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Research article

What attributes are relevant for drainage culverts to serve as efficient road crossing structures for mammals?

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ABSTRACT

Roads increase wildlife mortality and present a movement barrier for many species. While wildlife passages have been advocated as a solution to many of the problems associated with roads, they are expensive and many roads still have none. However, roads usually have a series of drainage culverts designed to allow water to cross underneath the road, which might also be used by some mammals. This study aims to (1) determine what variables influence the number of successful passages of drainage culverts by mammals, and to (2) parse the effects that these variables have on the entry into and subsequent full passage of drainage culverts by individual mammals, using cameras and animal track stations along a 20 km stretch of autoroute 10 in Southern Quebec (Canada). Overall, 20 species were observed outside of the drainage culverts, but only about half of them were detected making full crossings. While various species were often seen outside, only animals highly tolerant to water, including raccoons (*Procyon lotor*) and American mink (*Neovison vison*), were observed fully crossing the structures with regularity, whereas the number of full crossings was small (<8) for all other species. High-water levels and use of polyethylene as a construction material were the strongest deterrents for both the number of successful passages and the probability of entry into the culverts. While several variables (e.g., water level, structure material, moon luminosity, distance to forest) influenced culvert entry, none had an influence on a mammal's probability of complete passage once it had entered. The results imply that ordinary drainage culverts are unsuitable as substitutes for designated wildlife passages for mammals. We recommend the installation of designated wildlife passages and fences, and that in places where wildlife passages are not feasible, dry ledges be installed in existing drainage culverts to better allow small and medium-sized mammals to safely cross under roads while avoiding the water inside of the culverts. To our knowledge, this study is the first to successfully combine trail cameras inside of drainage culverts with track-box data in the adjacent habitat.

1. Introduction

Global road development is expected to increase dramatically, by 14%–23% by 2050 (an additional 3.0 to 4.7 million kilometres of roads compared to around 2015) according to Meijer et al. (2018) and by 35%–60% (i.e., 14.8 to 25.3 million km of additional paved-lane length between 2010 and 2050) according to Dulac (2013), with estimates differing due to choice of methods and underlying data. The effects of roads on wildlife are numerous; road mortality presents a substantial threat to the populations of many species without the installation of proper fences and crossing structures (van der Ree et al., 2015). In many cases, roads create a barrier effect that can result in the disruption of wildlife movement (Grilo et al., 2015). Large mammals with extensive home ranges are affected most heavily (Ng et al., 2004). This decrease in movement can lead to changes in genetic flow within subpopulations as well as between populations and to isolation or local extinction (Banks et al., 2005; Mata et al., 2008; Sawaya et al., 2014).

One measure for mitigating the negative effects of roads on animals regards the placement of wildlife passages designed to allow animals to cross either below or above the road surface. They have been supported for their effectiveness at encouraging wildlife to safely cross roads, as well as their ability to educate and engage the public regarding conservation efforts (Niemi et al., 2014). If wildlife fences are used in combination with such passages, they can drastically reduce

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wildlife-vehicle collisions (Beben, 2012; Rytwinski et al., 2016) while wildlife movements between habitat patches on either side of the road can occur (Marangelo and Farrell, 2016).

Canadian case studies have been shining examples in the world of road ecology, among them a series of under- and overpasses in Banff National Park in Alberta (Clevenger and Barrueto, 2014). However, while the placement of wildlife passages is an attractive solution to many of the ecological problems posed by roads, they are often prohibitively expensive, making them unattainable in many areas (Viani et al., 2016). In such situations of financial constraint, it becomes important to explore cost effective (yet still functional) alternatives to designated wildlife crossing structures, while highlighting regions of importance to prioritize future efforts (Rodriguez et al., 1996; Bissonette and Adair, 2008).

Drainage culverts have received increasing attention for their potential as pseudo-wildlife-passages, facilitating animal movement under highways while serving their original purpose of water drainage. It is their ubiquity that shows the greatest potential; an even spacing of tunnels under roads, some conceivably at preferential crossing locations, may already be mitigating the effects that roads have on animals to some degree, and may be improved upon with retrofitting (Krawchuk et al., 2005; Grilo et al., 2008). Indeed, drainage culverts have been suggested as a cost-effective alternative to designated wildlife passages when funds for large mitigation projects are lacking (Mata et al., 2008). Some wildlife species have been observed regularly using drainage culverts to cross under roadways, lending support to this argument (Ascensão and Mira, 2007).

However, can drainage culverts truly act as substitutes for designated wildlife crossing structures? Ascensão et al. (2016) found that road mortality of small mammals was lower in areas where drainage culverts were present, suggesting that in some cases they act as effective ad-hoc passages. However, the intended purpose of the drainage culvert may prove to be its undoing as a passage for wildlife: It facilitates water movement. In many cases, fish and aquatic mammals are the only visitors to drainage culverts, with primarily terrestrial mammals avoiding them altogether (Marangelo and Farrell, 2016). Still, for some species, Clevenger et al. (2001) argued that drainage culverts may be critical for maintaining habitat connectivity, making them potentially valuable conservation tools that deserve more in-depth analysis. Furthermore, with projected increases in the frequency and severity of storms due to climate change, most drainage culverts will need to be modified or replaced by larger structures to properly deal with flooding (van Vliet et al., 2013). This presents an opportunity to install wildlife-friendly features such as dry ledges or dry walkways in an attempt to improve the drainage culvert's ability to move both water and wildlife (Villalva et al., 2013).

Ecological corridors, linear segments of habitat that facilitate the movement of organisms among patches otherwise separated by unsuitable matrix, have been considered to be valuable tools in conservation for maintaining habitat connectivity in an increasingly fragmented world (Pino and Marull, 2012). Proposed ecological corridors identified using remote-sensing technologies but not validated on-site provide useful theoretical information regarding which areas should be prioritized for conservation efforts, including the identification of potential road-crossing sites (Cushman et al., 2013; Wierzchowski et al., 2019). Our study area contains seven proposed ecological corridors in four priority areas (Salvant, 2017; Daguet and Lelièvre, 2019), which may result in higher levels of animal activity for drainage culverts laying within them.

Drainage culverts are made of various materials, each of which provide different benefits at different price points. While concrete drainage culverts are quite durable, they are expensive. Steel culverts, while more affordable than concrete ones, have a lower weight threshold that can result in their collapse. Lastly, polyethylene culverts have emerged as an inexpensive and longer-lasting alternative to those made of steel. No study to our knowledge has analyzed the influence these materials may have on their use by mammals, which is an aspect deserving more attention.

To determine the suitability and ultimately the substitutability of drainage culverts to designated wildlife crossing structures, we addressed three research questions: (1) How many individuals from which species fully cross, and which drainage culvert characteristics affect the rates of full passages? For individuals that are detected outside of the structure, what factors influence their (2) entry and (3) subsequent full passage of drainage culverts? To answer these questions, we evaluated the relationship between culvert use by mammals and 12 explanatory variables divided into two categories: structural characteristics of drainage culverts and surrounding environmental characteristics.

Structural characteristics often include physical dimensions of the drainage culvert (Ng et al., 2004; Seiler and Olsson, 2009) as well as the type of structure (Mata et al., 2008). To our knowledge, structure material has not been included in a study of this nature before, but has been included here due to the fairly even distribution of materials used to construct the drainage culverts in our study area, and due to our personal observation that structures made with concrete echoed less and had greater traction similar to natural substrates in the surrounding habitat, factors which may influence an animal's willingness to cross. Surrounding environmental variables used in past studies include the distance from a culvert entrance to the nearest forest edge (Clevenger et al., 2001) and water-related variables (Grilo et al., 2008). While Grilo et al. (2008) analyzed the effect of stream width on mammal use of drainage culverts, we were interested in the effect that water depth might have on the behaviour of mammals in our culverts, a variable that to our knowledge has not yet been included in a study of this type. The effect of the luminosity of the moon has been included in unrelated wildlife studies (Penteriani et al., 2013; Griffin et al., 2005) with results suggesting that the activity of animals changes considerably with the moon's luminosity. To our knowledge, this and all other environmental variables used in this study have not been included in past wildlife passage studies.

We hypothesized that (1) the number of full passages will be influenced by water level (−), the distance from culvert entrance to habitat edge (−), length of the culvert (−), and the presence of proposed ecological corridors (+); (2) the factors influencing entry of culverts will be the distance from the culvert entrance to habitat edge (−), use of concrete as construction material (+), as well as water level (−); and finally, (3) an individual fully crossing a culvert once it has been detected entering will be influenced by culvert length (−), use of concrete as construction material (+), and water level (−) inside the culvert.

2. Methods

2.1. Study area

The project area lies within the Quebec Appalachians, which vary considerably in elevation, ranging from sea level to over 1200 m, resulting in a wide variety of habitat types. Vegetation in this area transitions from forests of sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) to alpine tundra dramatically (Li and Ducruc, 1999). This shift in ecosystems provides ample habitat types for many species, resulting in a high species richness in the area. Within the Quebec region of the Appalachians alone, mammals include, among others, bobcat (*Lynx rufus*), Canada lynx (*Lynx canadensis*), moose (*Alces americanus*), caribou (*Rangifer tarandus*), North American river otter (*Lontra canadensis*), fisher (*Martes pennanti*), and American marten (*Martes americana*) (Li and Ducruc, 1999).

