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LETTER

Use of road infrastructure for movement by common terrestrial vertebrates

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Abstract

Wildlife-vehicle collisions are increasing with road expansion. This problem could be minimised if the use of existing infrastructure to cross roads could be enhanced. We aimed to determine whether common terrestrial vertebrates used drainage culverts to cross roads, relative to rates of surface crossings. Camera traps were deployed on road verges at 30 locations in southeast Queensland, Australia for 2 weeks each over a 3-month period. Of 1671 independent animal observations, 397 were direct observations of road crossings, either over-road (365) or under-road via culverts (32). Native species and small species were found more commonly at roadsides than culverts and where vegetation density was lower. Our data showed that animals used culverts only about 6% of the time. Management such as funnel fencing or vegetation manipulation could encourage wildlife to use culverts, but this would require a substantial investment given the propensity for animals to cross via the road surface.

KEYWORDS

culvert, drainage culvert, landscape connectivity, movement ecology, road crossing structure, road ecology, road management, roadkill, wildlife road crossing structure, wildlife-vehicle collisions

INTRODUCTION

With increasing urbanisation there is increasing expansion of road infrastructure globally (Laurance et al., 2015; Rutz et al., 2020). Fragmentation of wildlife habitat by roads can restrict gene flow, reduce dispersal, and reduce biodiversity in ecological communities (Crooks et al., 2017; Magioli et al., 2016). Roads also cause direct mortality of wildlife, a phenomenon which was highlighted during the 2020/2021 COVID-19 lockdowns when travel restrictions decreased roadkill between 19% to over 40% globally (Bíl et al., 2021; Driessen, 2021). The response of wildlife to roads is varied (Van Der Ree et al., 2015), with avoidance behavior by some species decreasing incidences of wildlife-vehicle collisions (Zimmermann Teixeira et al., 2017), while others are attracted to roads for scavenging, foraging on resources provided by the road verge, or thermoregulation (Bond & Jones, 2014; Hill et al., 2020; Rytwinski & Fahrig, 2013; Van Der Ree et al., 2015). This has implications for biodiversity and road management because species will not be uniformly affected. Understanding how ecological communities respond to road networks is necessary for effective road management, biodiversity conservation, and human safety.

Purpose-built wildlife crossing structures have been installed on new roads since the mid-1900s (Bond & Jones, 2008; Goldingay & Taylor, 2017a; Taylor & Goldingay, 2010; Taylor & Goldingay, 2012), a trend which is increasing, particularly in North America and Europe (Bond & Jones, 2008; Little et al., 2002). These include under-road structures such as drainage pipes, box drainage culverts, and dry passage bridges; and over-road structures such as dedicated wildlife land bridges, combined wildlife-vehicle overpasses, pole/rope/canopy bridges, and glide poles (Goldingay & Taylor, 2017b; Taylor & Goldingay, 2010). A meta-analysis of road mitigation measures found that purpose-built crossing structures can minimise wildlife-vehicle collisions by up to 40% but only when fencing was used to funnel animals towards these structures (Rytwinski et al., 2016). While purpose-built crossing structures have potential to mitigate wildlife-vehicle collisions, the majority of road networks worldwide lack these structures. Retro-fitting roads with crossing structures is expensive and can disrupt the primary function of the road (Bond & Jones, 2008; Brunen et al., 2020). Thus, to understand the use of roads by wildlife and road-crossing behavior more generally, we need knowledge on how wildlife interacts with existing road networks.

Existing road infrastructure, such as drainage culverts (hereafter "culverts"), have potential to reduce wildlife-vehicle collisions and, in many cases, may be the only viable option (Brunen et al., 2020). How wildlife use existing culverts is likely to depend on their traits, such as body size, habitat generalisation, evolutionary history (e.g., native vs. exotic [i.e., introduced species]) and mode of dispersal. Large generalist species might be more likely to encounter roads than small or specialist species with limited dispersal and greater sensitivity to anthropogenic disturbance (Gehring & Swihart, 2003). One study found that large species used culverts to cross roads, while smaller species avoided them, probably because of the presence of water inside the culvert (Grilo et al., 2008). Culvert use is also influenced by culvert dimensions and openness, with *Canis lupus* (wolves) and *Odocoileus* sp. (deer), respectively, using culverts with high and low openness ratios (i.e., length, relative to width) (Clevenger & Waltho, 2000; Grilo et al., 2008; Hill et al., 2020). In Australia, the invasive exotic mammals *Vulpes vulpes* (red fox) and *Felis catus* (cat) use roads for movement, which increases rates of predation on native wildlife (Dawson et al., 2018; Raiter et al., 2018). This kind of trait-based knowledge can help develop appropriate management of wildlife around roads. For example, modifying culverts to include dry passage ledges could encourage culvert use for small species that tend to avoid them (Grilo et al., 2008).

