Differential use of highway underpasses by bats

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A B S T R A C T

Roads can form barriers to movement for many species, and may reduce the ability of individuals to access foraging and breeding habitat. The impacts of roads on terrestrial fauna has been well studied, however little is known of the impact of roads on insectivorous bats. Wildlife crossing structures (e.g. fauna underpasses) may reduce the barrier impacts of roads and improve connectivity across roads. Use of underpasses by wildlife likely varies among species depending on their movement behaviour. In this study, we investigated whether the flight patterns of insectivorous bats influenced their use of underpasses. We monitored bat activity under and above 6 open-span bridges, 6 box culverts and 6 unmitigated sites along a major highway in Australia. We used Poisson regression models within a Bayesian framework of inference to compare the activity of 12 bat species (grouped into three guilds based on their flight patterns: clutter-adapted, edge-adapted, and open-adapted species) under the structures, over the road above the structures, above unmitigated segments of the highway, and in the vegetation adjacent to the roads. Bats were less active above the road than they were in the surrounding vegetation or under bridges. Two of the three guilds (i.e. seven species) crossed the highway more under bridges than they did under culverts or by going over the road, which suggests that bridges may reduce barrier effects of the road better than culverts. Installing bridges instead of culverts may better reduce the impacts of roads on multiple insectivorous bats species with a single structure type.

1. Introduction

Roads and traffic can reduce the persistence of wildlife populations, particularly when they restrict the access of individuals to breeding or foraging habitats (Forman et al., 2003). Fauna crossing structures are commonly installed to facilitate the safe movement of animals across landscapes fragmented by roads or other linear infrastructure, which helps to increase habitat accessibility (Smith et al., 2015). Environmental or structural factors, such as their position within the landscape, accessibility by individuals, and structure size, are often thought to influence the rate at which fauna crossing structures are used (e.g. Ascensão and Mira, 2007; Chambers and Bencini, 2015; Clevenger and Waltho, 2000, 2005), however, species traits and ecologies may also influence structure use (e.g. Abbott et al., 2012a; Abbott et al., 2012b). In addition to environmental factors, it may be informative to evaluate species' ecologies and behaviour in order to predict their response to roads (Rytwinski and Fahrig, 2012) and crossing structures (Abbott et al., 2012a; Abbott et al., 2012b).

Categorising species into guilds using ecological traits can help us to infer the response of a group of species to environmental change without having to study each species individually, increasing ecological transferability of knowledge. For example, ecological traits have been used to determine guilds of drought-tolerant plant species (e.g. Ouedraogo et al., 2013), urban-sensitive bat species (Caryl et al., 2016), and habitat-fragmentation-sensitive vertebrate species (e.g. Vetter et al., 2010), among others. These guilds can be used to guide conservation and management actions, and to identify threats that impact a group of similarly responsive species. This approach moves away from actions that are focused on a single species to those encompassing multiple species. In a similar way to anticipating or predicting the response to impacts, guilds can be used to predict the outcome of management or conservation strategies, such as the traits that influence the use of crossing structures along highways (Abbott et al., 2012a; Abbott et al., 2012b; Boonman, 2011; Kerth and Melber, 2009).

Roads can have a negative impact on the activity and movement of insectivorous bats (hereafter referred to as "bats"; e.g. Abbott et al., 2015, Bennett and Zurcher, 2013, Fensome and Mathews, 2016, Kitzes

and Merenlender, 2014, Medinas et al., 2013). Some species are less active closer to a major road than they are further away from the road (Berthinussen and Altringham, 2012; Kitzes and Merenlender, 2014), with individuals often not crossing the road when traffic and/or lighting is present (Bennett and Zurcher, 2013; Hale et al., 2015; Zurcher et al., 2010). There is variation among species responses to the presence of a road. Some species are more sensitive to barrier effects, as they require continuous forest cover and are less likely to cross gaps in the canopy caused by roads (Bennett and Zurcher, 2013; Hale et al., 2015; Kerth and Melber, 2009). Alternatively, species that typically fly in open spaces, such as over the canopy, are likely to be more tolerant because gaps created by roads would be less of a barrier (Ciechanowski, 2015; Helbig-Bonitz et al., 2015; Kerth and Melber, 2009). For the more sensitive species, fauna crossing structures may mitigate the impacts of the road by providing a sheltered, connected pathway across a landscape that is otherwise fragmented. Using guilds may assist in predicting the impact of roads (e.g. Abbott et al., 2015; Kerth and Melber, 2009; Kitzes and Merenlender, 2014) and, as in the present study, the effectiveness of crossing structures to mitigate this impact for bats (Abbott et al., 2012a; Abbott et al., 2012b).