The highway of interest in this study was Quebec's autoroute 10, the province's fourth longest highway at 147 km, stretching from Montreal in the north-west to the south-east-lying city of Sherbrooke (Fig. 1). Fragmenting ecologically important regions including northern Estrie and Monteregie, autoroute 10 was opened to motorists in 1964. It borders the southern boundary of Parc national du Mont-Orford, an IUCN category II provincial park. The portion of autoroute 10 between kilometre markers 82 and 114.6, encompassing 13 drainage culverts (Table 1), received on average 30,950 vehicles per day in 2017 according to data from the Quebec Ministry of Transportation. Species killed most often by passing vehicles on this road include North American porcupine (*Erethizon dorsatum*), whitetail deer (*Odocoileus virginianus*), and unidentified micromammals (Quebec Ministry of Transportation, unpublished data; LoScerbo et al., resubm.).

2.2. Trail cameras

To monitor animal activity inside and outside the culverts, this project used *Reconyx Hyperfire* model HC600 motion-sensing infrared trail cameras at each entrance (four cameras per culvert, two at each entrance, one directed inside and one outside; see Fig. 2 for photos of installation) in summer and fall 2018 (May 21 – December 4). Trail camera photos allowed us to determine full drainage culvert crossing rates (where the animal crosses entirely from one entrance of the structure and exits out of the other without turning around within 10 min) compared to total number of visits. Visits include wildlife detections outside of the drainage culvert without the animal entering the culvert, full crossings, explorations (when the animal enters through one entrance and turns around, exiting out of the same entrance from which it entered), and unknown passages (when the outcome of the visit is not known, due to technical issues or non-detection due to high speed of the moving animal). These numbers provide an approximation of what proportion of animals are able to successfully use the structures to cross under the road. Unknown passages were excluded from statistical analyses.

Full crossings were confirmed if an individual was seen on at least one camera from each entrance crossing completely from one side to the other. Any combination of camera detections were permitted to confirm full crossings, including all four cameras, both inside-facing cameras, both outward-facing cameras, or combinations of these. Our count dataset was constructed by taking the sums of full crossings, outside detections, explorations, and unknown passages per two-week sampling period, respectively, per species, per site.

Due to financial constraints, we did not have the number of cameras required to have one inward facing and one outward facing camera at each of the thirteen structure entrances simultaneously. We found a solution to this issue by rotating the cameras between every other site on a two-week rotation schedule. To minimize potential detection bias resulting from differences in detection sensitivity that may be present between cameras, potentially resulting in the failure of a camera to detect an animal (Jumeau et al., 2017), this project employed a continuous counter-clockwise rotation of cameras among sites. Every two-week session, cameras were moved to their counter-clockwise

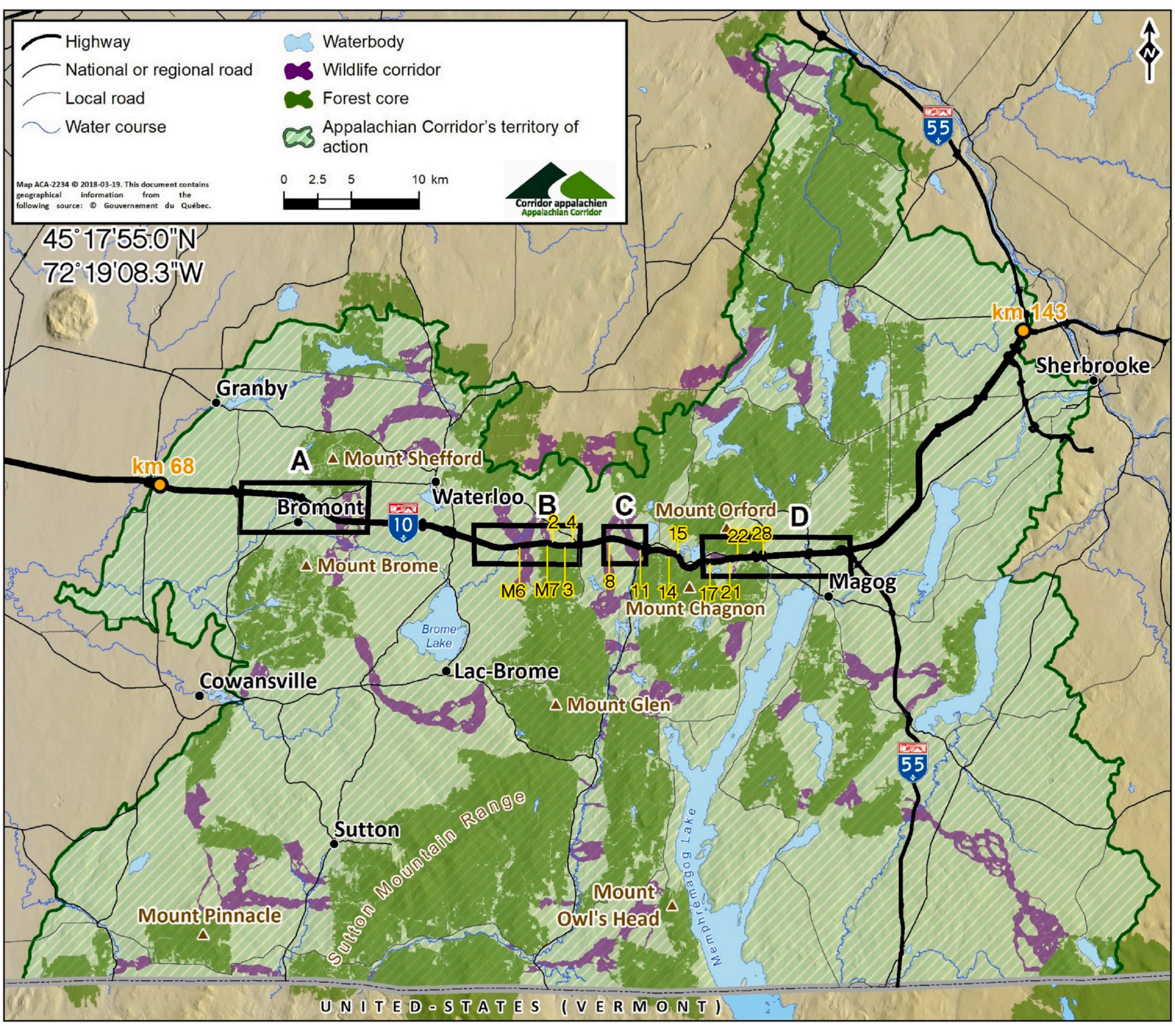

Fig. 1. Map of study area. Western boundary is approximately 80 km from Montreal, Quebec (courtesy of Appalachian Corridor). The locations of the 13 drainage culverts studied are indicated by yellow labels (Table 1). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Characteristics of the 13 drainage culverts studied.

Site ID	Length (m)	Width (m)	Height (m)	Shape	Material	Inside wildlife corridor?	Average distance from culvert entrance to forest (m)
M6	130.40	1.70	1.70	Circular	Steel	Yes	0
M7	50.00	1.05	1.05	Circular	Polyethylene	Yes	8.50
2	62.50	1.20	1.20	Circular	Steel	No	1.30
3	102.90	1.50	1.50	Circular	Polyethylene	No	0
4	89.00	1.00	1.00	Circular	Polyethylene	No	0
8	56.80	0.95	0.95	Circular	Polyethylene	No	17.80
11	56.00	1.00	1.00	Circular	Polyethylene	No	9.60
14	64.50	1.80	1.80	Circular	Concrete	No	0
15	60.85	1.35	1.35	Circular	Concrete	No	0
17	63.70	1.50	1.50	Circular	Concrete	Yes	0
21	57.00	0.80	0.80	Circular	Polyethylene	Yes	8.83
22	47.50	1.25	1.25	Circular	Polyethylene	Yes	3.50
28	63.50	6.00	3.00	Rectangular	Concrete	No	5.75

Fig. 2. Trail camera and track-box installation photos. (Photo credit: Jonathan Cole, Steffy Velosa, and Mehrdokht Pourali.)

neighbour, resulting in each structure hosting a different set of cameras for each sampling period. Data collected at any given structure was stored on SD cards labelled with the structure's ID to ensure accurate photo organization during the rotation process.

2.3. Track boxes

Animal footprint collection was employed as a tool to estimate species presence in the forest adjacent to the drainage culvert sites. Two footprint-collecting track boxes (Fig. 2) were placed outside of each structure entrance, 40 m away from the entrance on either side of the structure, and an additional 20 m away from the road surface in the adjacent habitat (Fig. 3). The goal of these track boxes was to detect individuals within the adjacent habitat away from the highway as a rough index of mammal activity, including animals that may not venture out into the cleared shoulder of the road.

Track boxes were constructed using two bent sheets of corrugated black coroplast fastened with tape and wooden poles to form a rectangular enclosure following the construction plan by Bélanger-Smith (2014) (Fig. 2). A thin layer of white polystyrene was fastened inside the bottom of the track box, proving a surface on which to attach the track papers. A layer of ink was applied to each entrance of the box, with brown kraft paper placed in the center of the box, both of which were replaced bi-weekly over a period of 14 weeks (June 6 – November 9). The ink was formulated using activated cosmetic charcoal powder and mineral oil, at a ratio of 0.5 cups of powder to 1 L of oil. To attract mammals, a lure was placed into the box as inspired by Bélanger-Smith (2014): a mixture of fish oil, anise oil, and a carnivore lure called K-9 Triple Take made by Forsyth Animal Lures. The lure was poured bi-weekly into red solo cups taped to the inside wall of the track box, and formulated using a ratio of 0.25 cups of fish oil to one tablespoon of anise oil to one popsicle-stick-dab of carnivore lure.