Vegetation properties might also influence whether or not wildlife use culverts (Clevenger & Waltho, 2000; Grilo et al., 2008; Hill et al., 2020). Some studies found that vegetation directly around culvert entrances increases their use, likely because it provides food and shelter (Brunen et al., 2020; Chisholm & Taylor, 2007; McLaren et al., 2011). Another study found that culvert use declined with increased proximity to forest edges, likely because predominantly generalist species were studied (Brunen et al., 2020). Similar results might be expected for macropods which prefer clear movement paths (Bond & Jones, 2014; Brunen et al., 2020; Yanes et al., 1995). Thus, there are likely to be interactions between species' traits and the environment that influence wildlife culvert use. If vegetation cover influences culvert use, vegetation could be managed around culvert entrances (e.g., through revegetation or habitat modification, depending on species' needs) to encourage wildlife towards them. Such a management strategy should be based on quantitative evidence related to species traits and environmental context (while also considering road user visibility) (Bond & Jones, 2014). Only a few studies have examined the extent to which environmental variables like vegetation structure and culvert properties affect different trait groups, and the contrasting results suggest more data are needed to develop generalisations and appropriate management methods.

In this study, we aimed to determine whether common terrestrial vertebrates in an Australian semi-natural, urban-agricultural system crossed roads via drainage culverts more frequently than via the road surface. We used a trait-based approach to determine whether animal associations with culverts depended on their body size and evolutionary history (native vs. exotic). We anticipated that smaller species would preferentially use smaller culverts, and larger species large culverts. We also expected exotic species to be less inclined to use culverts because of their generalist habitat preferences. Finally, we predicted there would be an interaction between species traits such as body size and vegetation density surrounding culverts. Results from our study could assist wildlife managers in deciding how to manage roadside vegetation and culvert infrastructure in a way that enhances culvert use, potentially reducing wildlife-vehicle collisions.

Practitioner points

- Existing drainage culvert networks are not generally used by wildlife to cross roads, relative to surface crossings.
- Additional infrastructure or vegetation management is required for culverts to reduce wildlife-vehicle collisions and, given the propensity for crossings via the road surface, this would require substantial investment.
- Current road verge management for driver visibility might increase animals at roadsides, which could increase wildlife-vehicle collisions.

MATERIALS AND METHODS

Study location

The study was conducted in Southeast Queensland at 30 sampling sites in the Lockyer Valley and Ipswich regions, where agricultural (mainly grazing) land is interspersed with residential areas and protected native vegetation (conservation areas) (Figure 1 and Supporting Information: Table SA1). The region has a temperate climate with a mean annual rainfall of 780 mm, and an average monthly diurnal temperature of 32°C in summer and 4°C in winter. Dominant vegetation includes *Eucalyptus* woodlands and forests, with patches of rainforests and vine scrubs, *Melaleuca* and *Acacia* dominated open forests and woodlands, and some wetland areas (Figure 1).

Sampling sites were selected with Google Earth Satellite Imagery to cover the range of variables relating to the study questions: (1) culverts of varying sizes, (2) sampling sites spaced at least 500 m from each other, and (3) variation in vegetation density. Sampling sites were then assessed on the ground to ensure safe access by car and foot, and the presence of appropriate attachment points for camera traps.

Survey methods

At each of the 30 sampling sites we established a culvert subsite (C1–C4, hereafter "culvert") and a nearby road