Bats can be classified into guilds based on their flight patterns which allow the individual species to occupy different niches within the shared environment (Denzinger and Schnitzler, 2013; Luck et al., 2013). These guilds may also predict a species' response to roads and underpasses (Abbott et al., 2012a; Boonman, 2011; Kerth and Melber, 2009). To date, most studies have investigated the use of culverts as crossing structures for bats (Abbott et al., 2012a; Boonman, 2011; Kerth and Melber, 2009), but few studies compare the use of different types of crossing structures by multiple guilds (see Abbott et al., 2012b for exception). By evaluating the response of guilds to multiple structure types, as opposed to single species and single type of structure, we can understand how several bat species respond to roads and crossing structures based on their ecological traits instead of environmental factors such as where in the landscape the crossing structures are located.

In this study, we recorded the activity of 12 bat species above the road and under the road using two types of underpasses: open-span bridges (n = 6) and box culverts (n = 6) (hereafter referred to as bridges and culverts, respectively; see Fig. 1) in south-east Australia. Our objectives were to determine if: i) bats travelled under underpasses; ii) the presence of underpasses reduced the activity of bats above the road (i.e. crossing at-grade); and iii) guilds varied in their level of activity under the two types of underpass and above the road. We assigned each species to one of three guilds based on flight patterns (i.e. clutter-adapted, edge-adapted or open-adapted, after Denzinger and Schnitzler, 2013, Luck et al., 2013), and compared the activity of each
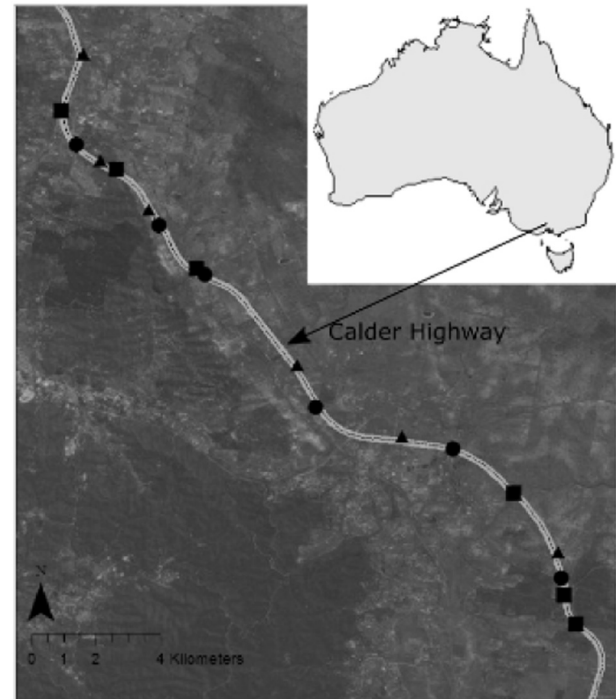

Fig. 2. The Calder Highway, in Victoria Australia. The highway extends approximately 150 km northwest from Melbourne. Map shows the 40 km span used in this study. The southernmost site is 120 km from Melbourne. Squares indicate bridge sites, triangles indicate culvert sites and circles indicate unmitigated sites. Inset shows study location within Australia. See Supplementary information for site-level images.
Source: Image from ARCMAP 10.2.2. and "maps" package in R.

guild above the road and under bridges, culverts, and above segments of the road that were unmitigated. We predicted that: i) clutter-adapted species would be more active under culverts than bridges due to the smaller, more enclosed shape of the culverts and these bats' ability to fly close to or within vegetation or other structures; ii) edge-adapted species would actively use bridges instead of culverts, due to the large size of the bridges and the foraging opportunity that may be available along the vegetated corridor; and iii) open-adapted species would not be active within either type of underpass but more active above the road because of their tendency to fly high above the tree canopy.

Fig. 1. Examples of one of the open-span bridges (left) and one of the box culverts (right) where bat movement was studied along the Calder Highway, in Victoria, Australia. Photos not to scale.
Source: Photos by Lee Harrison.

