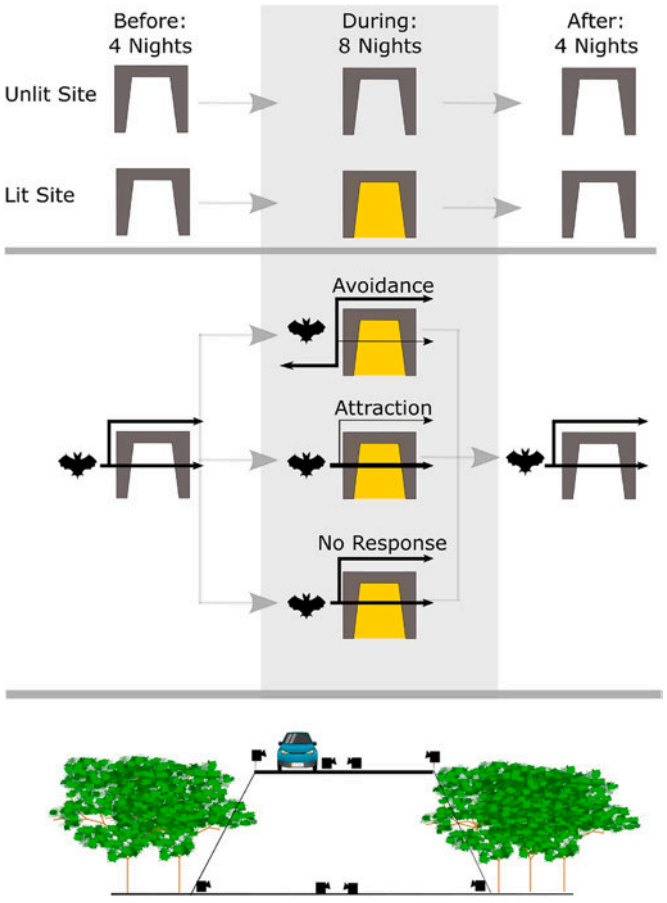

Fig. 1. Top: Experimental set up at lit and unlit crossing structures during the three phases of the trials: before, during and after. Note: the figure depicts two structures; these were replicated resulting in four structures used during each trial. Middle: Potential responses of bats to lighting in the underpasses: avoidance, attraction or no response. Arrow thickness indicates the change in crossing activity. Bottom: Detector placement above and under crossing structures to record the activity levels of bats. We installed four detectors under the underpass (under the road), and four detectors along the road above the underpass.

on both sides of the freeway (Costermans, 2006). Bridge sites were closed to the public, and only accessible by researchers and maintenance staff. Some culverts were used by local land-owners, where the highway transects their land. However, most of this usage would be during the day, and we would expect very little impact to the bats as they are only using these structures for foraging or commuting rather than roosting. For information on the structures, aerial images of sites, and map of sites, see supplementary information, Table S1, Figs. S1 and S2.

2.2. Experimental design

From December 2015 to March 2016 (Australian summer), we conducted a manipulative field experiment to test the effect of ALAN on bat use of underpasses. We compared bat activity before, during and after adding ALAN to underpasses (Fig. 1). In the before stage of the experiment, we collected bat passes for four nights to determine the baseline levels of activity at each underpass. In the during stage, we collected bat passes for eight nights to determine the immediate effect of lighting on bat activity at the underpasses. In the after stage, we monitored for a final four nights to determine if there were any lag effects of the light on behaviour (i.e. did crossing rates return to pre-light conditions after the lights were turned off). Each 16-night period is referred to as a 'trial'.

In each trial, we monitored four structures simultaneously: two

bridges and two culverts. One bridge and one culvert received the light treatment as described above, while the other bridge and culvert remained dark and acted as a control for the entire 16-night period (Fig. 1). This allowed us to account for nightly variation in bat activity unrelated to lighting in the underpasses. We had five independent bridge sites, and six independent culvert sites in our experimental design. Due to a limitation in availability of suitable sites, we rotated the lit and unlit treatments through the 11 sites to maximize replication (Table 1). Five sites that were initially used as an unlit site were used again. Two of these sites were unlit both times they were used, and three were treated with light in their subsequent trial. Sites were not used as an unlit site if light had been previously added, as this had potential to affect the response of bats. Simultaneously monitored structures were at least 2 km apart which is beyond the sampling range of the detectors and ensures independent sampling of each structure during an individual trial. We conducted four trials in total, thus, we had eight lit treatments (four bridges and four culverts) and eight complimentary unlit sites (four bridges and four culverts), across the 11 sites. A minimum of 10 nights elapsed between trials. Trials were not conducted on nights with a full moon or for four nights before and after the full moon.

We lit structures using cool white LED light strips (colour temperature 5500–6500 K) on 1 m × 1.2 m sheets of reflective metal, powered by 12 V batteries (henceforth referred to as a 'light fixture'). We used LED lighting due to its increasing use in urban lighting (Baumgartner et al., 2011; Kyba et al., 2017). In addition, LED lights attract fewer insects (Park and Lee, 2017), and therefore there are fewer foraging resources to attract bats and confound the comparisons, despite some bats continuing to forage near LED lights (Lewanzik et al., 2017). The number of light fixtures within each bridge or culvert varied according to size of the structure, with bridges lit with 8–12 light fixtures and culverts with 4–5 light fixtures. Light fixtures were evenly distributed along the sidewalls of the structure (Fig. 2), and were installed on the first day of the lighting period. Culverts only needed light fixtures on one side of the structure; whereas bridges had light fixtures on both sides in order to fully light the structure. We measured lux levels at 1 m intervals from each lighting fixture for the width of the crossing structure, by pointing an Extech HD450 light meter (Extech by FLIR Systems, Boston, Massachusetts, USA) towards the light strip in the middle of the fixture (bridges: mean 49.7 lux ± 2.8 s.e., culverts: mean 94.2 lux ± 4.1 s.e.; for reference, residential walkways are generally lit to 30 lux according to Australian & New Zealand Standards AS/NZS 1158.4; mean lux ± s.e. for each site is provided in supplementary information, Table S1). The lux levels in culverts were generally higher because of the confined space within the culvert compared to the bridges, resulting in more light reflectance throughout the structure.