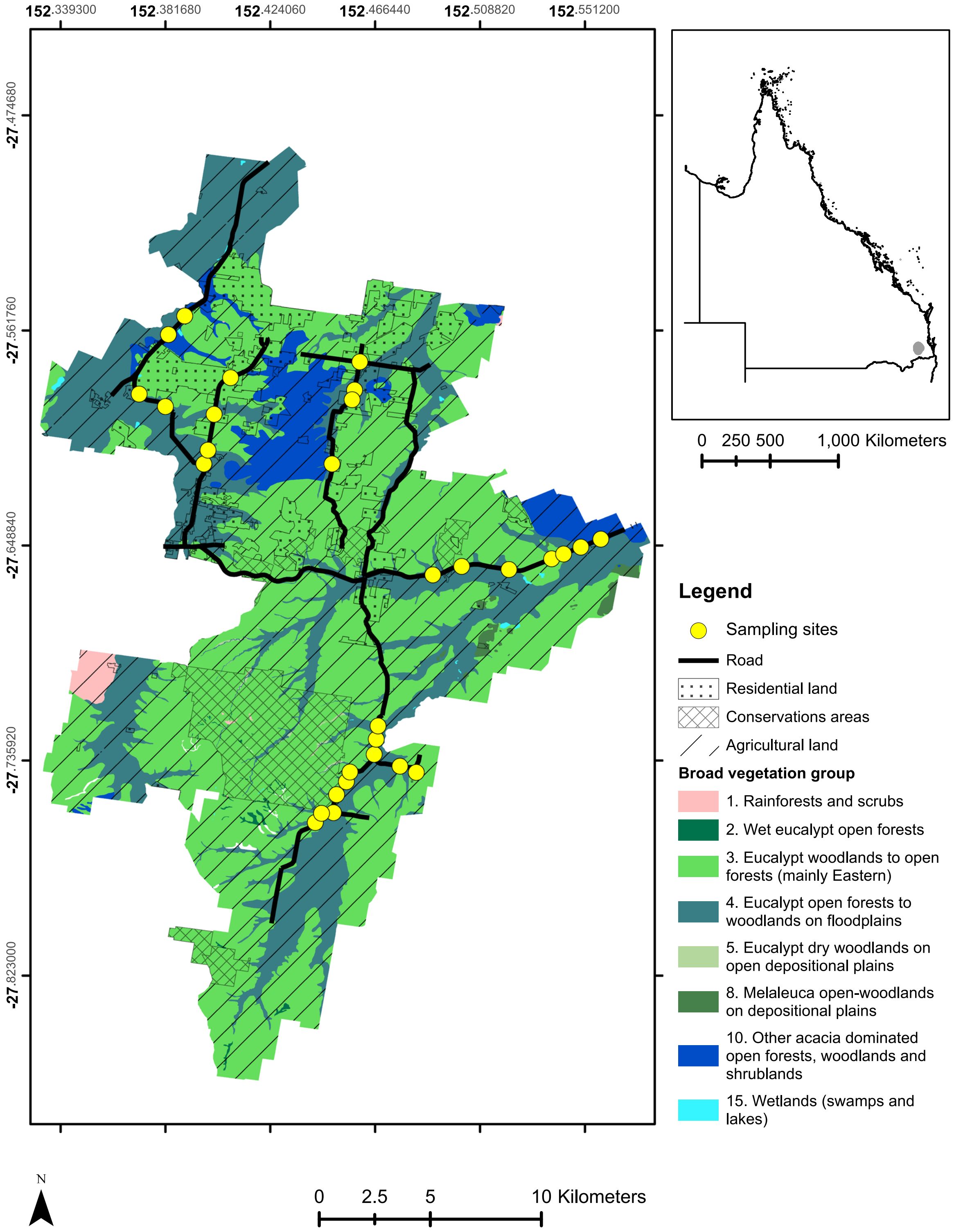

FIGURE 1 Culvert use in wildlife was studied at 30 sites in the Lockyer Valley and Ipswich region of Southeast Queensland (Neldner et al., 2019).

subsite (R1–R2, hereafter "roadside"), which were separated by an average of 3 m (Supporting Information: Figure SA1). At each site, we ensured the culverts and roadsides had generally similar vegetation density and height. We used digital motion sensor-activated infrared cameras to monitor wildlife. We established four camera points at each culvert and two camera points at each roadside (in anticipation of lower capture rates at culverts due to a narrow camera field of view) (Supporting Information: Figure SA1). We accounted for this variation in trap effort between subsites in our analysis, described below. Sampling was conducted over three 2-week sampling periods between October and December 2020, with 10 randomly chosen sites surveyed in each period. This research was conducted according to the guidelines of the Animal Ethics Committee of The University of Queensland.

Four types of camera trap were used: infrared Reconyx™ (Holmen) HC600 HyperFire™, Reconyx™ HP2X HyperFire™ 2 Professional, Swift (Outdoor Cameras Australia) ENDURO, and Swift 3 C. Within sites, the same camera brand was used for all six camera points. Cameras were positioned horizontally at varying heights depending on culvert size, being higher (approximately 70 cm above ground) for larger culverts and lower (approximately 10 cm above ground) for smaller culverts. This height variation catered for species expected to be observed at culverts of different sizes, with cameras at small culverts (<90 cm in height) positioned lower to ensure the culvert was within the camera frame. Each camera was set to passive infrared, high sensitivity with three shots per trigger, and no time delay between triggers. All cameras produced color daytime and monochromatic night-time photographs. Other settings varied across camera types including the picture interval (rapid fire for Reconyx™ and 4 s for Swifts) and image resolution (1080p for Reonyx™ HC600 HyperFire; ISO 1600 for Reconyx™ HP2X HyperFire™ 2 Professional; and 5MP for the Swift cameras).