2.4. Variables considered

To address research question 1, data were organized in two-week sampling periods. For research questions 2 and 3, daily sampling results were used. Accordingly, variables were defined to suit each research question (Table 2). For example, "track.avg", the average number of tracks detected per site per two-week period for each species, was only included in the statistical model for research question 1, according to the two-week frequency track paper collection. Similarly, "avg.rain (cm)", representing the two-week average rainfall in the study area, was used only in the model for research question 1, while "rain

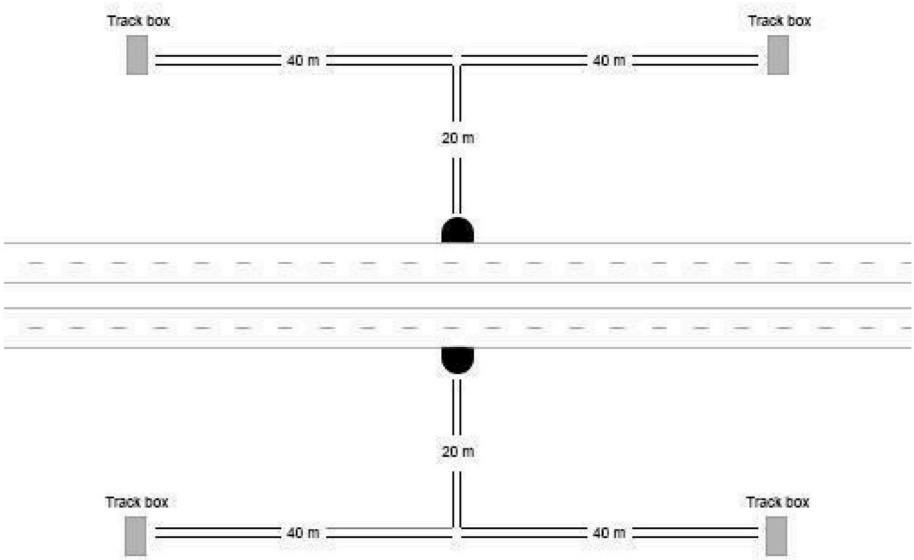

Fig. 3. Track-box layout in relation to each drainage culvert.

Table 2
Variables considered in the analysis of the use of drainage culverts ($n = 13$) monitored along autoroute 10, Quebec, Canada in summer and fall 2018.

Variable name	Definition/explanation and units	Structural or environmental variable	Range of values	Related to research question	Variable type
material	Culvert material	structural	Steel, polyethylene, concrete	1, 2, 3	Fixed
dist.forest	Distance from culvert entrance to habitat edge (m)	environmental	0–17.80 m	1, 2, 3	Fixed
track.avg	Average number of tracks detected per species per site (referred to as "tracks" in text)	environmental	0–0.50	1	Fixed
temp	Average temperature per two-week sampling period (°C)	environmental	−3.36–20.93 °C	1	Fixed
daily.temp	Daily temperature measurement from nearest weather station (°C)	environmental	−9 –32 °C	2, 3	Fixed
week	Two-week sampling session of each data point	–	1–7	1, 2, 3	Fixed
corridor	Whether or not the site lies within an ecological corridor	environmental	0 or 1	1, 2, 3	Fixed
length	Structure length (m)	structural	47.50–130.40 m	1, 2, 3	Fixed
water	Water depth at culvert entrance (cm)	structural	0–55 cm	1, 2, 3	Fixed
avg.rain	Average precipitation per two-week session (cm)	environmental	0–15.4 cm	1	Fixed
rain	Precipitation per day (cm)	environmental	0–38.1 cm	2, 3	Fixed
qmoon	Quantified moon cycle	environmental	0 (new moon), 0.25, 0.5, 0.75, 1 (full moon)	2, 3	Fixed
Site	Drainage culvert ID	–	13 sites	1, 2, 3	Random
species	Species of each event observed	–	–	1, 2, 3	Random

(cm)", the daily rainfall measurement, was employed in the models for research questions 2 and 3. All other variables were used in all three models.

2.5. Statistical analysis

2.5.1. Model selection

All statistical models were tested for multicollinearity using variance inflation factors (VIF) (Alin, 2010). A common rule states that if any variable returns a VIF coefficient of 10 or greater, the variable is considered to be collinear with at least one other variable (O'Brien, 2007). However, we followed Ringle et al. (2015) using a more rigorous VIF threshold of 5 to ensure there was no multicollinearity within our datasets and to avoid any unreliable parameter estimates (Mansfield and Helms, 1982).

We performed model selection for fixed effects by stepwise backward model reduction (Zuur et al., 2009) and compared models using Akaike's Information Criterion (AIC_c) (Hurvich and Tsai, 1989). When a model excluding a given variable resulted in an AIC_c score difference of two or greater (indicating a lower degree of parsimony) compared to the global model, the variable was considered significant and was included in the final model. This was performed for each fixed effect in the global model until all variables were either discarded or included in the final model. We acknowledge the criticism calling for the cautious use of stepwise model reduction (Flom and Cassell, 2007), but elected to use the method for its computational efficiency, clear interpretation, and very common usage in the field of ecology (Zuur et al., 2009; Alexandre et al., 2018).

2.5.2. Zero inflation

To address research question 1, we modeled full crossing counts of mammals per two-week sampling period ($n = 7$) using zero-inflated negative binomial (ZINB) generalized linear mixed models (GLMM) to assess the effect that some variables may have on making sites uninteresting for mammals to use. Our count data of full crossings exhibited considerable overdispersion resulting from higher variation in the data than expected under a Poisson distribution (overdispersion parameter = 2.2, $p = 7.3e\text{-}60$, with zeros comprising 87.76% of the data for outside presence and 89.95% for full passages), necessitating the use of negative binomial regression. Because we suspected that some variables (water depth and the distance between the drainage culvert entrance to the nearest habitat edge) may be causing absences (called structural zeros) separate from those naturally occurring (called true zeros) due to the low population densities of some mammal species in our study area, zero-inflation was utilized for its ability to assess which component in a model may be causing structural zeros. Generally, zero-inflation is used when there is a significant excess of zeros that is higher than the number that would be expected according to a Poisson or negative binomial distribution, leading to overdispersion (Zuur et al., 2009). Studies over the past five years have shown that statistically ignoring the presence of zero inflation in count datasets often causes bias in the estimation of parameters and leads to inaccuracies in model interpretation (Bouyer et al., 2015).

We estimated coefficients using maximum likelihood under R version 3.3.3 (R Core Team, 2017) with the package *glmmTMB* (generalized linear mixed models using Template Model Builder) version 0.2.3 (Brooks et al., 2017; Alexandre et al., 2018). Structurally very similar to the package *pscl* (Zeileis et al., 2008), *glmmTMB* allows for the estimation of correlation within sampling units (random effects) through mixed models, of which *pscl* is not yet capable (Brooks et al., 2017). The *glmmTMB* zero-inflation model has two central components: (1) a conditional model that reports the coefficients of the negative binomial generalized linear mixed model using the same syntax as *lme4* (Bates et al., 2007), and (2) a zero-inflation component that reports the probability of a fixed effect resulting in the observation of an extra zero that is not generated by the conditional model (Brooks et al., 2017).

To account for repeated measurements at both the species and site scales, categorical variables "species" and "site" were included in the model as random effects. Only species with at least fifteen detections were included in this analysis to reduce zero-counts, resulting in seven species: common raccoon (*Procyon lotor*), whitetail deer (*Odocoileus virginianus*), American mink (*Neovison vison*), eastern gray squirrel (*Sciurus carolinensis*), weasel spp. (including *Mustela nivalis*, *M. frenata*, and *M. erminea*), muskrat (*Ondatra zibethicus*), and red fox (*Vulpes vulpes*). To account for potential temporal variation in mammal activity, a numeric value for each two-week sampling period was included as a fixed effect in the global model.

2.5.3. Logistic regression

For mammals that were detected by trail cameras outside of the drainage culverts (for research questions 2 and 3), we modeled binary outcomes for both entry into and full crossing through the culverts with logistic regression using generalized linear mixed models with binomial distributions and logit links. Through this method, we determined which structural and environmental factors affect entry into, and once inside, which factors affect full crossing of drainage culverts by mammals. Generalized linear mixed effects models were required for this data type due to the non-normal binomial distribution. Additionally, the random effects of the model required a mixed model type. All statistical tests for this section were performed in R version 3.3.3. (R Core Team, 2017) with the package *lme4* (Bates et al., 2015).

As before, repeated measures of species and sites were accounted for by including them as random effects. Moon luminosity as a function of the moon phase has been shown to affect the movement of some species (Prugh and Golden, 2014; Penteriani et al., 2013). To account for this potential effect, moon luminosity was included as a fixed effect. See Table 2 for full list of variables considered.