2. Materials and methods

2.1. Study area

We monitored bat activity along the Calder Highway in Victoria, Australia. The Calder Highway extends approximately 150 km northwest from Melbourne, Victoria (Fig. 2). The native vegetation in this region consists mainly of heathy dry forest, with some grassy woodlands and box ironbark forest (Costermans, 2006). There were patches of forest on both sides of the highway, however much of the landscape is used for agriculture (Fig. 2). Between 2003 and 2009, approximately 40 km of the Calder Highway was upgraded which included the installation of 23 purpose-built wildlife crossing underpasses: nine bridges and 14 culverts. This section of the highway is a four-lane divided highway (two lanes in each direction, each carriageway approximately 12 m wide, separated by a grassy median approximately 5 m in width, with a maximum speed limit of 110 km/h and an average daily traffic volume ranging from 8000 to 14,000 vehicles/day, VicRoads, 2015). In this study, we assessed the activity of bats at six bridges, six culverts (Fig. 1) and at six unmitigated sites. Bridges were large, open-span underpasses that varied in width (10–90 m), height (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. Three of the six bridges crossed over dry creek beds. Culverts were 3–3.6 m wide by 3–3.6 m high box culverts with a concrete floor, and were 24–67 m long (span of double carriageway). The dimensions of each of these structures are provided in the supplementary information. Unmitigated sites were sections of the highway in between the mitigated sites that had no underpasses installed under them. Unmitigated sites were similar in surrounding habitat and likely presence of insectivorous bats as mitigated sites.

2.2. Study species

The study area supports 12 species of insectivorous bat which we categorized into guilds based on their flight patterns and their typical foraging location (i.e. cluttered habitat, edge habitat or open habitats; adapted from Denzinger and Schnitzler, 2013, Luck et al., 2013; Table 1). Clutter-adapted species typically have short broad wings, slow flight and high manoeuvrability, flying and foraging within and close to vegetation, often flying closer to the ground among the understorey, under the canopy. Edge-adapted species have average wingspans and fly faster than clutter-adapted, but slower than open-adapted species, and typically fly and forage around the edges of patches of habitat and gaps between trees. Open-adapted species have

Table 1
Total number and percent of calls identified of each species of insectivorous bat. Calls were identified using AnaScheme Bat Call Analysis System, using a key developed for this region.

Species	Guild	Total number of calls identified	Percentage of total identified calls
Nyctophilus-Myotis- complex[a]	Clutter	2194	9.2
Chalinolobus gouldii	Edge	2809	11.8
Chalinolobus morio	Edge	2067	8.7
Scotorepens balstoni	Edge	82	0.3
Vespadelus darlingtoni	Edge	6156	25.9
Vespadelus regulus	Edge	331	1.4
Vespadelus vulturnus	Edge	3758	15.8
Mormopterus ridei	Open	1237	5.2
Mormopterus planiceps	Open	2680	11.3
Austronomus australis	Open	2446	10.3
	Total	23,760	99.9

[a] The *Nyctophilus-Myotis* complex consists of *Nyctophilus geoffroyi*, *Nyctophilus gouldi* and *Myotis macropus*.

long, narrow wings and fly faster than the other two guilds, typically flying and foraging above the canopy and in open areas.

2.3. Data collection

We monitored bat activity using Anabat SD1 and SD2 acoustic detectors (Titley Electronics, Ballina, New South Wales, Australia). Six detectors were deployed at each underpass: two within the structure, facing towards the centre of the structure; two detectors on the road edge above the structure, facing towards the centre median; and two detectors 10 m outside of the structure, facing into the vegetation surrounding the highway (Fig. 3). This design was intended to record the activity of bats crossing under the structures, bats crossing above the road, and of bats in the vegetation surrounding either side of the road. Anabat detectors are relatively directional (Titley Scientific, 2012) with calls detected from approximately 5 m to 50 m depending on the species. Detectors were pointed away from each other, to reduce the number of calls that were captured on more than one detector, and the detectors under each structure were set well into the structure to reduce the possibility of recording bats flying outside the structure. There was no evidence of bats roosting in any of the structures (Bhardwaj *pers. obs.*). At unmitigated sites, we installed four detectors: two on the road edge, facing towards the median and two detectors 10 m away from the road, facing into the vegetation surrounding the highway. Henceforth, "position" refers to the detector position, representing where the bats crossed the road: under or above bridges, under or above culverts, or above unmitigated sites.