Environmental characteristics

Environmental characteristics were measured for each camera point following Grilo et al. (2008) with some modifications. To estimate vegetation density (D) at each camera point, we measured the vegetation height at three points and used the average of these measurements for vegetation density. An average vegetation density for each site (1–30) was calculated for site-level analysis, by averaging vegetation density across all camera points. We calculated the difference in vegetation density between the culverts and roadsides as:

$$\text{Vegetation difference} = D_{\text{Culvert}} - D_{\text{Road}}.$$

Culvert and road characteristics

Culvert length (which also represented road width) was recorded using Google Earth Satellite Imagery. Following Grilo et al. (2008), numerical culvert properties, including culvert length l, height h, width w, and openness O were recorded for each site. Culvert size was recorded as a categorical variable: small <90 cm in height (corresponding to approximate sizes of small animals in our study region); and large ≥90 cm in height (corresponding to approximate sizes of medium and large animals in our study region) (Supporting Information: Table SA2). The culvert openness ratio O was determined as:

$$O = \frac{w \times h}{l}.$$

Image processing

All images were processed visually, and animals were classified into class, genus, and, where possible, species (Supporting Information: Table SA2). Due to low detection rates, species in *Amphibia*, *Rodentia*, and *Reptilia* subclass *Serpentes* were not identified to species level. The exotic *C. lupus* sp. and the native *C. lupus dingo* were grouped together as they could not be distinguished. Following Sollmann (2018), an animal was considered an independent individual when images were separated by 30-min. Where possible, markings and orientation of wildlife when entering/exiting the camera frame were used to identify individual animals.

Animals were categorised into the following functional groups: (1) all animals; (2) *Macropus giganteus* (eastern gray kangaroo) (analysed as a distinct group as they were numerically dominant in the data); (3) native species; (4) exotic species; (5) small species; and (6) large species (Supporting Information: Table SA2).

Animal images were categorised into four behavioral categories: sitting/standing still, foraging (including any movement that did not include a road surface crossing), a culvert crossing (an animal crossed the road through a culvert), and a road surface crossing (an animal crossed the road via the road surface). To increase temporal independence of the crossing behavior data set (which included multiple observations of individual animals crossing the road in a short period [e.g., less than an hour]), the data were filtered to include only one observation of an animal performing a behavior in a 60-min period.

Analysis

We examined culvert use and road crossings indirectly and directly. Our indirect method examined the probability of animals occurring at culverts and roadsides using a binomial variable to indicate whether an animal was seen (1) or not (0). This method assumed that seeing an animal in proximity to the culvert (within 2 m of the culvert entrance) indirectly indicated its use. The data set for the indirect method consisted of 180 independent observations (i.e., the number of camera points) and we subset the data for different animal functional groups. We accounted for spatial dependence among cameras within sites in the model (described below). By analysing the camera point at the observation level, presence/absence data could be used directly without adjusting for the higher trap effort at culvert subsites as the model accounted for the number of observations within each treatment.

Our direct method examined the actual behavior of animals in relation to culverts. This data set consisted of 26 independent observations (i.e., the number of sites with any type of road crossing observed). We only used culvert crossings (hereafter "CC") captured on culvert cameras and road crossings (hereafter "RX") from roadside cameras to calculate the total number of crossings. That is, we discarded a small number of observations of road crossings seen in the periphery of the culvert cameras, and vice versa. To standardise the number of crossings relative to trapping effort, we doubled RX, accounting for roadside trap effort being half that of culverts. We then calculated the proportion of total crossings that were under a culvert as:

$$\text{Proportion of crossings via a culvert} = \frac{\text{Number of CC}}{(\text{Number of CC} + \text{Number of RX})}.$$

Prior to modelling, we conducted Pearson's product-moment correlation analyses (r) to ensure that models did not include multiple correlated variables ($r > 0.20$). For the probability of occurrence data, vegetation density was positively correlated with culvert length ($r = 0.23$; $p = 0.001$) but not with culvert size (Supporting Information: Figure SA2). Culvert size was not correlated with culvert length (Supporting Information: Figure SA2). Vegetation density, which incorporated variation in culvert length, and culvert size were used in the probability of occurrence models.