2.3. Monitoring the crossing activity of bats

In order to monitor the activity levels of bats above and under each structure, we deployed eight ultrasonic bat detectors (Anabat SD1 and SD2 model detectors, Titley Electronics, Ballina, New South Wales, Australia) at each underpass for the full 16 nights of each trial. We used four detectors under the structure (two in the middle and one at each entrance, all facing towards the middle of the structure), and four detectors on the freeway above the structure (two in the centre median and one on each edge, facing towards the middle of the carriageway; Fig. 1). Detectors were equipped with directional microphones and were orientated 45° towards the sky, pointing towards the middle of the freeway. By using directional rather than omnidirectional microphones, echolocation calls were only detected when the bat flew directly in front of the microphone ([redacted]). The orientation of the four microphones towards the centre of the freeway was to reduce the risk of recording individuals flying along the roadside, and instead primarily detect those bats that flew through the structures or above the freeway respectively. This was checked by comparing the mean number of bat passes at each detector location (supplementary material Figs. S3 and S4). Henceforth, detector locations are referred to as "position," and

Table 1
Arrangement of sites used in each trial of the experiment. Grey shading indicates the structure surveyed in each trial, with sites marked 'L' and 'U' showing which sites were lit and unlit, respectively, during each trial. Letters beside site names correspond to the site letters in tables and figures in the supplementary information. Note: some sites were used in two trials; however, they were always unlit in the first trial.

		Trial			
Structure Type	Site Name	1	2	3	4
Bridge	A. Barker's Creek	U		L	
Bridge	B. Coliban River			U	U
Bridge	C. Forest Creek		U		L
Bridge	D. Post Office Rd		L		
Bridge	E. South Black Jack Rd	L			
Culvert	F. Bendigo-Sutton Grange Rd			U	
Culvert	G. Black Jack Rd		U		L
Culvert	H. Ellery's Rd			L	
Culvert	I. Specimen Gully trail		L		
Culvert	J. Specimen Gully Rd	L			
Culvert	K. Symes Rd	U			U

Fig. 2. Examples of a lit bridge (left; South Black Jack Rd) and a lit culvert (right; Ellery's Rd) used in this study.

there are 2 possible positions: above structure, under structure. Recording began half an hour before sunset and ended a half hour after sunrise. We downloaded data from detectors every day. Batteries were replaced at each morning of the trials with fully charged batteries, and the structures were observed from the highway above the underpasses at the start of each night to ensure all lights turned on each night.

Bats can have three possible responses to lit underpasses: (1) they avoid the lit underpass, (2) they are attracted to the lit underpass and (3) there is no observable response to the lighting (Fig. 1). When there is less activity under lit structures, compared to when they are unlit, this is deemed an 'avoidance'. When there is more activity when the structures are lit, compared to when they are unlit, this is deemed an 'attraction'. Finally, when there are similar levels of activity under structures between lit and unlit conditions, this is deemed 'no response'.

We identified the recorded bat passes to species level using the automated AnaScheme Bat Call Analysis System v1.0 (Gibson and Lumsden, 2003; Adams et al., 2010) with a key developed for this region using locally-collected reference calls (Lumsden and Bennett, 2005). Species identification was only attempted if there were five or more valid pulses in the bat pass, and deemed successfully identified when >50% of the pulses in a bat pass were assigned to the same species. We assigned bat passes to 10 species/species groups: *Austronomus australis, Chalinolobus gouldii, C. morio, Ozimops planiceps, O. ridei, Nyctophilus-Myotis* species group*, Scotorepens balstoni, Vespadelus darlingtoni, V. regulus,* and *V. vulturnus.* The key was unable to reliably differentiate *Nyctophilus geoffroyi, N. gouldi* and *Myotis macropus* calls, therefore we grouped these calls into a '*Nyctophilus-Myotis* species group.' The key was also prone to misattributing insect or background noise to *A. australis* calls, so we visually confirmed all files identified as this species. Each species had different detectability and the key had some biases in identifiability due to the overlap in call characteristics, and therefore, we do not compare the number of bat passes among species but only within species between treatments. We calculated the mean number of bat passes per night from all detectors above or under each structure (i.e. at each position: above bridge, under bridge, above culvert and under culvert) for each species and rounded to the nearest whole number, as an indication of nightly crossing activity above and under the structures (mean and standard error number of each species' passes collected each night at each structure is given in the supplementary information, Tables S2 and S3). 'Overall number of passes' reflects the sum of the number of passes from all species and the species group. Finally, as we cannot identify individuals from bat passes, it is important to remember the results refer to levels of activity and not as an indication of population size.

2.4. Statistical analysis

To explore the change in number of bat passes throughout the trials, we fitted Poisson regression models to the count of nightly crossings (R) as a response. Preliminary analyses indicated over-dispersion in the data, compared to a Poisson model. To account for this over-dispersion, we estimated additional variance in the rate of the Poisson using a gamma distribution. This formulation of the negative binomial model as a Poisson-gamma mixture is often used for count data with over-dispersion (Plummer, 2003). Models were fitted for the overall number of bat passes (sum of passes for all species combined), and for each species/species group separately. Bridge data was modelled separately from culvert data. So, for each data point, i (number of passes in each position per night) the Poisson-gamma regression models can be described as follows:

$$R_i \sim Poisson(\lambda_i * r)$$
$$\lambda_i \quad \exp(\beta_1 a_i + \beta_2 b_i + \beta_3 c_i + \beta_4 d_i + \beta_5 e_i + \beta_6 f_i + \beta_7 T_i + \beta_8 M_i + \beta_9 S_i + \varepsilon_{x(i)})$$
$$r \sim gamma\,(z, z)$$