We simultaneously surveyed bat activity at one bridge, one culvert and one unmitigated site (i.e. 16 detector positions) for two consecutive nights. Bats were surveyed during the Australian summer, in December and January, and each site was surveyed once in 2013/2014 and again in 2014/2015 (totalling four nights per site). Each detector was programmed to begin recording calls half an hour before sunset and end half an hour after sunrise. Detectors were housed in 3 L rectangular plastic containers, with microphones protruding through a 50 mm hole in one of the short sides, placed at a 45° angle towards the sky. Moon phase (i.e. first quarter, full moon and last quarter) was recorded based on data available from Museum Victoria (http://museumvictoria.com. au/planetarium/discoverycentre/moon-phases/). Daily maximum temperature data were obtained from the Australian Government, Bureau of Meteorology (http://www.bom.gov.au/climate/data/).

We identified 33,444 Anabat calls sequences to species using the automated AnaScheme Bat Call Analysis System (Version 1.0, Adams et al., 2010, Gibson and Lumsden, 2003) with a key developed for this region using locally collected reference calls (Lumsden and Bennett, 2005). To reduce misidentifications, species identification was only attempted if there were five or more valid pulses in the call, and deemed successfully identified when > 50% of the pulses were assigned to the same species (23,760 calls; Lumsden and Bennett, 2005). 29% of calls (9684 calls) were excluded due to containing too few valid pulses or being of poor quality. The average proportion of calls identified did not significantly differ at each position among the site types, so the exclusion of these poor quality calls did not influence the comparisons between positions (pairwise 2-sample test for equality of proportions for all combinations of detector positions, all p > 0.15; average proportion of identified calls at each position is provided in supplementary information). The key was unable to reliably differentiate *Nyctophilus geoffroyi*, *Nyctophilus gouldi* and *Myotis macropus* calls, therefore these calls were grouped into a "*Nyctophilus-Myotis* complex." These three species are also the same three that comprise the clutter-adapted guild (Table 1). The key was also prone to misattributing insect or background noise to *Austronomus australis* calls, so any files identified as this species were confirmed visually. We used the nightly average number of calls in each detector position for each species or species-complex. Total call activity reflects the sum of calls identified across all species. Guild activity (clutter, edge or open) reflects the sum
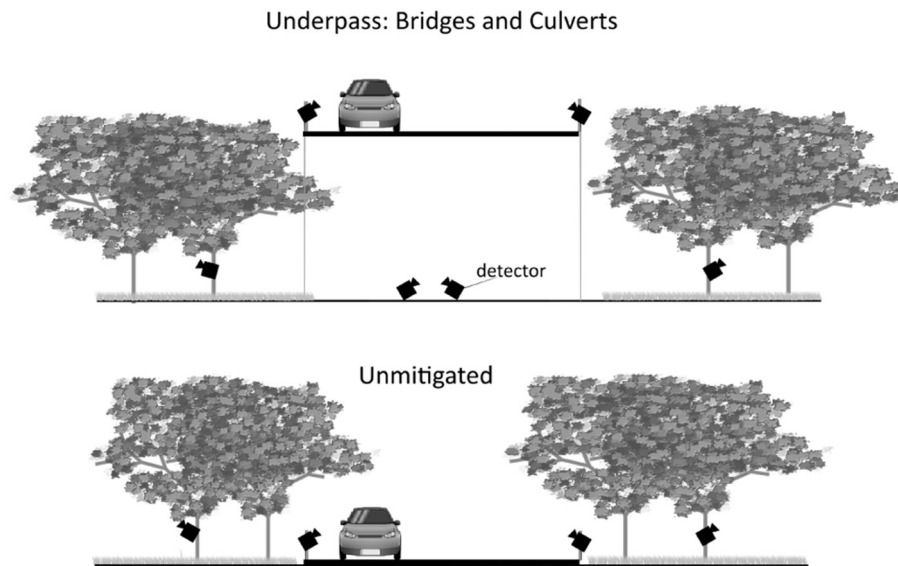
Underpass: Bridges and Culverts

Fig. 3. Detector position under and above bridges and culverts, and at unmitigated control sites. We installed 2 detectors under the underpasses (under the road), 2 detectors along the road above the underpasses, and 2 detectors in the surrounding habitat, 10 m from the entrance of the underpasses. At the unmitigated sites the detectors were set facing across the road, and 10 m away facing into the vegetation.

of the nightly average number of calls from all species belonging to the guild.