In order to reduce the chance of fitting correlated variables in the same model we ran a series of correlation tests and selected a single variable that represented correlations among multiple variables. Based on the results from this analysis (Supporting Information: Figure SA3), we used culvert size to represent culvert openness, height, and width for the crossing behavior data. We used the average vegetation density to represent vegetation density at the culvert and roadside, and culvert length (Supporting Information: Figure SA4).

We analysed the probability of occurrence data (indirect culvert use) using binomial generalised linear mixed-effects models with a logit link function in the lme4 package (Bates et al., 2015) in R version 4.0.3 (R Core Team, 2020). We fitted eight models for each functional group: three univariate models including main effects for camera position (road vs. culvert), vegetation density, and culvert size; two models including camera position and additive effects of the covariates vegetation density and culvert size; two interactive models between camera position and the covariates; and a null model with no variation against which to compare the other models. We included a random effect for site to account for potential spatial dependence among cameras within sites.

For the crossing behavior data analysis (proportion data, direct culvert use) we used beta regression in the mgcv package (Wood, 2011). We fitted three models for each functional group: two univariate models for vegetation difference and culvert size; and a null model with no variation against which to compare the other models. We did not include a random effect because these data were analysed at the site level.

For both data sets, we used Akaike's information criterion corrected for small sample sizes (AIC_c) in AICcmodavg 2.3-1 (Mazerolle, 2020) to rank models. The best model was chosen as the one with the lowest $AIC_{c,}$ and which improved the model fit over the null model by $\Delta AIC_c > 2$. If two models had AIC_c values within $\Delta 2$, they were assumed to be equivalent.

RESULTS

We collected 2,323,693 images, of which 14,139 included images of wildlife (with three images per photographic event) after filtering for false triggers. There were 4714 photographic events (i.e., one image per event), which included 1165 animals. Among the 1165 individual animals there were 16 species (although nine animals could not be identified to species level) (Supporting Information: Table SA2). Some animals were observed multiple times so the probability of occurrence data set included 1365 wildlife observations after filtering.

After filtering for temporal independence, the crossing behavior data set included 1676 photographic events, of which 32 were culvert crossings, 948 foraging, 330 sitting still, and 365 road crossings. After filtering for culvert crossings and road crossings on their corresponding cameras (i.e., not including road crossings or culvert crossings recorded on nonroad or nonculvert cameras, respectively), the crossing behavior data included 32 culvert crossings and 482 road crossings (accounting for trapping effort, i.e., 241 × 2).

Probability of occurrence

For all animals and native species, the top-ranked model included an additive effect of vegetation density and camera position (Table 1). This model showed a higher probability of observing an animal at roadsides and a consistent negative effect of vegetation density (Figure 2a,b). The interactive model for both of these groups also had support from the data (Table 1), showing the camera position effect was only evident at low vegetation density (Supporting Information: Figure SA4). For small species, the camera position only model was ranked highest, showing that small species have a higher probability of observation at roadsides than culverts (Table 1 and Figure 2c). There was also support for an additive effect of vegetation density, showing fewer small species with increasing vegetation density (Table 1 and Supporting Information: Figure SA5). For large species, the culvert size model was ranked highest, showing more large species at small culverts than large ones (Table 1 and Figure 2d). However, this was not a strong effect since the null model was approximately equivalent (Table 1). For exotic species and *M. giganteus* the null model was ranked highest, indicating no effect of the measured variables on these groups (Table 1).

Crossing behavior

Road crossing behaviors were observed at 26 of the 30 sampling sites, with 32 independent culvert crossings and 246 independent road crossings observed. Species crossing through culverts were *F. catus* ($n = 2$), *Bos taurus* ($n = 5$), *M. giganteus* ($n = 23$), *Varanus varius* ($n = 1$), and *Notamacropus parryi* ($n = 1$). Species crossing the road surface were *B. taurus* ($n = 6$), *C. lupus* ($n = 8$), *V. vulpes* ($n = 4$), *Lepus europaeus* ($n = 7$), *M. giganteus* ($n = 194$), and *N. parryi* ($n = 27$). We did not observe any other species crossing over or under the road.

Accounting for the increased trap effort at culverts, our data show that common terrestrial vertebrates in this system use culverts to cross roads approximately 6% of the time (32/[[241 × 2] + 32]). The propensity for wildlife to use culverts to cross roads was not significantly influenced by any culvert or environmental properties, with the null model being top-ranked for all crossing behavior analyses (Supporting Information: Table SA3).

TABLE 1 Models used to test hypotheses regarding the influence of camera position, vegetation density, and culvert size on the probability of occurrence (indirect culvert associations) for six different animal groups.