with λ_i the mean number of passes for data point i, and z the shape and rate parameters of the gamma distribution. Indicator variables a_i to f_i represent the combination of light treatment phase and detector position. Indicator variables a_i and b_i, take value 1 when data point i comes from "above the structure", or "under the structure" respectively, and represent when the structures are unlit; otherwise, their value is 0. Variables c_i and d_i are the indicators (above/under respectively) when the underpasses are lit underneath. Indicator variables e_i and f_i are equivalent indicators, after the lights are turned off in the structures. Together, these indicator variables (c_i to f_i) represent an additive effect to their respective intercept (a_i, b_i, i.e. the baseline pulse rate), so e.g. for data from under bridge before lighting, only b_i 1, but for data from under bridge while it is lit, b_i 1 and f_i 1). This structure represents a model with full interaction between the position in the crossing structure and the phase of the experiment before/during/after, both categorical variables). We chose this over a simple additive effect to allow for more complex responses (i.e. different effect of light at different positions), for example to allow for the effect above bridge/culvert to be different from the effect under bridge/culvert. The model also accounts for other nuisance parameters: T_i represents maximum daily temperature; M_i represents the moon phase (0 for new moon; 1 for first or last quarter; we did not conduct any trials during a full moon) and S_i is a categorical variable that represents the trial (1–4) to account for any changes in bat activity throughout the season and between trials. We also included a random effect for the eleven sites, $\varepsilon_{x(i)}$ to account for site-level (spatial) variation, and the fact that some sites were sampled twice,

during different trials.

All model fitting was conducted within a Bayesian framework of inference using Markov Chain Monte Carlo (MCMC) sampling, by calling JAGS 4.1.0 (Plummer, 2003) from R (v3.3.2; R Core Team, 2019) using package R2jags (Su and Yajima, 2015). Vague uninformative priors were used for all regression coefficients: uniform distributions U (10,10). We ran three MCMC chains for each parameter, keeping 50,000 samples from each chain after discarding a burn-in of 50,000. We assessed convergence by visual inspection of the chains and using the statistic R-hat (assuming no evidence of lack of convergence for values below 1.01).

To test for model fit, we conducted posterior predictive checks by calculating Bayesian p-values based on the Freeman-Tukey statistic as a measure of discrepancy (0.5 indicating perfect fit, with values between 0.2 and 0.8 deemed acceptable; King et al., 2009). At bridges, Bayesian p-values for most species were between 0.29 and 0.59, however low p-values suggest some lack of fit for *S. balstoni* (Bayesian p-value 0) and *V. regulus* (Bayesian p-value 0.06). At culverts, Bayesian p-values for all species were between 0.17 and 0.78, suggesting some lack of fit only for *V. regulus* (Bayesian p-value 0.17); the results for these two species should be taken with some scrutiny.

3. Results

When the structures were lit, the overall number of bat passes of all species combined decreased under the structures and increased above the structures, relative to the baseline levels (Fig. 3). After the lighting was removed, the overall number of bat passes was closer to the baseline levels over the next four nights, but did not return to baseline levels entirely. Species varied in their response to lighting in culverts and bridges and therefore these are discussed separately below.

3.1. Species-specific response to ALAN in bridges

Eight out of ten species/species groups avoided lit bridges (i.e. the number of passes under bridges was lower when they were lit compared to when they were unlit; Fig. 4, for mean and standard error see supplementary information Table S4). These species are: *C. gouldii*, *C. morio*, the *Nyctophilus-Myotis* species group, *O. planiceps, O. ridei, V. darlingtoni, V. regulus* and *V. vulturnus*. When structures were lit, *C. gouldii, C. morio, O. planiceps, O. ridei, V. darlingtoni,* and *V. regulus* were more active above the road than when the structures were unlit. Contrastingly, the *Nyctophilus-Myotis* species group had fewer bat passes over bridges when they were lit, and *V. vulturnus* had similar levels of bat passes above bridges when the bridges were lit compared to baseline levels. After the lights were turned off, activity tended to return to baseline levels for each species under bridges. The only exception being the *Nyctophilus-Myotis* species group, which had more than baseline activity under bridges after the lighting was turned off. Above bridges, the number of bat passes of *C. gouldii*, the *Nyctophilus-Myotis* species group, and *O. ridei,* approached their baseline activity after lighting was turned off, however the average activity of *C. morio, O. planiceps, V. darlingtoni, V. regulus,* and *V. vulturnus,* was higher than baseline during the four nights after the lighting was turned off. *Austronomus australis* was the only species to be attracted to the lit bridges (Fig. 4), and it was more active both under and above lit bridges compared to baseline levels. After the lighting treatments, the number of passes of *A. australis* under and above bridges returned to before-light levels. Finally, *S. balstoni* showed no response to the lit bridges, as their number of passes under bridges did not change when the structures were lit (Fig. 4).

3.2. Species-specific response to ALAN in culverts

In general, there were fewer bat passes under culverts than under bridges, even without the addition of ALAN (Supplementary information, Tables S3 and S5; Figs. S3 and S4). *C. morio*, the *Nyctophilus-Myotis* species group, *O. ridei*, and *V. regulus* avoided lit culverts (Fig. 5). *C. morio* and *O. ridei* had more bat passes above lit culverts compared to baseline levels, while the *Nyctophilus-Myotis* species group had fewer, and *V. regulus* had similar amount of bat passes compared to before the structure were lit. Comparatively, *A. australis* and *C. gouldii* were attracted to lit culverts and also had a higher number of bat passes over