2.4. Statistical analysis

To explore the difference in the crossing rates of bats at each detector position, we fitted Poisson regression models, separately for each guild, using average number of calls per night (which we term "crossing rate", R) as a response. So, for each data point, i (each position, per night):

$$R \sim Poisson \lambda_i$$

$$\log \lambda_i = \beta_0 + \beta_1 B_i + \beta_2 b_i + \beta_3 C_i + \beta_4 c_i + \beta_5 v_i + \beta_6 T_i + \beta_7 M_i$$

where λ was the mean call rate per night, B, b, C, c are indicator functions (which take value '1' when calls were collected: above bridge, under bridge, above culvert and under culvert respectively); v is the standardised mean call rate in the surrounding vegetation; T is standardised daily maximum temperature; M is the moon phase. The intercept, β_0, represents the baseline (control sites, the road without any structure), and $\beta_1, \beta_2, \beta_3, \beta_4$, are the incremental effects of each structure type and position compared to the road. The mean call rate per night is represented as a count, and fits the assumptions of a Poisson distribution. Daily maximum temperature, and moon phase were included to account for nightly variation. Mean call rate in the surrounding vegetation, and daily maximum temperature were standardised to have a mean of 0 and standard deviation of 1 to aid model fitting. The number of calls recorded in the surrounding vegetation were used as a reference to account for possible spatial and temporal variation across sites and nights (thus the rest of the log regression actually models the difference in call activity compared to the surrounding vegetation at each site). We used vague uninformative priors for all parameters: normal distributions $N(0,10^6)$ for the regression coefficients of moon phase (first/last quarter, versus the reference: full moon; no sampling was undertaken during new moon), and detector position, uniform distributions $U(-10,10)$ for the regression coefficients of maximum daily temperature and the number of calls in the surrounding vegetation.

To compare the activity over the road to the activity in the surrounding vegetation, we estimated and compared the mean call activity in the vegetation surrounding the road and the mean call activity above the road at all sites, using Poisson regression models in a

similar fashion as described above. We fitted these models for all species combined, and for each guild separately. The comparison of these means was used to evaluate if the roads were impeding the movement of bats.

All model fitting was conducted within a Bayesian framework of inference using Markov Chain Monte Carlo (MCMC) sampling, by calling OpenBUGS 3.2.3 (Spiegelhalter et al., 2011) from R (v3.3.1; R Core Team, 2016) using package R2OpenBUGS (Sturtz et al., 2005). We ran 3 MCMC chains for each parameter, keeping 100,000 iterations after discarding a burn-in of 50,000. Convergence was assessed by visual inspection of the chains and using the statistic R-hat (assuming no evidence of lack of convergence for values below 1.01).

3. Results

We assigned 23,760 Anabat call sequences to species or species complex (average 76 identified calls per detector per night, ranging from 0 to 793 calls per night, median = 35 calls). On average, we identified 98 calls at bridge sites (in and above the structures, ranging from 0 to 793 calls, median = 39 calls), 39 calls at culvert sites (in and above the structures, ranging from 0 to 527, median = 10 calls) and 46 calls at unmitigated sites (ranging from 0 to 216 calls, median = 36 calls) per detector per night. In comparison, there were on average 98 calls per detector per night (ranging from 0 to 485 calls, median = 56) at the locations facing into the vegetation surrounding each site.