Animal group	Model structure	Number of parameters	AIC_c	ΔAIC_c	Log Likelihood
All animals	Camera position + vegetation density	3	246.91	0.00	−119.34
	Camera position × vegetation density	3	248.87	1.96	−119.26
	Camera position	2	249.26	2.35	−121.56
	Null model	2	250.64	3.73	−123.29
	Camera position + culvert size	3	251.31	4.39	−121.54
	Culvert height	2	252.66	5.74	−123.28
	Vegetation density	2	252.67	5.76	−123.28
	Camera position × culvert size	3	253.42	6.50	−121.54
Exotic species	Null model	2	233.44	0.00	−114.69
	Camera position	2	234.12	0.68	−113.99
	Vegetation density	3	234.83	1.39	−114.35
	Culvert size	2	235.32	1.87	−114.59
	Camera position + culvert size	3	235.99	2.55	−113.88
	Camera position + vegetation density	3	236.18	2.74	−114.35
	Camera position × vegetation density	3	237.61	4.17	−113.63
	Camera position × culvert size	3	238.10	4.66	−113.88
Native species	Camera position + vegetation density	3	213.43	0.00	−102.60
	Camera position × vegetation density	3	214.07	0.63	−101.86
	Camera position	2	221.87	8.44	−107.87
	Camera position + culvert size	3	223.35	9.91	−107.56
	Null model	2	224.03	10.60	−109.98
	Camera position × culvert size	3	225.39	11.96	−107.52
	Culvert size	2	225.56	12.12	−109.71
	Vegetation density	2	226.04	12.61	−109.95
Macropus giganteus	Null model	2	112.06	0.00	−54.00
	Camera position	2	113.96	1.90	−53.91
	Culvert size	3	114.13	2.07	−53.99
	Vegetation density	2	114.13	2.07	−54.00
	Camera position + vegetation density	3	115.73	3.67	−53.75
	Camera position + culvert size	3	116.05	3.99	−53.91
	Camera position × vegetation density	3	116.15	4.09	−52.90
	Camera position × culvert size	3	117.50	5.44	−53.58
Small species	Camera position	2	244.33	0.00	−119.10
	Camera position + vegetation density	3	245.57	1.24	−118.67
	Camera position × vegetation density	3	245.87	1.54	−117.76
	Camera position + culvert size	3	246.39	2.06	−119.08
	Null model	2	247.56	3.23	−121.75
	Vegetation density	2	248.09	3.76	−120.98
	Camera position × culvert size	3	248.50	4.17	−119.08
	Culvert size	2	249.62	5.29	−121.74
Large species	Culvert size	2	189.44	0.00	−91.65
	Null model	2	190.16	0.72	−93.05

TABLE 1 (Continued)

Animal group	Model structure	Number of parameters	AIC_c	ΔAIC_c	Log Likelihood
	Camera position + culvert size	3	191.53	2.09	−91.65
	Vegetation density	2	191.90	2.45	−92.88
	Camera position	2	192.23	2.79	−93.05
	Camera position + vegetation density	3	193.33	3.88	−92.55
	Camera position × culvert size	3	193.42	3.98	−91.54
	Camera position × vegetation density	3	195.06	5.62	−92.36

Note: Models within groups are ranked from lowest to highest AIC_c.