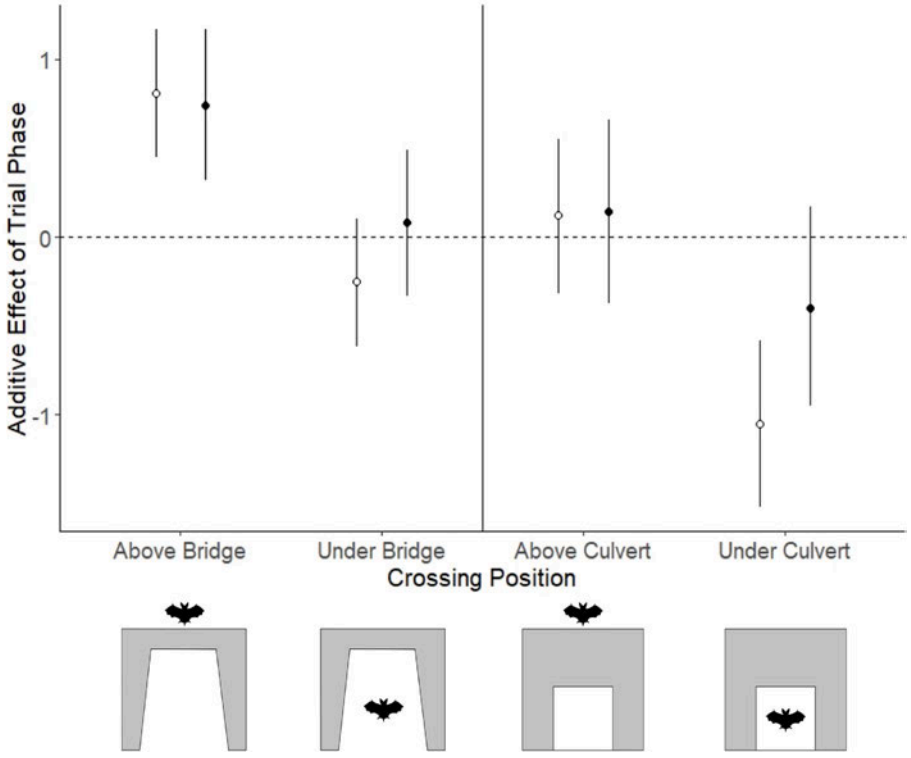

Fig. 3. Estimates of the regression coefficients from the model estimating nightly number of bat passes of all species combined. Estimates depict the additive effect of each phase: during lighting (open circles, β_3 β_4) and after lighting (closed circles, β_5 β_6), relative to baseline (dotted line at 0, β_1 β_2), above and under bridges (n = 5), and culverts (n = 6). Error bars show 95% credible intervals. Credible intervals that overlap zero show no significant change from baseline, > 0 indicate a significant positive effect and <0 indicate a significant negative effect.

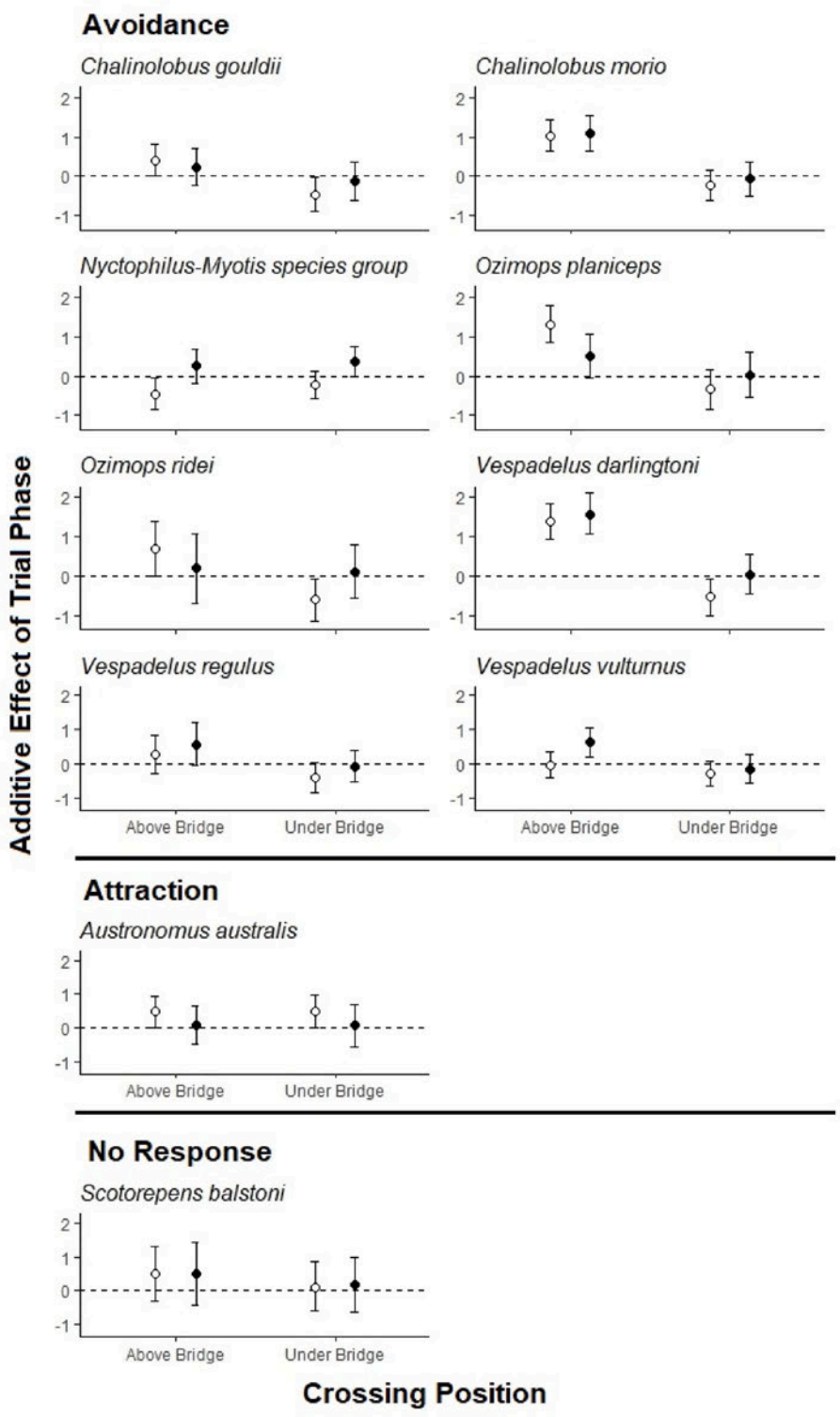

Fig. 4. Estimates of the regression coefficients from the models estimating nightly numbers of bat passes for each species above and under bridges (n = 5), during lighting (open circles, β_3 and β_4) and after lighting (closed circles, β_5 and β_6) relative to baseline activity levels (dotted line at 0, β_1 β_2). Error bars show 95% credible intervals. Credible intervals that overlap zero show no significant change from baseline, > 0 indicate a significant positive effect and <0 indicate a significant negative effect.

lit culverts compared to baseline levels. Finally, *O. planiceps, S. balstoni, V. darlingtoni,* and *V. vulturnus* showed no response to lighting in culverts.