3. Results

Across 13 sites and 99 observation days at each site, we collected a total of 193,867 trail camera photos that included a total of 1145 unique animal detections, 261 of which resulted in a full crossing (22.79%). Regarding research question (1), detections spanned 20 species (Figs. 4 and 5), though only species with at least 15 detections were included in further analysis for research question one. Common raccoons fully crossed drainage culverts most often (37.54% of interactions with drainage culverts resulted in a full passage, 217 full crossings out of 587 detections), 2.8 times more likely to make a full crossing than the next highest full crossing species, the American mink (13.39%, 17 full crossings out of 127 detections). Species of special interest that were detected inspecting the drainage culverts included 3 observations of bobcats and 3 observations of American black bear (*Ursus americanus*), but no full crossings were attempted. Track boxes detected 15 species, with mouse spp., Eastern gray squirrel, and common raccoon being the most commonly detected species (Fig. 6).

3.1. Number of full crossings per two week period

The ZINB GLMM model containing only three variables after stepwise model selection (Zuur et al., 2009) was more parsimonious than the global model (Table 3), and included tracks per species per site per sampling unit, temperature, and week as fixed effects, with site and species kept as random effects. We collected a total of 638 two-week sampling period data points across our sites, which were included in our statistical analysis. We found that excess absences of full crossings significantly rose as a result of water level ($\beta = 0.13$ [0.03 to 0.23], $p = 0.01$), while no significant effect on excess zeros was measured by the distance from a drainage culvert entrance to the nearest habitat edge (Table 4). These excess absences of full crossings resulting from water

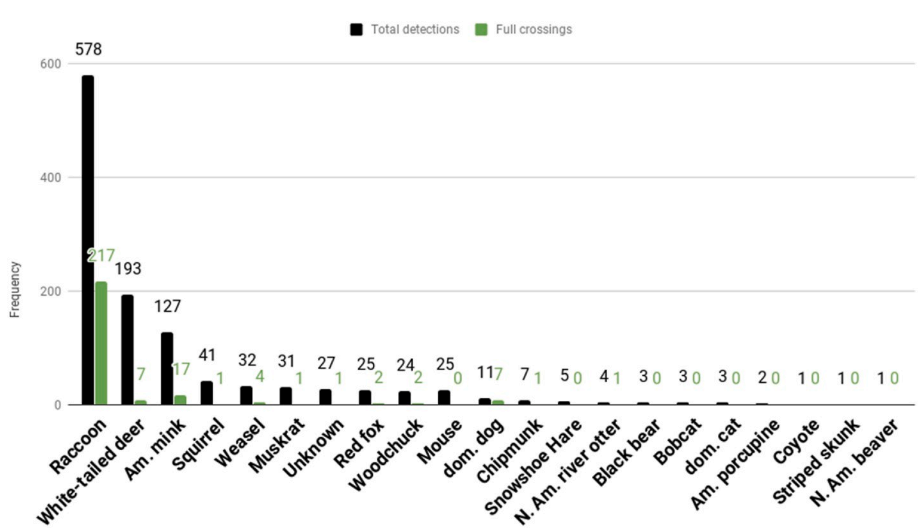

Fig. 4. Total number of detections (black) and full crossings (green) by species (observed based on camera data). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

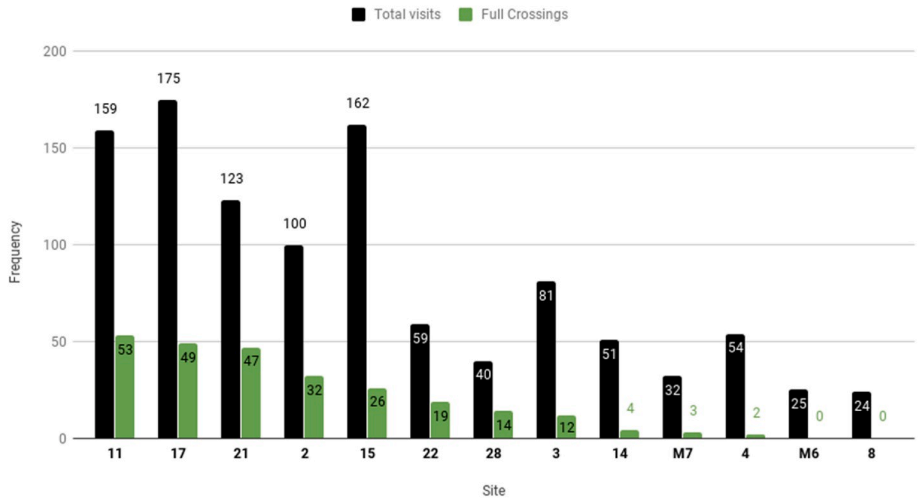

Fig. 5. Total number of detections (black) and full crossings (green) per drainage culvert site (observed based on camera data), ordered by number of full crossings. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

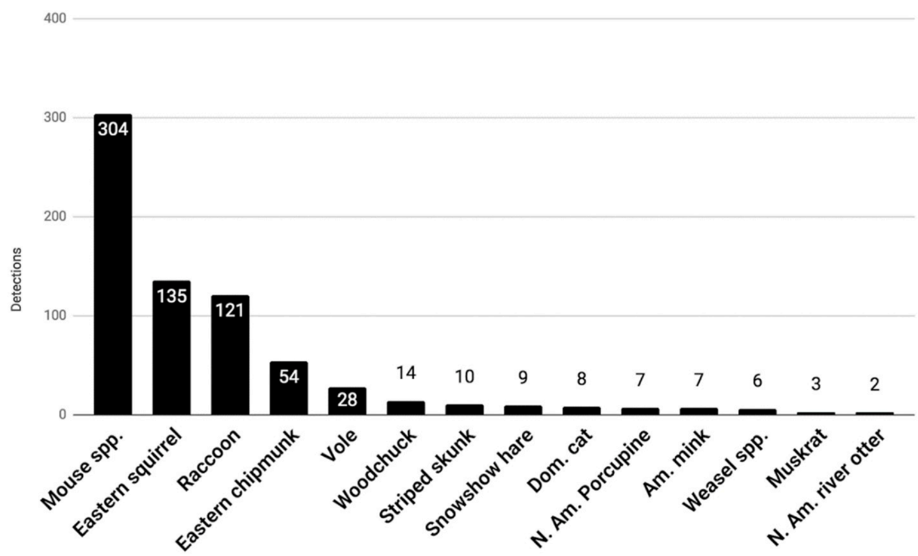

Fig. 6. Total numbers of track-box results by species.

level (or excess "true" zeros) mean that the zero-inflation model predicted that due to the level of water at each site, animals were not able to enter the detection zone of the trail cameras, resulting in an inflated number of zeros in the data. With absences accounted for, the number of full passages per species was found to be higher when tracks from that particular species were also detected in the adjacent habitat ($\beta = 5.52$ [1.69 to 9.35], $p = 0.005$), as well as when temperatures were higher ($\beta = 0.10$ [0.05 to 0.14], $p<0.001$). Sampling period did not have a significant effect on full passages. Unexpectedly, culvert material, the distance from culvert entrance to forest edge, the location within an ecological corridor, the length of the culvert, and average two-week rain levels were not selected for the final model.

3.2. Entry into and full crossing of drainage culverts

For estimating which factors influenced the entry of mammals that were first detected outside of drainage culverts, the model containing only variables selected during the model selection process was marginally better performing than the global model (Table 3). A total of 409 outside detections across 15 species were collected across all sites throughout the 99-day sampling period. Comparing conditional pseudo-R^2s revealed that the final model explained 6 percentage points more (global model $R^2 = 0.76$, final model $R^2 = 0.82$) of the variance than the global model. Regarding research question (2), entries into drainage culverts were found to be significantly affected by the material of the structure, with polyethylene negatively affecting entries ($\beta = -3.36$ [-5.28 to -1.44], $p<0.001$), and steel and concrete showing no difference. Surprisingly, the distance from the drainage culvert entrance to the nearest forest edge showed a positive relationship with entry ($\beta = 0.76$ [0.22 to 1.30], $p = 0.006$). Environmental factors also significantly influenced entries, with water level negatively affecting entry ($\beta = -0.17$ [-0.28 to -0.06], $p = 0.06$) and moon luminosity positively influencing entry ($\beta = 2.25$ [0.63 to 3.87], $p = 0.006$). Variables not selected from the global model included the location within an ecological corridor, culvert length, daily temperature, and daily rain level.

Using a subset of the above dataset containing only observations of individuals having entered the drainage culvert ($n = 78$ across 4 species), several models provided an equally reasonable fit following stepwise model selection, and therefore none of them could be discarded. We therefore elected to construct all suitable models and use the most parsimonious model (Table 3). The most effective model contained only the location within an ecological corridor and the distance from the

Table 3
Results of model-selection procedure evaluating number of full crossings, entry success, and crossing success by mammals over seven two-week sampling periods. The most parsimonious model is indicated with an asterisk.