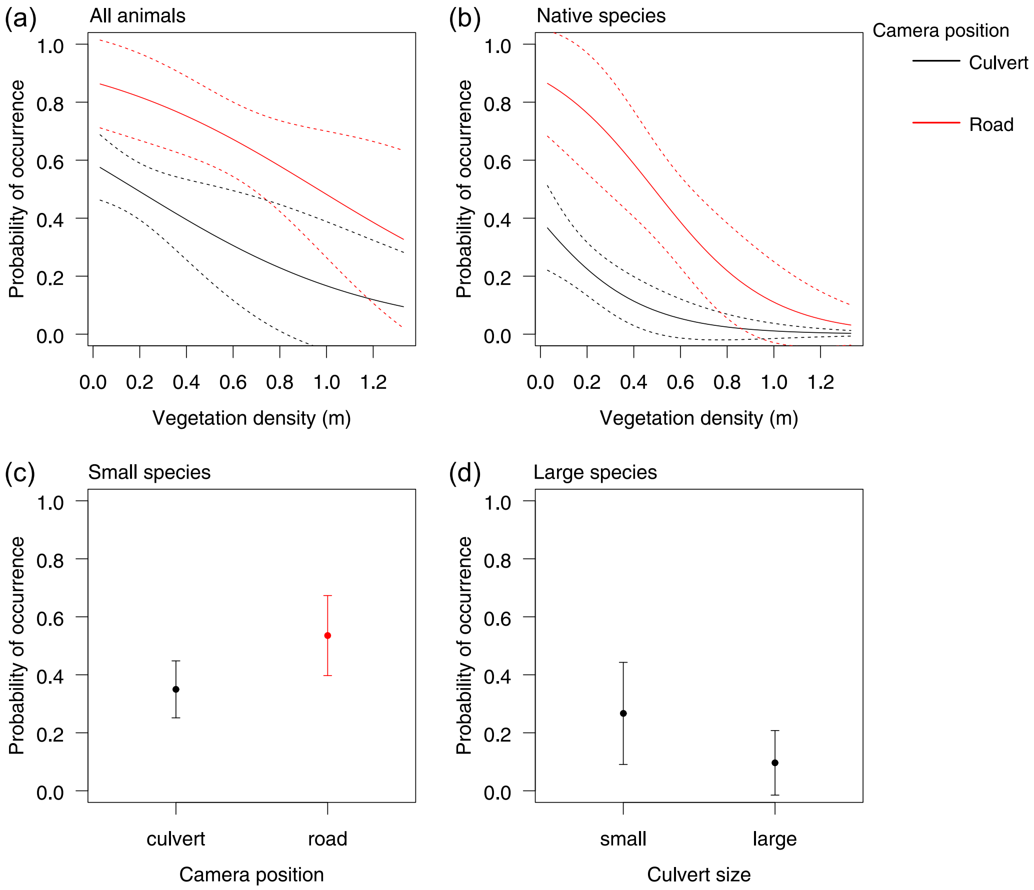

FIGURE 2 The estimated effect (and 95% confidence intervals) of camera position, vegetation density, and culvert size on the probability of observing different functional groups of terrestrial vertebrates. (a) All animals were influenced by an additive effect of camera position and vegetation density. (b) Native species were influenced by an additive effect of camera position and vegetation density. (c) Small species were influenced by camera position, with higher probabilities of occurrence on roadsides than at culverts. (d) Large species were influenced by culvert size, with higher probabilities of occurrence around small culverts than large culverts.

DISCUSSION

This study explored if and how common Australian terrestrial vertebrates use existing culvert infrastructure to cross roads in a semi-natural, agricultural landscape. Our large data set of 1676 independent wildlife observations, including 273 direct observations of road crossings, indicated that animals used culverts to cross roads approximately 6% of the time. This indicates very low culvert use relative to the number of road surface crossings. This does not necessarily indicate an aversion of wildlife towards these structures, but a current ineffectiveness of culverts to enable movement of wildlife across roads at a broader scale. Additional infrastructure (e.g., funnel fencing) or vegetation management might be needed if culverts are to substantially reduce wildlife-vehicle collisions, but this would require a substantial investment given the propensity for animals to cross via the road surface.

Many of our results point to the generalist nature of the species captured in our study. For example, we found the probability of occurrence of all animals and native species to be greater on roadsides than culverts. These groups were numerically dominated by the large generalist *M. giganteus* (eastern gray kangaroo, although this species did not show a response to camera position when analysed as a separate group) and also included *L. europaeus* (European hare) and native species, *N. parryi* (whiptail wallabies) and *Rodentia* (rodent species). The probability of observing animals was higher where vegetation density was lower—contrary to expectations given that vegetation provides shelter and food. However, this might have reflected that generalists prefer open environments and clear movement paths (Bond & Jones, 2014; Brunen et al., 2020; Yanes et al., 1995). Thus, animals might be avoiding areas that obscured their view of the road and associated environment.

Species such as bandicoots (Peramelemorphia) occur in our study region (Hidden Vale Wildlife Centre, 2022), but were not detected in our study. These species often have more specialised habitat requirements and fall within the critical weight range (35–5500 g, Chisholm & Taylor, 2007) that makes them susceptible to predation by introduced cats and foxes. Our data set thus appears biased towards habitat generalist species which are potentially less sensitive to roadside effects (Gehring & Swihart, 2003). However, it is possible that smaller, specialist species, were present in sites with higher vegetation density but remained unobserved due to lower detectability. Thus, future studies could supplement our results using methods that specifically target such groups (e.g., sand tracking, Bond & Jones, 2008; Taylor & Goldingay, 2003).