After lighting, the number of bat passes for most species under the culverts returned to baseline, with the only exception being *O. ridei*, which had fewer bat passes than baseline under culverts during the four nights after the lighting was turned off (Fig. 5). Above culverts, after lighting was turned off, the number of bat passes *for O. ridei, V. regulus*, and *C. gouldii* returned to baseline, while *C. morio* and *A. australis* had higher bat passes and the *Nyctophilus-Myotis* species group had fewer bat passes compared to baseline levels.

4. Discussion

In this study, we evaluated the impact of ALAN on the rate of use of underpasses by insectivorous bats while holding other confounding variables, such as vegetation structure and traffic disturbance, constant. We determined that lighting in underpasses reduced the activity levels

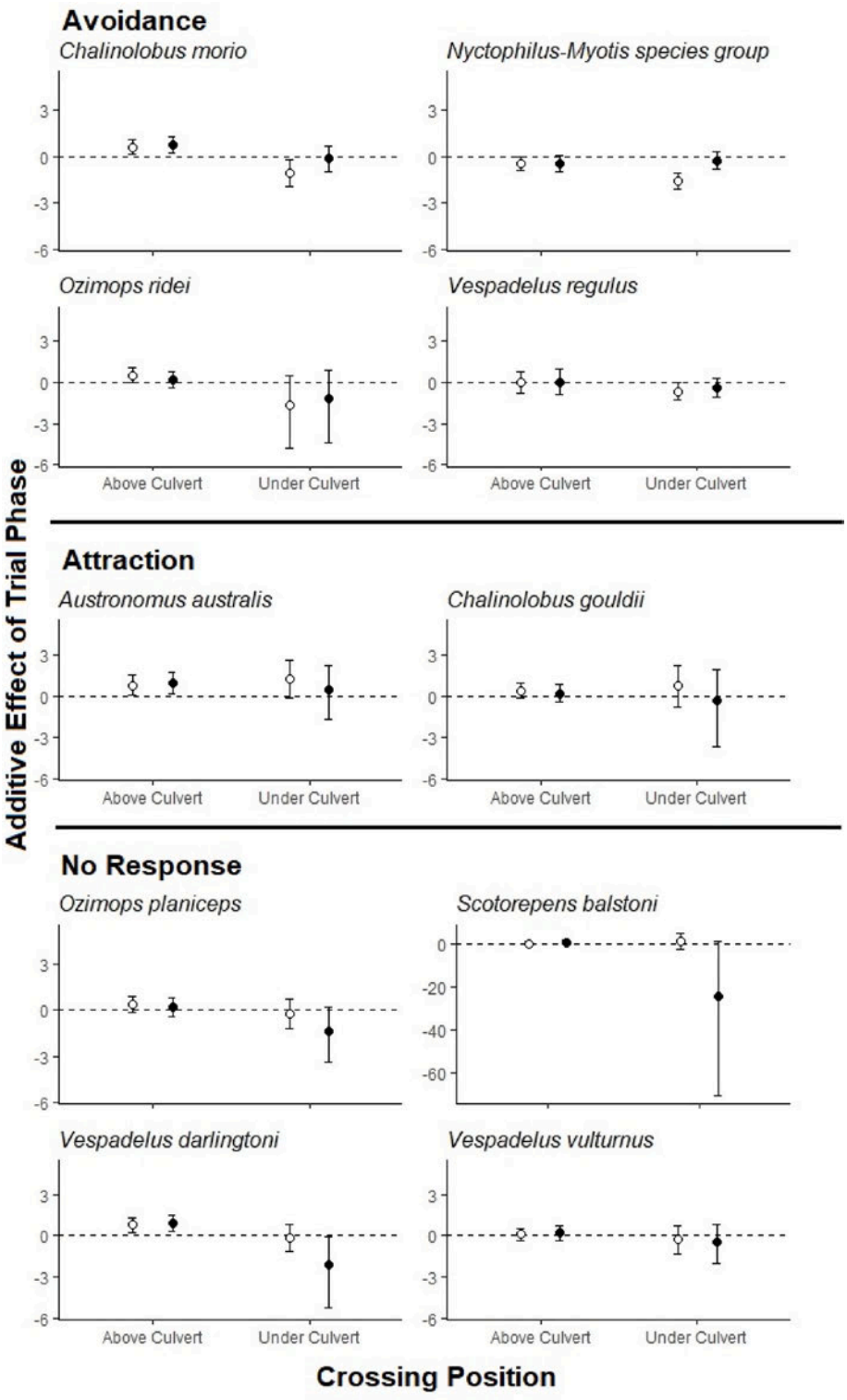

Fig. 5. Estimates of the regression coefficients from the models estimating the nightly number of bat passes for each species above and under culverts (n = 6), during lighting (open circles, β_3 and β_4) and after lighting (closed circles, β_5 and β_6)) relative to baseline activity levels (dotted line at 0, β_1 β_2). Error bars show 95% credible intervals. Points and credible intervals that overlap zero show no change from baseline, > 0 indicate a significant positive effect and <0 indicate a significant negative effect.

of most bat species. Similar patterns have been found for other nocturnal terrestrial mammals (Bliss-Ketchum et al., 2016), suggesting that lights are likely to overall have a negative impact on underpass use by a range of nocturnal wildlife. When wildlife crossing structures are primarily installed to provide a safe pathway for fauna to move across roads, then modifications that reduce the likelihood of achieving these objectives should be avoided, even if the modifications could make underpasses more accessible for human-use.

4.1. Species-specific response to ALAN in bridges

Eight species (or species group) of bats in this study avoided lit bridges (Fig. 4). Furthermore, we hypothesized two potential ecological consequences of ALAN in underpasses: increased risk of road-mortality (i.e. increased activity levels above the freeway compared to baseline levels - *C. gouldii, C. morio, O. planiceps, O. ridei, V. darlingtoni,* and *V. regulus*), or increased barrier effects (i.e. reduced activity levels above the freeway compared to baseline levels - the *Nyctophilus-Myotis* species

group and *V. vulturnus*) as a result of avoiding lit bridges. Species such *as C. gouldii, C. morio, V. regulus,* and *V. darlingtoni* tend to fly at close to the edge of landscape features (e.g. trees, and in our case, the freeway and vehicles; O'Neill and Taylor, 1986; Fullard et al., 1991), which may potentially increase their susceptibility of colliding with vehicles when crossing the freeway. On the other hand, the *Nyctophilus-Myotis* species group, and *V. vulturnus* did not compensate for the reduction in crossing under bridges by crossing more above the freeway. These species may avoid the freeway due to the gap created in the canopy (e.g. Hale et al., 2015), noise impacts (e.g. Schaub et al., 2008; Siemers and Schaub, 2011), or due to the presence of vehicles (e.g. Zurcher et al., 2010), but will often cross the freeway through unlit bridges (Bhardwaj et al., 2017). Therefore, for the *Nyctophilus-Myotis* species group, and *V. vulturnus,* ALAN in the bridges hypothetically exacerbates the barrier effect of roads and reduces connectivity in the landscape. Overall, ALAN reduces the effectiveness of underpass bridges and thus should be avoided where wildlife crossing is a primary aim of the underpasses.