To determine if bats used crossing structures, we estimated the average crossing rate in each detector position using a Poisson regression model. In the model, we incorporated the average number of calls in the surrounding vegetation to account for any site-level variations, so the following results represent the estimated crossing rates for each site type. The crossing rate of all species combined ("overall crossing rate") was highest under bridges, and lowest under culverts (Fig. 4). On average, bats crossed at a rate of 51.6 [48.3, 55.1] (hereafter number in square brackets refer to symmetrical 95% Bayesian Credible Intervals from the Poisson regression model) crosses per night under bridges and 8.9 [7.8, 10.0] crosses per night under culverts. When bridges were available, bats crossed above the bridge half as much as they did above unmitigated sites (above bridge = 19.4 [17.8, 20.9] crosses per night; above unmitigated sites = 36.6 [34.0, 39.3] crosses per night). In contrast, the overall crossing rate above a culvert was 39.0 [36.4, 41.7] crosses per night, which was not
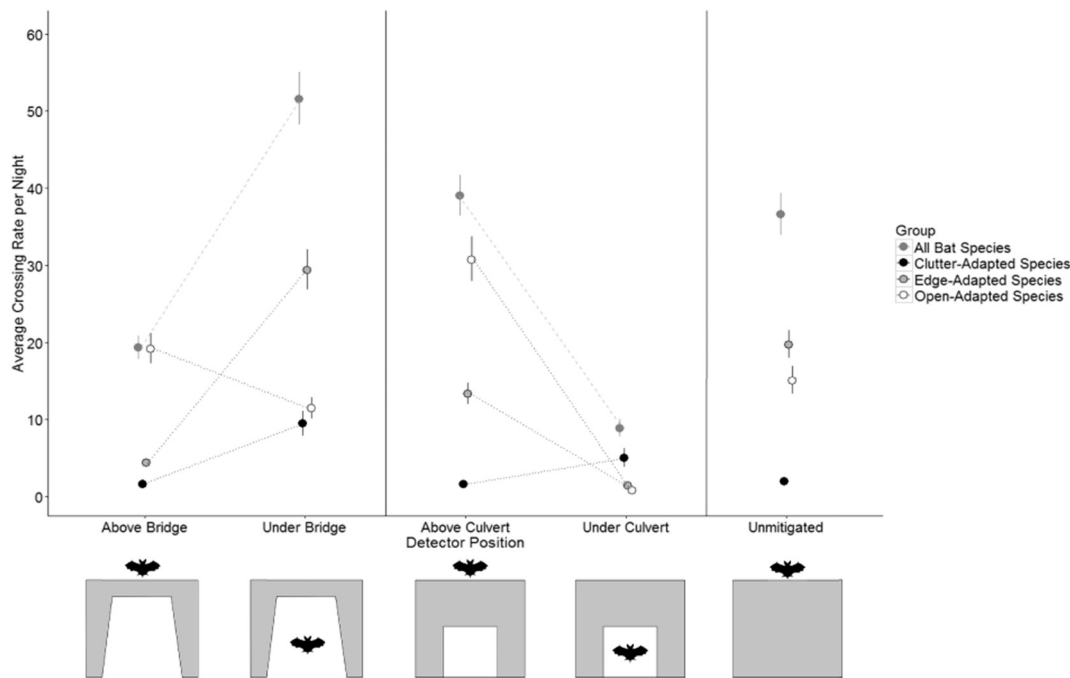
Fig. 4. Estimated average crossing rate per night above and under bridges (n = 6), above and under culverts (n = 6), and above unmitigated sites (n = 6). Estimated call rates were obtained from a Poisson regression model, and fit within a Bayesian framework of inference. Error bars show 95% credible intervals. Dotted lines show change in activity above and under bridges and culverts for each guild as well as for all bat species combined.

significantly different from the overall crossing rate above an unmitigated site. The overall crossing rate was approximately 3 times higher under bridges than above bridges, but approximately 4 times higher above culverts than under culverts.

The crossing rate for clutter-adapted species was highest under bridges compared to all other positions (Fig. 4). They crossed under bridges nearly twice as much as they crossed under culverts (under bridge = 9.5 [7.9, 11.1] crosses per night; under culvert = 5.0 [3.7, 6.3] crosses per night). Their crossing rate was lowest above the road, and did not significantly differ among site types (above bridge = 1.6 [1.2, 2.2] crosses per night; above culverts = 1.6 [1.1, 2.1] crosses per night; above unmitigated sites = 2.0 [1.5, 2.5] calls). Of the three guilds, clutter-adapted species were least active above the road, and they were the primary guild to make consistent use of culverts.