Dataset	Models[a]	df[b]	LLR[b]	AIC_c[b]	R^{2}[b,c]
Full crossings per two week session (Negative binomial; count)	Tracks + temp + week*	10	−253	526	–
	Material + dist.forest[d] + tracks + temp + week + corridor + log (length) + water + rain	17	−250	533	–
Outside detections that lead to entry (Logit; binomial)	Material + log (dist. forest+1) + water + moon*	8	−93.4	203	0.82
	Corridor + material + log (dist.forest+1) + log (length) + water + moon + temp + log (rain+1)	12	−90.2	204	0.76
Inside detections that lead to full crossing (Logit; binomial)	Corridor + log (dist. forest+1)*	5	−29	70	0.09
	Corridor + material + log (dist.forest+1) + log (length) + water + moon + temp + log (rain+1)	12	−27	78	0.19

[a] See Table 2 for detailed information about the variables.
[b] Degrees of freedom (df), Log Likelihood (LLR), Akaike's Information Criterion adjusted for small sample size (AIC_c), and conditional pseudo-R^2 value.
[c] Pseudo-R^2 values not shown for ZINB GLMM because this statistic is not suitable for two-step regression models.
[d] The distance to forest variable was not log-transformed for research question one due to model convergence errors.

Table 4
Regression coefficients for final models.

Response variable	Variable	Coefficient	CI	*p*-value
Number of full passages	Track average	5.52	[1.69, 9.35]	0.005
	Temperature (°C)	0.10	[0.05, 0.14]	<0.001
	Water (cm)[a]	0.13	[0.03, 0.23]	0.01
	Distance to forest (m)[a]	−0.25	[-0.93, 0.43]	0.47
Individual culvert entries	Material (polyethylene)	−3.36	[-5.28, −1.44]	0.001
	Material (steel)	−1.07	[-3.37, 1.24]	0.36
	Distance to forest (m)	0.76	[0.22, 1.30]	0.006
	Water (cm)	−0.17	[-0.28, −0.06]	0.002
	Moon luminosity	2.25	[0.63, 3.87]	0.006
Individual full crossings	Location within corridor	1.21	[-0.31, 2.74]	0.12
	Distance to forest	0.73	[-0.15, 1.62]	0.10

[a] Indicates zero-inflation coefficient, where positive values indicate the variable's likelihood of producing excess zeros in the data.

culvert entrance to the nearest habitat edge as fixed effects, though all models had low pseudo-R^2 values (<0.19).

Regarding research question (3), no significant effects were found to influence the full crossing of mammals once they had entered a drainage culvert (Table 4).

4. Discussion

4.1. General results

Our results highlight that despite the multitude of species present near the habitat edge and roadside, only a small fraction of species were documented entering and even fewer fully crossing drainage culverts in our study area. Only common raccoons, American mink, and whitetail deer were observed fully crossing drainage culverts with some regularity during our sampling period, while other species often observed outside of the structures, including weasel spp (including *Mustela nivalis*, *M. frenata*, and *M. erminea*), red fox, and snowshoe hare (*Lepus americanus*), were rarely if ever observed fully crossing the structures. All of the drainage culverts in our study received entry by mammals, while all but two culverts received full crossings (Fig. 5).

4.2. Influence of variables

Animal track data have been a valuable tool in wildlife studies for decades (Ward, 1982; Clevenger and Waltho, 2000). When used for assessing wildlife crossing through passages, track stations have served as a cost-effective method of detecting which species were present in a structure over a given sampling period (Ng et al., 2004). However, using animal tracks as a means of determining full crossings and general behaviour of animals can be problematic, in that it is difficult to infer information beyond presence/absence using only the tracks of a species over a given period of time (Seiler and Olsson, 2009). Here, we used track data as a method of determining whether species are present in the adjacent habitat to then compare with animal activity in and around the drainage culverts using motion-sensing trail cameras. We found that track data are highly predictive of the number of full crossings observed in drainage culverts. As a fixed-control variable, the average number of tracks found per species per site was found to significantly improve the performance of our ZINB GLMM, accounting for 7.98% more variance of the data within the fixed effects (marginal R^2) than our final model without track data (Table B4 in suppl. Material).

Water level was found to be both negatively correlated with mammal entry into drainage culverts and a source of structural zeros in our count data. This has very important implications for drainage culverts as alternatives to designated wildlife crossing structures: The drainage culvert's inherent purpose of facilitating water movement makes it entirely unsuitable as a passage under roads for most species in our study area. While this is a highly intuitive result, and while some studies have discussed the need for alterations to drainage culverts for animals to avoid water (Niemi et al., 2014), very few studies (for instance, Marangelo and Farrell, 2016) have quantified the effect that water has on the entry and full crossing of drainage culverts by mammals.

The distance from the entrance of a drainage culvert to the nearest habitat edge was found to have a positive effect on the entry of mammals into the structures. This result was surprising due to past research findings that even small linear clearings in habitat act as impenetrable barriers for many species, small mammals in particular (Rico et al., 2007). Indeed, because density of mammal populations is known to be generally higher away from road surfaces (Pocock and Lawrence, 2005; Torres et al., 2016), we expected that greater distance between a culvert entrance and habitat edge – often indicating an entrance closer to the road surface – would result in fewer entries into culverts by mammals. However, reviewing the results by species revealed that this result may largely be a result of generalist species dominating the dataset that are more tolerant of non-ideal habitat types, including common raccoon and larger species with greater mobility including whitetail deer. It is also conceivable that individuals entering the open area between the road and adjacent forest may already be habituated to the open area and may even be aware of the location of the drainage culvert.

Structure material is rarely considered in wildlife passage studies (for instance, Beben, 2012), but due to drainage culverts coming in various shapes, sizes, and materials, we included this variable in our analysis to assess the effect that material might have on entry and full crossing of mammals. We found that culverts constructed with polyethylene, a sturdy and affordable plastic, strongly deters entry by mammals, while steel and concrete displayed no significant difference on mammal response. To our knowledge, the effect of the material of a crossing structure on animal use has rarely been analyzed (e.g., Woltz et al., 2008), and has important ramifications for transportation authorities and decision makers wishing to consider wildlife-friendly drainage culverts. While polyethylene culverts are a cost-effective alternative to traditional concrete or steel drainage culverts, decision makers should be wary of them when considering drainage culverts that both facilitate water movement and allow for the passage of wildlife. From observations taken in the field, polyethylene culverts had a distinct plastic smell and were much more slippery than either steel or concrete culverts. While we cannot say with certainty what may be deterring animals from polyethylene culverts, we suspect that a mixture of these factors likely plays a role in their disfavour among wildlife. To our knowledge, this result has not been reported in previous studies.

Ecological corridors can be essential links between otherwise isolated patches of habitat in an increasingly fragmented landscape (Hilty et al., 2006). We followed the hypothesis that properly functioning ecological corridors should have more animals travelling within them, and that drainage culverts lying within the path of these corridors ($n = 5$) would therefore have more animal activity than those outside of them ($n = 8$). The ecological corridors in our study area were determined in a past study as having potential to act as links between patches of habitat in southern Quebec (Salvant, 2017; Daguet and Lelièvre, 2019). Our results, however, showed that the location within a corridor played no significant role in predicting animal presence, entry, or full crossing of mammals through drainage culverts. We suspect that while the corridors certainly have potential to act as linkages between habitat patches, at present they are likely fragmented by roads to such an extent that they are not functioning as proper ecological pathways. This inference is supported by the results of a Welch two-sample t-test between the average number of tracks detected within versus outside of the ecological corridors, that did not find a significant difference between the two groups (t (474.56) = 0.78, $p = 0.44$).

Indeed, when highways are constructed through ecological corridors, the resulting habitat fragmentation often acts as a major constraint on the movement of animals in the area (Forman, 2005). If the barrier presented by the road is severe enough, animals will not be able to cross in large enough numbers resulting in loss of ecological connectivity and isolation of fragmented habitat patches (Dupras et al., 2016). To help combat this, we recommend constructing wildlife passages that align with the paths of ecological corridors, allowing animals moving along them to safely cross the highway without having to significantly deviate from their paths (Clevenger and Huijser, 2009). In our study area, several drainage culverts are already placed within ecological corridors, and retrofitting these structures to better suit animals should therefore be a high priority. Additionally, constructing wildlife fencing that would lead to either drainage culverts or designated wildlife crossing structures in these corridor areas would be necessary for lowering the amount of roadkill in these areas, as Rytwinski et al. (2016) found in their meta-analysis of mitigation measures intended to reduce road mortality.

Moon luminosity was found to have a significant effect on the entry of mammals into drainage culverts. Because the grand majority of animal detections in our study were during nighttime hours (Fig. 7), it follows that nights with greater moon luminosity – and therefore higher visibility – would result in higher animal activity. The effect that the moon's luminosity has on animal activity has been assessed in other studies (Griffin et al., 2005; Prugh and Golden, 2014), but to our knowledge has been included in animal studies relating to roads only very recently (Colino-Rabanal et al., 2018). We suspect that road mortality would peak during periods of higher moon luminosity, and we encourage the inclusion of this variable in future roadkill studies.

4.3. Species of special interest

Although we observed low numbers of detections from species of special interest, for example American black bear and bobcat, their naturally low population densities and large home ranges mean that their detection in our study is still highly significant. Both American black bears and bobcats were observed from the drainage culverts' outward-facing trail cameras approaching and investigating the entrance to the structures, but no entries were recorded. This result is very important as it shows that these species are present along the habitat edge and close to the highway barrier and the drainage culverts, but found the drainage culverts in our study area to be unsuitable as passages across the road. Since mammals with large home ranges are often impacted the most by fragmentation of their habitat, monitoring and mitigating this fragmentation is of high importance. We strongly recommend the implementation and monitoring of larger structures that are better suited to facilitate the movement of medium-sized and large mammals.