Austronomus australis was attracted to lit underpasses. It is a high-flying species (Luck et al., 2013), that rarely uses underpasses (Bhardwaj et al., 2017), however when bridges were lit, they were more active under the bridges than when the bridges were unlit. This species can exploit light as a foraging resource (Threlfall et al., 2012), and it may be possible that the lighting drew the species in, with individuals spending more time around the light due to the increased availability of forage, despite LED lights attracting fewer insects than other lighting. Thus, lighting crossing structures could potentially be advantageous for *A. australis.*

Species of the *Ozimops* genus are high-flying species (Reside and Lumsden, 2011) that tend to be tolerant of roads. They typically fly in open landscapes (Reside and Lumsden, 2011), and are more active near freeways than the other species in this region (Bhardwaj et al. *unpub*). *Ozimops* species rarely use underpasses, and instead readily cross the canopy gap by flying high above the road (Bhardwaj et al., 2017). Despite this apparent tolerance of the freeway, *Ozimops* species avoided lit crossing structures. This is in contrast to the current literature which suggests that those species within the 'high and fast flying' guild, are more tolerant and potentially exploitive of urban lighting (Threlfall et al., 2012; Schoeman, 2016). Therefore, further study into the species-specific response of bats to ALAN is necessary, and broad generalizations should be used with caution.

4.2. Species-specific response to ALAN in culverts

Bats rarely used culverts in comparison to bridges (Supplementary information, Tables S3 and S5; Figs. S3 and S4). This may be because bridges are more open and taller than culverts, with a natural floor of grassy vegetation and shrubs throughout that provides an almost continuous connection to the surrounding habitat (Bhardwaj et al., 2017). Alternatively, culverts are smaller and concrete throughout, and likely do not connect the landscape as well as bridges or provide foraging habitat (Bhardwaj et al., 2017). For the species where we were able to determine a response to lighting, the trends were similar to those shown at lit bridges. *C. morio* and *O. ridei* avoided lit culverts, while compensating by flying over the culverts more. The *Nyctophilus-Myotis* species group avoided lit culverts and did not go over the freeway more in compensation, thus a lit culvert hypothetically exacerbated the barrier effect of the freeway for these species. Interestingly, *V. regulus* did not have more passes over lit culverts as they did over lit bridges, and thus also hypothetically had increased susceptibility to the barrier effect of the freeway. As *V. regulus* activity over lit bridges was only marginally higher than unlit bridges, it stands to reason that lighting in underpasses may contribute to barrier effects at both location types, but more data may be necessary to draw precise conclusions. *C. gouldii* showed an interesting response and they avoided lit bridges, but were attracted to lit culverts. This may suggest that the use of culverts can be improved for *C. gouldii* with lighting, but like *V. regulus,* more data would be necessary to test this.

One could argue that culverts would be the ideal underpass to adapt for human co-use, as it would have negligible impacts on bat use, however, this would compromise the conservation goals of the culverts. Despite their low use, if culverts are the only wildlife crossing structures present in the landscape, they should not be lit because that can have adverse effects on the few species that do benefit from the structures.

4.3. Future directions and conclusions

The impact of ALAN on bats can differ based on the spectra, extent and intensity of light. For example, research has shown that some bats are more averse to white LEDs compared to other LED light spectra (Spoelstra et al., 2017). It may be possible that structures lit with different colours of light (e.g. red LED light) would attract more insects (Park and Lee, 2017), and repel fewer bats (Spoelstra et al., 2017, 2018), and therefore may potentially increase crossing structure use by bats, while still providing enough light for visibility for people. It is essential to note that if lighting of different spectra has the potential to increase the activity of bats, the lighting should be placed within the structure and not near the opening or along the roadside, lest bats be inadvertently attracted to the road, which may increase the risk of road-mortality. Secondly, bats may habituate to the presence of lighting. Bats inhabit urban areas with high levels of lighting (e.g. Caryl et al., 2016) and it is possible that the exposure to light in this experiment was over too few nights to capture the ability of bats to habituate to lighting. Finally, the findings from our study contradict one previous study which shows no change in culvert use by *Myotis daubentonii* in the Netherlands (Spoelstra et al., 2018), however this may be because the structures in our study were lit more intensely (i.e. higher lux) than those in the European study. This raises the question: is there a threshold to which light intensity may be tolerable for more species? Future studies into the impacts of different light spectra, lighting durations and lighting intensities would be valuable to fully understanding the impacts on wildlife of ALAN in underpasses.

Our results support other studies that show ALAN has a negative impact on bats. ALAN leads to reduced commuting (Stone et al., 2009; Laforge et al., 2019), or drinking behaviour in bats, (Russo et al., 2017, 2018), and can also contribute to roost abandonment (Boldogh et al., 2007; Rydell et al., 2017). The only documented benefit ALAN offers appears to be to provide increased foraging opportunity for some species (Rydell 1992, 2013; Blake et al., 1994). However, these results are not consistent across all bat species, and other studies have also demonstrated reduced foraging behaviour near ALAN (Stone et al., 2009; Russo et al., 2019). Overall, the current literature suggests that ALAN has more negative impacts on insectivorous bats than positive ones, but further investigations on the impact of ALAN on specific behaviours is warranted to better understand the effect of ALAN on the ability of bats to persist in a lit landscape.