We found that vegetation density and culvert size had no influence on the propensity for animals to cross roads via culverts. Increased vegetation density at culvert entrances might have discouraged culvert use as animals could not see what was inside or through to the other side of the culvert (Bond & Jones, 2014; Yanes et al., 1995). Vegetation density was also correlated with increasing road width and culvert length. We expected wider roads would create barriers to movement and encourage culvert use due to increased risk of wildlife-vehicle collisions (Bond & Jones, 2008; Rytwinski & Fahrig, 2015), but this was not the case.

Body size matching has been observed in previous studies (Rivera Roy, 2020; Yanes et al., 1995), however, this was not observed in our study. The direct method for crossing behavior indicated no body size effect, however, we found large species to have more indirect associations with small culverts. Since small culverts are unlikely to accommodate passage by large species this was possibly due to an unmeasured correlated variable. Thus, we found no strong effect of body size on these direct associations with culverts. Large species are often targets for mitigation of wildlife-vehicle collisions given their high movement ability and potential for extensive, even fatal, damage to human life (Gehring & Swihart, 2003). Previous research has suggested that artificial crossing structures positioned in movement paths are effective at encouraging culvert use (Dexter et al., 2016; Taylor & Goldingay, 2003). In our study, large animals often were present near culverts (within ~2 m), but rarely used them. Small species, such as *Trichosurus vulpecula* (common brushtail possum) and *L. europaeus* (European hare) were also common on roadsides in our study but were not observed using culverts of any size. Thus, wildlife are not limited by exposure to the culvert but appear to avoid using them.

Invasive exotic species such as lagomorphs and foxes were only observed crossing via the road surface, known to use roads for movement (Dawson et al., 2018; Raiter et al., 2018); they sometimes approached culverts but did not enter them. *F. catus* (cats) and *B. taurus* (cows) were the only exotic species observed directly using culverts to cross roads. There was one instance in which a cat entered a small culvert and did not emerge for over 4 h. Thus, roadside culverts provide shelter, not just movement corridors, for exotic vertebrates.

Our study found that existing networks of culverts are not necessarily useful on their own as wildlife road-crossing structures. Previous studies have shown that culvert use can be increased by adding "furniture" such as timber railings, dry passage ledges, rocks, and logs within the culvert (Bond & Jones, 2008; Goldingay et al., 2019; McGregor et al., 2015). Funnel fencing and other alterations are likely to be prohibitively expensive in a system where culvert use is so low. Furthermore, if rare or specialised species are not present on roadsides, these have the effect of encouraging invasive species rather than assisting native species. In other studies, vegetation manipulation (McGregor et al., 2015) has been used to attract wildlife into culverts. These might be more cost-effective solutions but whether or not they increase culvert use for species of conservation concern is not clear. Road verges are generally managed to increase driver visibility (Bond & Jones, 2014), but our data suggest that could increase animals on roadsides. Vegetation manipulation would likely need a mosaic pattern leading up to culvert entrances, with more open spaces for movement and foraging of large generalist species such as kangaroos (Bond & Jones, 2014; Yanes et al., 1995) and patches of more dense vegetation for small species such as rodents to shelter and avoid predation (Brunen et al., 2020; Chisholm & Taylor, 2007; McLaren et al., 2011). An alternative solution, previously unutilised, would be use of biological attractants and repellents such as pheromones which could potentially produce an associated learned behavior, therefore, not requiring constant replenishment of pheromones. Our study region only contained under-road infrastructure which did not cater for arboreal species, which apart from the common brushtail possum (only observed crossing over the road surface), were not observed. Therefore, further research of road crossing infrastructure should also investigate over-road crossing structures such as land or canopy bridges, and glide poles, to cater for arboreal species at the same time.

AUTHOR CONTRIBUTIONS

Felicity E. Charles: Conceptualization (equal); data curation (lead); formal analysis (equal); methodology (equal); writing—original draft (lead); writing—review and editing (equal). **Megan J. Brady**: Conceptualization (equal); formal analysis (supporting); methodology (equal); supervision (supporting); writing—original draft (supporting); writing—review and editing (equal). **Annabel L. Smith**: Conceptualization (equal); formal analysis (equal); methodology (equal); supervision (lead);

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CONFLICT OF INTEREST STATEMENT

Annabel L. Smith is on the editorial board of *Wildlife Letters* and recused herself from discussing this manuscript during the submission and review process.

DATA AVAILABILITY STATEMENT

Data and code (Charles & Smith, 2023) are available in Zenodo at https://doi.org/10.5281/zenodo.8026119.

ETHICS STATEMENT

This research was conducted according to the guidelines of the animal ethics committee of the University of Queensland (approval number: ANFRA/SAFS/242/20). Animals were not interfered with or handled during the process of this research; all contact with animals was indirect via camera trapping.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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