4.4. Novel findings and techniques

One of the most intriguing results in our study was that for mammals fully crossing under highways, several factors influenced their entry into drainage culverts, while no effects were found influencing their full crossing once inside. Factors including water level, structure material, and moon luminosity affected an animal's entry into a drainage culvert, but once it was inside, no variables included in our study affected whether it would fully cross. Low pseudo-R^2 values were observed for all of our potential models for this test, with no statistical significance among them. Because of this, we felt confident in selecting the final

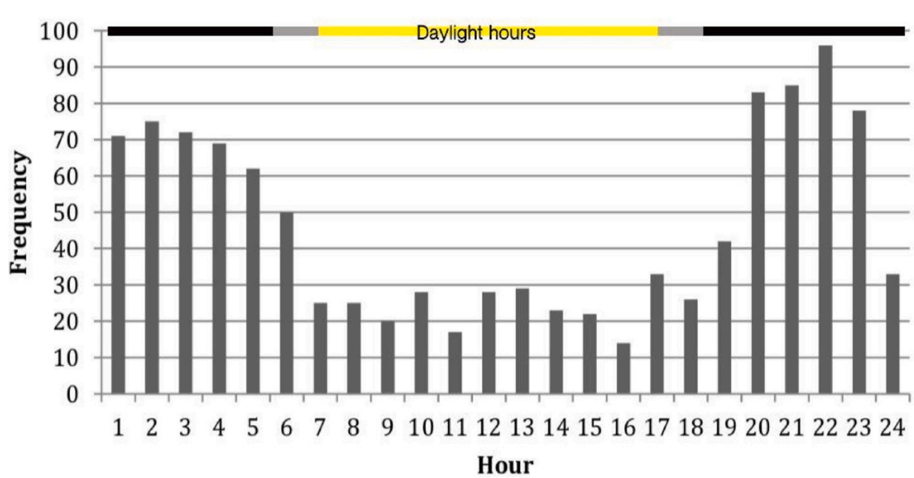

Fig. 7. Times of camera detections across all species (by hour).

model for this research question solely by AIC_c score, due to no variables being significant regardless of the outcome of the model selection process. This result suggests that mammals in our study area consider multiple factors before entering a structure, and that once inside, few factors change their initial decision. This too has significant implications for wildlife passage planners, as it suggests that while the passage in its entirety should be designed with care, entrances to wildlife passages should receive the utmost attention to make them as attractive to wildlife as possible. In our study, mammals preferred structures with little to no water running through them, as well as structures that were not constructed with polyethylene. Other studies have found that vegetation around the passage entrance (Clevenger and Barrueto, 2014), a soil substrate along the passage floor (Krawchuk et al., 2005), and passages with a high structural openness (Seiler and Olsson, 2009) are also strongly favored by many species.

We assessed the factors affecting mammals' entry and full crossing of culverts while employing several novel data collection methods and statistical techniques. To our knowledge, this is the first research project that has (1) used a scheduled rotating motion-sensing camera study design to minimize detection bias present in individual cameras, (2) utilized both outward- and inward-facing cameras to determine outside presence of animals as well as inside of drainage culverts, (3) combined animal track data with motion-sensing camera data to assess the relationship between mammals present in the habitat adjacent to the road versus animals within detection-range of the trail cameras, and finally (4) utilized zero-inflated negative binomial generalized linear mixed effects models to test for the presence of structural zeros in a road-related wildlife study.

One method that is very likely to become standard procedure in ecological studies to determine factors that lead to habitat unsuitability, much like culvert water depth in this study, is the use of zero-inflated modelling. The utilization of zero-inflated mixed models in ecology is currently on the cutting edge of statistical analyses, with only a handful of publications using the method since its creation in 2010 and widespread introduction in 2017 (Brooks et al., 2017; García-Romero et al., 2019; Williams et al., 2019). Due to ecologists' interest in not only determining what factors contribute to a response, but what variables may entirely prevent a response from occurring, such as animals not being present in a sampling area, we feel that zero inflated modelling is a natural fit for ecological studies.

4.5. Limitations

While this study employed particularly strong sampling techniques, including the use of four motion-sensing trail cameras per drainage culvert, as well as the two-week rotation of trail cameras to reduce detection bias in individual cameras, it could have benefitted from several small changes to its general design and duration. For example, a longer sampling period would lend support to a stronger statistical analysis due to a larger sample size. This study covered 99 days at each site, with cameras active in each site for half of the sampling period from May 21 to December 4 due to the rotation of trail cameras. However, a longer sampling period in this study would have extended into the winter months, when many of the species in our study area would either be in hibernation or be exhibiting lower activity. Starting the sampling period earlier in the spring season would undoubtedly have resulted in a larger sample size. Additionally, having multiple sampling seasons and a larger number of drainage culverts would potentially further strengthen our findings.

Although the variation in drainage culvert characteristics including construction material and dimensions was as large as possible given the study area, having a larger sample of drainage culvert materials and sizes would have increased the strength of the study considerably. In particular, this study would have benefitted from a higher number of large box culverts. Because of the small sample of box culverts in this study (1 out of 13), it will be difficult to draw confident conclusions regarding their ability to allow animals to cross through them. In particular, the large box culvert in this study showed good potential to allow for the passage of deer and other large mammals of special interest, so increasing the sample size of this type of culvert could have ecologically significant implications.

This research was also limited by its dependence on ecological corridor data that were originally collected as part of another study. A broader environmental evaluation such as inclusion of variables of landscape pattern into the statistical models could have contributed to a stronger study.

4.6. Suggestions for future research

While wildlife monitoring studies with a one-season sampling period, as this study was, provide ecologically significant information, conducting a multi-timeframe study that assesses the activity of animals both before and after a variable is introduced provides an excellent opportunity to test the effect of the variable on the response variable (Rytwinski et al., 2015). Regarding this study's survey area, the potential for the installation of wildlife fencing along the highway presents a unique opportunity to measure both animal activity around the highway as well as animal mortality on the road surface before and after the fence's installation. Ideally, fences would be constructed where roadkill hotspots exist (Spanowicz et al., 2020), with fence ends placed in conjunction with existing drainage culverts to allow animals venturing to the end of the fence to cross under the highway. This study design type, known as a before-after-control-impact (BACI) study (Roedenbeck et al., 2007), has the potential to show the impact that a wildlife fence may have on the movement patterns and mortality on the road surface of mammals along autoroute 10. These results would be essential for determining the value of such fencing, and would have the potential to influence the installation of wildlife fencing in other areas.

The plastic smell of the polyethylene culverts may be related to the fact that those culverts were relatively new. It is conceivable that mammals might eventually get used to them after some time. To test this possibility, the age of polyethylene culverts should be studied as a variable in future research. Including habitat types (Clevenger et al., 2001) and landscape connectivity metrics (Mimet et al., 2016) or functional connectivity assessments (Girardet et al., 2015; Valerio et al., 2019) could also be an interesting step toward better understanding road crossing behaviour and the use of culverts.

5. Conclusions and recommendations

For 13 drainage culverts along a high-traffic 4-lane highway in southern Quebec, we assessed the effect that structural and environmental factors have on the entry, full crossing, and number of full crossings by mammals. We found that, (1) the presence of water outside of and within drainage culverts resulted in site avoidance, (2) polyethylene drainage culverts were strongly disfavored, (3) increasing distance from culvert entrance to habitat edge was related to more entries, (4) the luminosity of the moon had a positive effect on mammal activity and entry of culverts, and (5) that many more factors play a role in an animal's entry into a drainage culvert than its full crossing once it is already inside.

We recommend the installation of designated wildlife crossing structures to allow safe passage by all species present in the study area. Larger structures should be considered to facilitate the movement of larger mammals. Where this is not feasible, we recommend dry ledges be installed inside of drainage culverts to allow for mammals to cross through drainage culverts without water levels deterring their passage, in accordance with Glista et al. (2009), Villalva et al. (2013), and Smith et al. (2015). In times of climate change, extreme weather events are expected to occur more frequently in many regions, and many water culverts will need to be replaced by larger structures. In this situation, types of culverts should be selected that are more suitable for wildlife movement or can be retrofitted with ledges more easily to make them more suitable. Furthermore, retrofitting and conservation priority regarding drainage culverts should be given to those that are situated within ecological corridors. Improving these structures could help restore ecological functionality of ecological corridors that have lost it as a result of the barrier effect of the road, since they are optimally placed, at least in principle. Additionally, we recommend installing wildlife fencing along our study area, with sections that end at the entrances to drainage culverts, and that culvert entrances be situated on the habitat-side (rather than the highway-side) of the fence (Ford and Clevenger, 2018). This is in accordance with the meta-analysis by Rytwinski et al. (2016) that found that animal mortality on roads significantly decreases when wildlife passages are employed in combination with wildlife fencing, whereas wildlife passages without fences do not reduce road mortality. Mortality reduction graphs can be used to determine the length of fencing required to achieve any given mortality reduction target, as part of an adaptive fence implementation plan (Spanowicz et al., 2020). In lieu of designated crossing structures, ending fence sections at culvert entrances would be the best possible strategy in the current situation and might increase the use of the culverts by more individuals from a larger range of species.

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Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2020.110423.

References

Alin, A., 2010. Multicollinearity. WIREs Computational Statistics 2 (3), 370–374. https://doi.org/10.1002/wics.84.