While we found that ALAN had mostly a negative effect on bat use of underpasses, there are still ways in which wildlife crossing structures can be adapted for human co-use. Including a walking or cycling path under a bridge would cause minimal disturbance to bats as long as the structures remained unlit, vegetation was maintained throughout and the recreational path was clearly defined and fenced to keep people from venturing into the 'wildlife-side' of the structure (van der Ree and van der Grift, 2015). Where ALAN cannot be avoided, the aim should be to reduce the level of disturbance as much as possible. Shielding and directing light so it only illuminates the recreational path could be one solution (Blackwell et al., 2015). Alternatively, structures may be lit on a push-button, sensor or timer system, reducing the amount of time they are lit. Finally, if these options are not available, co-use should be restricted to culverts (the lesser-used structure type) where possible. Human co-use of culverts may have negligible impacts on wildlife, provided there are more effective structures like bridges available nearby for them to use instead of culverts. Creating mitigation strategies

that are both wildlife and human-friendly may be the way forward in conservation management, however careful design and planning is necessary before changing existing strategies designed specifically for wildlife to accommodate human-use.

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.

CRediT authorship contribution statement

M. Bhardwaj: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing, Visualization, Funding acquisition. **K. Soanes:** Conceptualization, Methodology, Formal analysis, Writing - review & editing, Supervision. **J.J. Lahoz-Monfort:** Formal analysis, Writing - review & editing, Supervision. **L.F. Lumsden:** Conceptualization, Methodology, Formal analysis, Writing - review & editing, Resources, Supervision. **R. van der Ree:** Conceptualization, Methodology, Formal analysis, Writing - review & editing, Resources, Supervision, Funding acquisition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at [redacted]

References

Abbott, I.M., Harrison, S., Butler, F., 2012. Clutter-adaptation of bat species predicts their use of under-motorway passageways of contrasting sizes - a natural experiment. J. Zool. 287, 124–132.

Adams, M.D., Law, B.S., Gibson, M.S., 2010. Reliable automation of bat call identification for eastern New South Wales, Australia, using classification trees and AnaScheme software. Acta Chiropterol. 12, 231–245.

Baumgartner, T., Wunderlich, F., Wee, D., Jaunich, A., 2011. Lighting the Way: Perspectives on the Global Lighting Market. New York City, NY, USA.

Bennett, V.J., Zurcher, A.A., 2013. When corridors collide: road-related disturbance in commuting bats. J. Wildl. Manag. 77, 93–101.

Bhardwaj, M., Soanes, K., Straka, T.M., Lahoz-Monfort, J.J., Lumsden, L.F., van der Ree, R., 2017. Differential use of highway underpasses by bats. Biol. Conserv. 212, 22–28.

Blackwell, B.F., DeVault, T.L., Seamans, T.W., 2015. Understanding and mitigating the negative effect of road lighting on ecosystems. In: van der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology. John Wiley & Sons, Ltd., Chichester, West Sussex, pp. 143–150.

Blake, D., Hutson, A.M., Racey, P.A., Rydell, J., Speakman, J.R., 1994. Use of lamplit roads by foraging bats in southern England. J. Zool. 234, 453–462.

Bliss-Ketchum, L.L., de Rivera, C.E., Turner, B.C., Weisbaum, D.M., 2016. The effect of artificial light on wildlife use of a passage structure. Biol. Conserv. 199, 25–28.

Boldogh, S., Dobrosi, D., Samu, P., 2007. The effects of the illumination of buildings on house-dwelling bats and its conservation consequences. Acta Chiropterol. 9, 527–534.

Caryl, F.M., Lumsden, L.F., van der Ree, R., Wintle, B.A., Minderman, J., 2016. Functional responses of insectivorous bats to increasing housing density support 'land-sparing' rather than 'land-sharing' urban growth strategies. J. Appl. Ecol. 53 [redacted] Publishing,

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

Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., Fahrig, L., France, R., Goldman, C.R., Heaue, K., Jones, J.A., Swanson, F.J., Turrentine, T., Winter, T.C., 2003. Road Ecology: Science and Solutions. Island Press, Washington, DC, USA.

Fullard, J.H., Koehler, C., Surlykke, A., McKenzie, N.L., 1991. Echolocation ecology and flight morphology of insectivorous bats (Chiroptera) in South-Western Australia. Aust. J. Zool. 39, 427–438.

Gibson, M., Lumsden, L., 2003. The Anascheme automated bat call identification system. The Australasian Bat Society Newsletter 20, 24–26.

Hale, J.D., Fairbrass, A.J., Matthews, T.J., Davies, G., Sadler, J.P., 2015. The ecological impact of city lighting scenarios: exploring gap crossing thresholds for urban bats. Global Change Biol. 21, 2467–2478.

Jung, K., Threlfall, C.G., 2016. Urbanisation and its effects on bats—a global meta-analysis. In: Voigt, C.C., Kingston, T. (Eds.), Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer Science+ Business Media, pp. 13–33.

King, R., Morgan, B., Gimenez, O., Brooks, S., 2009. Bayesian Analysis for Population Ecology. Chapman and Hall/CRC.

Kyba, C.C.M., Kuester, T., Sanchez de Miguel, A., Baugh, K., Jechow, A., Holker, F., Bennie, J., Elvidge, C.D., Gaston, K.J., Guanter, L., 2017. Artificially lit surface of Earth at night increasing in radiance and extent. Sci. Adv. 3, e1701528.

Laforge, A., Pauwels, J., Faure, B., Bas, Y., Kerbiriou, C., Fonderflick, J., Besnard, A., 2019. Reducing light pollution improves connectivity for bats in urban landscapes. Landsc. Ecol. 34, 793–809.

Lesiński, G., Sikora, A., Olszewski, A., 2011. Bat casualties on a road crossing a mosaic landscape. Eur. J. Wildl. Res. 57, 217–223.

Lewanzik, D., Voigt, C.C., Minderman, J., 2017. Transition from conventional to light-emitting diode street lighting changes activity of urban bats. J. Appl. Ecol. 54, 264–271.

Longcore, T., Rich, C., 2004. Ecological light pollution. Front. Ecol. Environ. 2, 191–198.

Luck, G.W., Smallbone, L., Threlfall, C., Law, B., 2013. Patterns in bat functional guilds across multiple urban centres in south-eastern Australia. Landsc. Ecol. 28, 455–469.