The crossing rate for edge-adapted species was also highest under bridges than all other positions (Fig. 4). Edge-adapted species crossed approximately seven times more under bridges (29.4 [26.9, 32.1] crosses per night) than above bridges (4.4 [3.8, 5.0] crosses per night). In contrast, they crossed the road almost 10 times more above culverts (13.3 [12.0, 14.7] crosses per night) than under culverts (1.4 [1.0, 1.8] crosses per night). They crossed under bridges 21 times more than under culverts (under bridge = 29.4 [26.9, 32.1] crosses per night; under culvert = 1.4 [1.0, 1.8] crosses per night). Edge-adapted species crossed above the road at a significantly higher rate where the road was unmitigated (19.7 [18.0, 21.5] crosses per night) than they did above bridges (4.4 [3.8, 5.0] crosses per night) or above culverts (13.3 [12.0, 14.8] crosses per night), however their crossing rate above the road was lower than their crossing rate under bridges.

Open-adapted species responded differently than the other two guilds (Fig. 4). Their crossing rate was higher above culverts (30.7 [27.9, 33.7] crosses per night), than above bridges (19.2 [17.2, 21.3] crosses per night); or above unmitigated sites (15.0 [13.3, 16.9] crosses per night). They crossed the road approximately 38 times more above culverts than under culverts (above culvert = 30.7 [27.9, 33.7] crosses per night; under culvert = 0.8 [0.5, 1.3] crosses per night). They were also the only guild that crossed the road more above bridges (19.2 [17.3, 21.3] crosses per night); than under bridges (11.5 [10.2, 12.9]

crosses per night).

Finally, we estimated and compared the mean call activity over the road and in the vegetation surrounding the road. The estimated mean call activity of all species combined was significantly lower over the road than it was in the vegetation surrounding the road (over the road = 52.7 [50.9, 54.5] calls per night; in the surrounding vegetation = 96.3 [93.9, 98.7] calls per night). This was also true for clutter-adapted species (over the road = 3.3 [2.8, 3.7] calls per night; in the surrounding vegetation = 7.9 [7.3, 8.6] calls per night) and edge-adapted species (over the road = 22.8 [21.6, 24.0] calls per night; in the surrounding vegetation = 68.9 [66.9, 70.9] calls per night). In contrast, open-adapted species were significantly more active over the road than they were in the surrounding vegetation (over the road = 28.2 [26.9, 29.6] calls per night; in the surrounding area = 21.0 [19.9, 22.2] calls per night).

4. Discussion

Our findings revealed that underpasses were used by bats, and that bridges were more effective at facilitating movement across highways than culverts. Our findings also revealed that there were some differences in crossing behaviour among the guilds. The activity of clutter- and edge-adapted species was lower over roads compared to in the vegetation surrounding the road, suggesting that the road was at least a partial barrier to bat movement, and is reducing the rate at which bats fly over that part of the landscape. In contrast, the activity of open-adapted species was not impeded by the road. Clutter- and edge-adapted species frequently crossed under bridges rather than over them. In contrast, open-adapted species flew over the road more than they flew under bridges. Finally, clutter-adapted species were the only guild to fly under the culverts more frequently than crossing above the road, whereas edge- and open-adapted species made little use of the culverts, and flew over the road significantly more than they flew under the culverts.

While the road inhibited activity, it was not a complete barrier to the movement of bats. Across all site types, there was some activity over the road, regardless of whether a crossing structure was present or not.

However, clutter- and edge-adapted species were significantly more active in the vegetation surrounding the road than over the road. Clutter- and edge-adapted bats may be less active over the road because the road area may not provide as rich of a foraging resource as the surrounding vegetation. However, this may not always be the case, as nocturnal insects can be attracted to the road due to the heat of the surface and light from cars (Muñoz et al., 2015), and the grassy median strip present at all sites was likely to have insects flying within it. It may be more likely that the road is creating a gap in the canopy and individuals that prefer flying close to vegetation, like clutter- and edge-adapted species, avoid crossing due to the risk of predation or avoidance of light, noise and vehicles (Abbott et al., 2015; Bennett and Zurcher, 2013; Hale et al., 2015; Kerth and Melber, 2009; Schaub et al., 2008). Therefore, although the road is not completely impeding the movement of bats, for some species, it is significantly reducing their activity.

The level of bat activity in the vegetation surrounding each site did not appear to have a strong influence on the rate of crossing over the road or through the crossing structure by either guild. By using the number of calls recorded in the surrounding vegetation as a reference for the activity that occurred at each site, we were able to control for any site-level variation. Therefore, bridges may appear to be situated in higher-quality habitat, since they go over waterways and connect adjacent forested areas, but these habitat variables are not the reason bats used bridges more than culverts. Nor do these habitat variables account for the reduction in clutter- and edge-adapted species' activity over the road where bridges were present. Instead, any differences in activity under the structures and above the road are due to structure presence and/or type, not quality of the surrounding habitat.