Alexandre, N.M., Humphrey, P.T., Gloss, A.D., Lee, J., Frazier, J., Affeldt III, H.A., Whiteman, N.K., 2018. Habitat preference of an herbivore shapes the habitat distribution of its host plant. Ecosphere 9 (9), e02372. https://doi.org/10.1002/ecs2.2372.

Ascensão, F., Mira, A., 2007. Factors affecting culvert use by vertebrates along two stretches of road in southern Portugal. Ecol. Res. 22 (1), 57–66. https://doi.org/10.1007/s11284-006-0004-1.

Ascensão, F., Mata, C., Malo, J.E., Ruiz-Capillas, P., Silva, C., Silva, A.P., et al., 2016. Disentangle the causes of the road barrier effect in small mammals through genetic patterns. PloS One 11 (3), e0151500. https://doi.org/10.1371/journal.pone.0151500.

Banks, S.C., Lindenmayer, D.B., Ward, S.J., Taylor, A.C., 2005. The effects of habitat fragmentation via forestry plantation establishment on spatial genotypic structure in the small marsupial carnivore, *Antechinus agilis*. Mol. Ecol. 14 (6), 1667–1680. https://doi.org/10.1111/j.1365-294X.2005.02525.x.

Bates, D., Sarkar, D., Bates, M.D., Matrix, L., 2007. The lme4 Package. R package version 2 (1), 74.

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. *lme4: Linear Mixed-Effects Models Using Eigen And S4*. R Package Version 1.1-10. http://CRAN.R-project.org/package=lme4.

Beben, D., 2012. Crossings for animals – an effective method of wild fauna conservation. J. Environ. Eng. Landsc. Manag. 20 (1), 86–96. https://doi.org/10.3846/16486897.2012.662753.

Bélanger-Smith, K., 2014. Evaluating the Effects of Wildlife Exclusion Fencing on Road Mortality for Medium-Sized and Small Mammals along Quebec's Route 175 (MSc thesis). Concordia University, Department of Biology. Available at: https://spectrum.library.concordia.ca/979605/. (Accessed 10 January 2018).

Bissonette, J.A., Adair, W., 2008. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. Biol. Conserv. 141 (2), 482–488. https://doi.org/10.1016/j.biocon.2007.10.019.

Bouyer, Y., Rigot, T., Panzacchi, M., Moorter, B.V., Poncin, P., Beudels-Jamar, R., et al., 2015. Using zero-inflated models to predict the relative distribution and abundance of roe deer over very large spatial scales. Ann. Zool. Fenn. 52 (1–2), 66–76. https://doi.org/10.5735/086.052.0206.

Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9 (2), 378–400. https://doi.org/10.3929/eth-zb-000240890.

Clevenger, A.P., Waltho, N., 2000. Factors influencing the effectiveness of wildlife underpasses in Banff national Park, Alberta, Canada. Conserv. Biol. 14 (1), 47–56. https://doi.org/10.1046/j.1523-1739.2000.00099-085.x.

Clevenger, A.P., Chruszcz, B., Gunson, K., 2001. Drainage culverts as habitat linkages and factors affecting passage by mammals. J. Appl. Ecol. 38 (6), 1340–1349. https://doi.org/10.1046/j.0021-8901.2001.00678.x.

Clevenger, T., Huijser, M.P., 2009. Handbook for Design and Evaluation of Wildlife Crossing Structures in North America. Montana State University, Bozeman (MT), and Federal Highway Administration, Washington (DC), p. 212 pp.

Clevenger, A.P., Barrueto, M., 2014. Trans-Canada Highway Wildlife and Monitoring Research, Final Report. Part B: Research. Prepared for Parks Canada Agency, Radium Hot Springs, British Columbia.

Colino-Rabanal, V.J., Langen, T.A., Peris, S.J., Lizana, M., 2018. Ungulate-vehicle collisions rates are associated with the phase of the moon. Biodivers. Conserv. 27 (3), 681–694. https://doi.org/10.1007/s10531-017-1458-x.

Cushman, S.A., Lewis, J.S., Landguth, E.L., 2013. Evaluating the intersection of a regional wildlife connectivity network with highways. Movement Ecology 1, 12. https://doi.org/10.1186/2051-3933-1-12.

Daguet, C., Lelièvre, M., 2019. Identification et protection des corridors naturels de part et d'autre de l'autoroute 10 (Estrie et Montérégie Est) et amélioration de sa perméabilité faunique: premiers résultats. Le naturaliste canadien 143 (1), 32–39. https://doi.org/10.7202/1054115ar.

Dulac, J., 2013. Global land transport infrastructure requirements. Estimating road and railway infrastructure capacity and costs to 2050. Information Papers (Paris: OECD, International Energy Agency). http://www.slocat.net/sites/default/files/transportinfrastructureinsights.pdf.

Dupras, J., Marull, J., Parcerisas, L., Coll, F., Gonzalez, A., Girard, M., Tello, E., 2016. The impacts of urban sprawl on ecological connectivity in the Montreal Metropolitan Region. Environ. Sci. Pol. 58, 61–73. https://doi.org/10.1016/j.envsci.2016.01.005.

Flom, P.L., Cassell, D.L., 2007. Stopping stepwise: Why stepwise and similar selection methods are bad, and what you should use. In: NorthEast SAS Users Group Inc 20th Annual Conference: 11-14th November 2007 (Baltimore, Maryland).

Ford, A.T., Clevenger, A.P., 2018. Factors affecting the permeability of road mitigation measures to the movement of small mammals. Can. J. Zool. 97 (4), 379–384. https://doi.org/10.1139/cjz-2018-0165.

Forman, R.T., 2005. Good and bad places for roads: Effects of varying road and natural pattern on habitat loss, degradation, and fragmentation. In: Irwin, C.L., Garrett, P., McDermott, K.P. (Eds.), Proceedings of the 2005 International Conference on Ecology and Transportation (ICOET). Center for Transportation and the Environment, North Carolina State University, Raleigh, NC, pp. 164–174.

García-Romero, A., Vergara, P.M., Granados-Peláez, C., Santibañez-Andrade, G., 2019. Landscape-mediated edge effect in temperate deciduous forest: implications for oak regeneration. Landsc. Ecol. 34 (1), 51–62. https://doi.org/10.1007/s10980-018-0733-x.

Girardet, X., Conruyt-Rogeon, G., Foltête, J.-C., 2015. Does regional landscape connectivity influence the location of roe deer roadkill hotspots? Eur. J. Wildl. Res. 61 (5), 731–742. https://doi.org/10.1007/s10344-015-0950-4.

Glista, D.J., DeVault, T.L., DeWoody, J.A., 2009. A review of mitigation measures for reducing wildlife mortality on roadways. Landsc. Urb. Plann 91 (1), 1–7. https://doi.org/10.1016/j.landurbplan.2008.11.001.

Griffin, P.C., Griffin, S.C., Waroquiers, C., Mills, L.S., 2005. Mortality by moonlight: Predation risk and the snowshoe hare. Behav. Ecol. 16 (5), 938–944. https://doi.org/10.1093/beheco/ari074.

Grilo, C., Bissonette, J.A., Santos-Reis, M., 2008. Response of carnivores to existing highway culverts and underpasses: Implications for road planning and mitigation. Biodivers. Conserv. 17 (7), 1685–1699. https://doi.org/10.1007/s10531-008-9374-8.

Grilo, C., Smith, D.J., Klar, N., 2015. Carnivores: struggling for survival in roaded landscapes. In: van der Ree, R., Grilo, C., Smith, D.J. (Eds.), Handbook of Road Ecology, pp. 300–312.

Hilty, J.A., Lidicker Jr., W.Z., Merenlender, A.M., 2006. Corridor Ecology: The Science and Practice of Linking Landscapes for Biodiversity Conservation. Island Press, Washington, DC.

Hurvich, C.M., Tsai, C.L., 1989. Regression and time series model selection in small samples. Biometrika 76 (2), 297–307. https://doi.org/10.1093/biomet/76.2.297.

Jumeau, J., Petrod, L., Handrich, Y., 2017. A comparison of camera trap and permanent recording video camera efficiency in wildlife underpasses. Ecology and Evolution 7 (18), 7399–7407. https://doi.org/10.1002/ece3.3149.

Krawchuk, A., Larsen, K.W., Weir, R.D., Davis, H., 2005. Passage through a small drainage culvert by mule deer, *Odocoilus hemionus*, and other mammals. Can. Field Nat. 119 (2), 296–298. https://doi.org/10.22621/cfn.v119i2.119.

Li, T., Ducruc, J.P., 1999. Les province naturelles. Niveau I du cadre écologique de référence du Québec. Ministère de l'Environnement, Direction de la conservation et du patrimoine écologique, 90 pp. (see also. http://www.mddep.gouv.qc.ca/biodiversite/aires_protegees/provinces/index.htm.

LoScerbo, D., Daguet, C., Jaeger, J.A.G. (resubm.): Can passages be shared? How human use of existing highway underpasses affects mammal crossing success. Canadian Field Naturalist (resubmitted).

Mansfield, E.R., Helms, B.P., 1982. Detecting multicollinearity. Am. Statistician 36 (3a), 158–160. https://doi.org/10.1080/00031305.1982.10482818.

Marangelo, P., Farrell, L., 2016. Reducing Wildlife Mortality on Roads in Vermont: Documenting Wildlife Movement Near Bridges and Culverts to Improve Related Conservation Investments. The Nature Conservancy, Vermont Chapter.