Lumsden, L.F., Bennett, A.F., 2005. Scattered trees in rural landscapes: foraging habitat for insectivorous bats in south-eastern Australia. Biol. Conserv. 122, 205–222.

Medinas, D., Marques, J.T., Mira, A., 2013. Assessing road effects on bats: the role of landscape, road features, and bat activity on road-kills. Ecol. Res. 28, 227–237.

Medinas, D., Ribeiro, V., Marques, J.T., Silva, B., Barbosa, A.M., Rebelo, H., Mira, A., 2019. Road effects on bat activity depend on surrounding habitat type. Sci. Total Environ. 660, 340–347.

O'Neill, M.G., Taylor, R.J., 1986. Observations on the flight patterns and foraging behavior of Tasmanian bats. Wildl. Res. 13, 427–432.

Park, J.H., Lee, H.S., 2017. Phototactic behavioral response of agricultural insects and stored-product insects to light-emitting diodes (LEDs). Appl. Biol. Chem. 60, 137–144.

Plummer, M., 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Reside, A.E., Lumsden, L.F., 2011. Resource partitioning by two closely-related sympatric freetail bats, *Mormopterus* spp. In: Law, B., Eby, P., Lunney, D., Lumsden, L. (Eds.), Biology and Conservation of Australasian Bats. Royal Zoological Society New South Wales, Sydney, pp. 155–166.

Rowse, E., Lewanzik, D., Stone, E., Harris, S., Jones, G., 2016. Dark matters: the effects of artificial lighting on bats. Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer Science+ Business Media, pp. 187–213.

Russo, D., Ancillotto, L., Cistrone, L., Libralato, N., Domer, A., Cohen, S., Korine, C., 2018. Effects of artificial illumination on drinking bats: a field test in forest and desert habitats. Anim. Conserv. 22, 124–133.

Russo, D., Cistrone, L., Libralato, N., Korine, C., Jones, G., Ancillotto, L., 2017. Adverse effects of artificial illumination on bat drinking activity. Anim. Conserv. 20, 492–501.

Russo, D., Cosentino, F., Festa, F., De Benedetta, F., Pejic, B., Cerretti, P., Ancillotto, L., 2019. Artificial illumination near rivers may alter bat-insect trophic interactions. Environ. Pollut. 252, 1671–1677.

Rydell, J., 1992. Exploitation of insects around streetlamps by bats in Sweden. Funct. Ecol. 6, 744–750.

Rydell, J., 2013. Bats and their insect prey at streetlights. In: Rich, C., Longcore, T. (Eds.), Ecological Consequences of Artificial Night Lighting. Island Press, pp. 43–60.

Rydell, J., Eklof, J., Sanchez-Navarro, S., 2017. Age of enlightenment: long-term effects of outdoor aesthetic lights on bats in churches. Royal Society Open Science 4, 161077.

Sawaya, M.A., Kalinowski, S.T., Clevenger, A.P., 2014. Genetic connectivity for two bear species at wildlife crossing structures in Banff National Park. Proc. Biol. Sci. 281, 20131705.

Schaub, A., Ostwald, J., Siemers, B.M., 2008. Foraging bats avoid noise. J. Exp. Biol. 211, 3174–3180.

Schoeman, M.C., 2016. Light pollution at stadiums favors urban exploiter bats. Anim. Conserv. 19, 120–130.

Siemers, B.M., Schaub, A., 2011. Hunting at the highway: traffic noise reduces foraging efficiency in acoustic predators. Proc. Biol. Sci. 278, 1646–1652.

Smith, D.J., van der Ree, R., Rosell, C., 2015. Wildlife crossing structures: an effective strategy to restore or maintain connectivity across roads. In: van der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology. John Wiley & Sons, Ltd., Chichester, West Sussex, pp. 172–183.

Soanes, K., Lobo, M.C., Vesk, P.A., McCarthy, M.A., Moore, J.L., van der Ree, R., 2013. Movement re-established but not restored: inferring the effectiveness of road-

crossing mitigation for a gliding mammal by monitoring use. Biol. Conserv. 159, 434–441.
Soanes, K., Taylor, A.C., Sunnucks, P., Vesk, P.A., Cesarini, S., van der Ree, R., Wiersma, Y., 2018. Evaluating the success of wildlife crossing structures using genetic approaches and an experimental design: lessons from a gliding mammal. J. Appl. Ecol. 55, 129–138.
Spoelstra, K., Ramakers, J.J.C., van Dis, N.E., Visser, M.E., 2018. No effect of artificial light of different colors on commuting Daubenton's bats (*Myotis daubentonii*) in a choice experiment. J. Exp. Zool. Part A: Ecological and Integrative Physiology 329, 506–510.
Spoelstra, K., van Grunsven, R.H.A., Ramakers, J.J.C., Ferguson, K.B., Raap, T., Donners, M., Veenendaal, E.M., Visser, M.E., 2017. Response of bats to light with different spectra: light-shy and agile bat presence is affected by white and green, but not red light. Proc. Biol. Sci. 284, 20170075.
Stone, E.L., Jones, G., Harris, S., 2009. Street lighting disturbs commuting bats. Curr. Biol. 19, 1123–1127.
Su, Y.-S., Yajima, M., 2015. R2jags: using R to Run 'JAGS'. R Package Version 0.5-7.
Threlfall, C.G., Law, B., Banks, P.B., 2012. Sensitivity of insectivorous bats to urbanization: implications for suburban conservation planning. Biol. Conserv. 146, 41–52.
van der Ree, R., Jaeger, J.A.G., van der Grift, E.A., Clevenger, A.P., 2011. Effects of roads and traffic on wildlife populations and landscape function: road ecology is moving toward larger scales. Ecol. Soc. 16, 48.
van der Ree, R., van der Grift, E.A., 2015. Recreational co-use of wildlife crossing structures. In: van der Ree, R., Smith, D.J., Grilo, C. (Eds.), Handbook of Road Ecology. John Wiley & Sons, Ltd., Chichester, West Sussex, pp. 184–189.
Zurcher, A.A., Sparks, D.W., Bennett, V.J., 2010. Why the bat did not cross the road? Acta Chiropterol. 12, 337–340.