Bridges may be important for clutter- and edge-adapted species to maintain unrestricted access to foraging and roosting habitat. Unmitigated roads can impede the access of some species to foraging habitat, and reduce their foraging area (Bennett et al., 2013; Kerth and Melber, 2009). In our study, we found that when a bridge is available, the crossing rate of clutter- and edge-adapted species above the road was reduced, which may result in a lower risk of vehicle-related mortality, while improving access to habitat. Given that clutter- and edge-adapted species cross under bridges at significantly higher rates than they cross above the road, bridges may be used to help reduce barrier impacts and maintain connectivity in the landscape for insectivorous bats.

We predicted that guilds would be an informative way to predict crossing structure use. Although we accurately predicted structure use based on guilds, we underestimated the extent to which bridges would be used by a broader range of species. We had predicted that clutter-adapted species would use culverts more than bridges, due to their preference for enclosed areas (Abbott et al., 2012b; Boonman, 2011). However, clutter-adapted species had a higher crossing rate under bridges than they did under culverts. Open-adapted species were the most distinct guild, as they crossed over the road more than they flew under either crossing structure type and were similarly active in the surrounding vegetation as they were over the road. Roads do not appear to be a barrier for open-adapted species, and because they fly high above vehicle heights, they may have a lower risk of collision. Therefore, our results broadly agree with our predictions, with a slight variation for the clutter-adapted species. Our results are also consistent with the current literature that suggests that larger structures are used by more bat species, and use of smaller structures is primarily limited to clutter-adapted species (Abbott et al., 2012b). Overall, this study displays the effectiveness of using guilds to predict the use of crossing structures by multiple species of bats.

Although guilds may be a useful way to infer the response of multiple species by evaluating the response of similarly behaving species, generalizing to a group may reduce the detail of understanding the response of each species individually. It is important to evaluate the need of individual species based mitigation approaches to larger group

based approaches, and determine which will provide a more meaningful result for the question at hand. Here, we argue that it is possible to infer the behaviour of similarly-behaving species by using guilds to make predictions where data may be lacking or deficient. If one can determine the traits responsible for the success of different mitigation techniques (in the present study, we used flight and navigation patterns to define use of crossing structures) it may be more efficient to use guilds to make broad-scaled inference. If it is not possible to determine which traits may be responsible for mitigation success, it may be better to undertake individual species-based investigations.

Larger, wider crossing structures are more likely to facilitate the movement of a larger variety of species better than smaller structures. This is true for grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), elk (*Cervus elaphus*), and deer (*Odocoileus* spp.; Clevenger and Waltho, 2000, 2005), among others. Given the present study, this is also true for bats. In our study, bridges were not just longer and wider than culverts, but also had near-continuous mid-storey vegetation throughout. The vegetation often connected the habitat on both sides of the highway, thereby promoting foraging and commuting under the bridge rather than over it. In contrast, culverts were less suitable for bats to commute through because they were smaller, had no vegetation in them, and provided few foraging resources, therefore, bats flew over the road instead. Despite the mounting evidence that small culverts are less effective fauna passages than larger, vegetated structures (e.g. Ascensão and Mira, 2007; Chambers and Bencini, 2015; Lesbarrèrs and Fahrig, 2012), culverts are still commonly installed to mitigate the barrier effects of roads on wildlife. This is largely a matter of cost: culverts are, on average, five times less expensive than bridges (A. White, VicRoads, *pers. comm.*). Landscape topography and road profile can also often constrain the type of structure that can be installed, and bridges may not always be feasible. However, if bridges are used more frequently and by a larger range of species, then one can argue that the larger bridges will ultimately save the time, money and effort of implementing a less effective strategy such as culverts. Therefore, if the goal of mitigation is to facilitate the movement of as many species as possible, bridges are a better crossing structure than culverts.

Author contributions

MB, TS, LL and RvdR conceived the ideas and designed methodology; MB collected the data; MB, KS, JL-M, LL and RvdR analysed and interpreted the data; MB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.05.022.

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