Mata, C., Hervás, I., Herranz, J., Suárez, F., Malo, J.E., 2008. Are motorway wildlife passages worth building? Vertebrate use of road-crossing structures on a Spanish motorway. J. Environ. Manag. 88 (3), 407–415. https://doi.org/10.1016/j.jenvman.2007.03.014.

Meijer, J.R., Huijbregts, M.A., Schotten, K.C., Schipper, A.M., 2018. Global patterns of current and future road infrastructure. Environ. Res. Lett. 13 (6), 064006 https://doi.org/10.1088/1748-9326/aabd42.

Mimet, A., Clauzel, C., Foltête, J.C., 2016. Locating wildlife crossings for multispecies connectivity across linear infrastructures. Landsc. Ecol. 31 (9), 1955–1973. https://doi.org/10.1007/s10980-016-0373-y.

Niemi, M., Jääskeläinen, N.C., Nummi, P., Mäkelä, T., Norrdahl, K., 2014. Dry paths effectively reduce road mortality of small and medium-sized terrestrial vertebrates. J. Environ. Manag. 144, 51–57. https://doi.org/10.1016/j.jenvman.2014.05.012.

Ng, S.J., Dole, J.W., Sauvajot, R.M., Riley, S.P., Valone, T.J., 2004. Use of highway undercrossings by wildlife in southern California. Biol. Conserv. 115 (3), 499–507. https://doi.org/10.1016/S0006-3207(03)00166-6.

O'Brien, R.M., 2007. A caution regarding rules of thumb for variance inflation factors. Qual. Quantity 41 (5), 673–690. https://doi.org/10.1007/s11135-006-9018-6.

Penteriani, V., Kuparinen, A., del Mar Delgado, M., Palomares, F., López-Bao, J.V., Fedriani, J.M., et al., 2013. Responses of a top and a meso predator and their prey to moon phases. Oecologia 173 (3), 753–766. https://doi.org/10.1007/s00442-013-2651-6.

Pino, J., Marull, J., 2012. Ecological networks: Are they enough for connectivity conservation? A case study in the Barcelona Metropolitan Region (NE Spain). Land Use Pol. 29 (3), 684–690. https://doi.org/10.1016/j.landusepol.2011.11.004.

Pocock, Z., Lawrence, R.E., 2005. How far into a forest does the effect of a road extend? Defining road edge effect in eucalypt forests of south-eastern Australia. In: Irwin, C. L., Garrett, P. (Eds.), Proceedings of the 2005 International Conference on Ecology and Transportation. McDermott KP. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC, pp. 397–405.

Prugh, L.R., Golden, C.D., 2014. Does moonlight increase predation risk? Meta-analysis reveals divergent responses of nocturnal mammals to lunar cycles. J. Anim. Ecol. 83 (2), 504–514. https://doi.org/10.1111/1365-2656.12148.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. https://www.R-project.org/.

Rico, A., Kindlmann, P., Sedlácek, F., 2007. Barrier effects of roads on movements of small mammals. Folia Zoologica 56 (1), 1–12.

Ringle, C.M., Wende, S., Becker, J.M., 2015. SmartPLS 3. Boenningstedt. SmartPLS GmbH.

Rodriguez, A., Crema, G., Delibes, M., 1996. Use of non-wildlife passages across a high speed railway by terrestrial vertebrates. J. Appl. Ecol. 33, 1527–1540.

Roedenbeck, I.A., Fahrig, L., Findlay, C.S., Houlahan, J., Jaeger, J.A.G., Klar, N., Kramer-Schadt, S., van der Grift, E.A., 2007. The Rauischholzhausen-agenda for road ecology. Ecol. Soc. 12 (1), 11. http://www.ecologyandsociety.org/vol12/iss1/art11/.

Rytwinski, T., van der Ree, R., Cunnington, G.M., Fahrig, L., Findlay, C.S., Houlahan, J., Jaeger, J.A.G., Soanes, K., van der Grift, E.A., 2015. Experimental study designs to improve the evaluation of road mitigation measures for wildlife. J. Environ. Manag. 154, 48–64. https://doi.org/10.1016/j.jenvman.2015.01.048.

Rytwinski, T., Soanes, K., Jaeger, J.A.G., Fahrig, L., Findlay, C.S., Houlahan, J., van der Ree, R., van der Grift, E.A., 2016. How effective is road mitigation at reducing road-kill? A meta-analysis. PloS One 11 (11), e0166941. https://doi.org/10.1371/journal.pone.0166941.

Salvant, F., 2017. Identification des zones d'intervention prioritaires pour les mouvements fauniques sur une portion de l'autoroute 10 (Québec, Canada). Essai présenté pour l'obtention du grade de Maîtrise en sciences géographiques (M.Sc.), cheminement de type cours en géodéveloppement durable. Université de Sherbrooke, Québec, Canada, Département de géomatique appliquée, Faculté des lettres et sciences humaines, 87 pages.

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 (1780), 20131705. https://doi.org/10.1098/rspb.2013.1705.

Seiler, A., Olsson, M., 2009. Are non-wildlife underpasses effective passages for wildlife?. In: Proceedings of the 2009 International Conference on Ecology and Transportation (ICOET 2009). North Carolina State University, Raleigh (NC), pp. 317–331.

Smith, D.J., van der Ree, R., Rosell, C., 2015. Wildlife crossing structures: An effective strategy to restore or maintain wildlife connectivity across roads. In: van der Ree, R., Grilo, C., Smith, D.J. (Eds.), Handbook of Road Ecology, pp. 172–183.

Spanowicz, A.G., Teixeira, F.Z., Jaeger, J.A.G., 2020. An adaptive plan for prioritizing road sections for fencing to reduce animal mortality. Conservation Biology. https://doi.org/10.1111/cobi.13502 in press.

Torres, A., Jaeger, J.A.G., Alonso, J.C., 2016. Assessing large-scale wildlife responses to human infrastructure development. PNAs 113 (30), 8472–8477. https://doi.org/10.1073/pnas.1522488113.

Valerio, F., Carvalho, F., Barbosa, A.M., Mira, A., Santos, S.M., 2019. Accounting for connectivity uncertainties in predicting roadkills: A comparative approach between path selection functions and habitat suitability models. Environ. Manag. 64, 329–343. https://doi.org/10.1007/s00267-019-01191-6.

van der Ree, R., Gagnon, J.W., Smith, D.J., 2015. Fencing: A valuable tool for reducing wildlife-vehicle collisions and funneling fauna to crossing structures. In: van der Ree, R., Grilo, C., Smith, D.J. (Eds.), Handbook of Road Ecology. John Wiley & Sons, Oxford, pp. 159–171.

van Vliet, M.T.H., Franssen, W.H.P., Yearsley, J.R., Ludwig, F., Haddeland, I., Lettenmaier, D.P., Kabat, P., 2013. Global river discharge and water temperature under climate change. Global Environ. Change 23 (2), 450–464. https://doi.org/10.1016/j.gloenvcha.2012.11.002.

Viani, F., Polo, A., Giarola, E., Robol, F., Benedetti, G., Zanetti, S., 2016. Performance assessment of a smart road management system for the wireless detection of wildlife road-crossing. In: Proceedings of the 2016 IEEE International Smart Cities Conference (ISC2), Trento, Italy, 12-15 September 2016, pp. 1–6. https://doi.org/10.1109/ISC2.2016.7580835.

Villalva, P., Reto, D., Santos-Reis, M., Revilla, E., Grilo, C., 2013. Do dry ledges reduce the barrier effect of roads? Ecol. Eng. 57, 143–148. https://doi.org/10.1016/j.ecoleng.2013.04.005.

Ward, A.L., 1982. Mule deer behavior in relation to fencing and underpasses on Interstate 80 in Wyoming. Transport. Res. Rec. 859, 8–13.

Wierzchowski, J., Kuas, A., Balciauskas, L., 2019. Application of least-cost movement modeling in planning wildlife mitigation measures along transport corridors: Case study of forests and moose in Lithuania. Forests 10, 831. https://doi.org/10.3390/f10100831.

Williams, S.L., Sur, C., Janetski, N., Hollarsmith, J.A., Rapi, S., Barron, L., et al., 2019. Large-scale coral reef rehabilitation after blast fishing in Indonesia. Restor. Ecol. 27 (2), 447–456. https://doi.org/10.1111/rec.12866.

Woltz, H.W., Gibbs, J.P., Ducey, P.K., 2008. Road crossing structures for amphibians and reptiles: Informing design through behavioral analysis. Biol. Conserv. 141 (11), 2745–2750. https://doi.org/10.1016/j.biocon.2008.08.010.

Zeileis, A., Kleiber, C., Jackman, S., 2008. Regression models for count data in R. J. Stat. Software 27 (8), 1–25. https://doi.org/10.18637/jss.v027.i08.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science & Business Media, New York, NY.

Additional reference cited in suppl. material

Meek, P.D., Ballard, G., Claridge, A., Kays, R., Moseby, K., O'Brien, T., O'Connell, A., Sanderson, J., Swann, D.E., Tobler, M., Townsend, S., 2014. Recommended guiding principles for reporting on camera trapping research. Biodivers. Conserv. 23, 2321–2343. https://doi.org/10.1007/s10531-014-0712-8.