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Co-use of existing crossing structures along roads by wildlife and humans: Wishful thinking?

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Abstract

This study assesses existing human-purpose underpasses below an unfenced high-traffic 4-lane highway in the Appalachian region of Quebec, Canada, as potential crossing structures for native mammal species. Eight underpasses of three types (five water culverts with minimum height and width of 1.8 m, one low-use gravel road byway, and two railroad underpasses) were continuously monitored by motion-detection infrared camera traps for time periods spanning up to 778 days (September 2016 to November 2018). We asked how the ratios of successful crossings through the structures (termed full crossings) and aversions to the structures (termed aversions) differed between species and we explored the influence of human activity levels on the use of these structures by wildlife. All monitored crossing structures had low human observations (with averages of less than 35 human activities per day). Our results provide evidence that 21 species of mammals in the study area successfully crossed through at least one of the eight observed underpasses on a minimum of one occasion. Some species were observed crossing through some of the underpasses on a regular basis, namely raccoon, red fox, and white-tailed deer. We propose a classification of mammal species into five human co-use classes (no or low co-use to very high co-use) to explore the relationship between mammal use of the structures and human presence. We found that humans and mammals were observed sharing passages for the four mammal species identified as tolerant of human co-use (high and very high co-use classes), but co-use was observed to be limited or not occurring for most other species. The strengths of this study include the length of time during which monitoring took place, as well as the placement of four cameras at each structure (two facing inward and two facing outward) to determine whether individuals successfully crossed through the structures or displayed avoidance behaviour. The results suggest select species of mammals show some co-use with humans at existing underpasses. The activity patterns of mammals documented over the two-year study can assist with future estimates of highway permeability. Further, measurements of human and mammal co-use have species-specific implications for retrofitting existing structures and constructing wildlife fences and purpose-built wildlife passages.

Keywords
Camera traps, culverts, existing structures, landscape connectivity, road mitigation, underpasses, wildlife movement, wildlife passages

Introduction

Roads have become ubiquitous features in landscapes around the world. In the contiguous United States, 82% of the total land area is within 1 km of a road (including unpaved and private roads) (Riitters and Wickham 2003); in Europe, 50% of all land area is located within 1.54 km of the nearest paved road or railway line (Torres et al. 2016). Roads and vehicular traffic have complex impacts on wildlife and biodiversity, such as increased wildlife-vehicle collisions (WVCs), habitat fragmentation, and decreased habitat quality (Forman and Alexander 1998; van der Ree et al. 2015). When an animal confronts a road, it is either forced to move in a different direction, i.e., access to habitats on the other side is inhibited, or it must attempt to cross, thus being exposed to traffic. In severe cases, road avoidance behaviour may significantly impede dispersal of individuals to new habitat patches, reducing genetic exchange and overall, decreasing population persistence (Jaeger et al. 2005).

A developing solution to habitat fragmentation by roads is the installation of crossing structures. Successful road crossings by way of under- and overpasses have been documented for numerous species such as black bear (*Ursus americanus*), grizzly bear (*Ursus arctos*), moose (*Alces americanus*), cougar (*Puma concolor*), wolf (*Canis lupus*), white-tailed deer (*Odocoileus virginianus*), weasel (*Mustela nivalis*), and stoat (*Mustela erminea*) (Rodriguez et al. 1997; LaPoint et al. 2003; Dodd et al. 2004; van Vuurde and van der Grift 2005; Ford et al. 2017). Facilitation of gene flow across subpopulations was shown in populations of Eurasian elk (*Alces alces*) through use of wildlife overpasses in Sweden (Olsson et al. 2008) and in populations of grizzly bear and black bear in Canada (Sawaya et al. 2013; Ford et al. 2017). Although implementing wildlife passages appears to be a simple solution, there are structural and functional factors that need to be considered to ensure their efficiency as wildlife crossing structures.

A poorly understood covariate of crossing structure use is the recreational co-use of wildlife passages by humans (van der Ree and van der Grift 2015). A crossing structure designed for both wildlife and recreational use by humans is called a multi-use crossing structure, whereas a structure designed intentionally for sole use by human transportation (i.e., road or train underpass) or water divergence (i.e., culvert or bridge) is termed an existing (or human-use) crossing structure. Wildlife may use existing structures to cross above or below roads, yet this type of use was not intended for in the construction or design. If humans and animals are able to use the same crossing structures (multi-use or existing), fewer additional structures would need to be constructed for wildlife, saving transportation agencies considerable expenses. This ideal situation of shared passages, however, cannot be assumed for all species, as human use of crossing structures may be a deterrent for many species and may defeat the intended mitigation efforts (Rodriguez et al.1997; Grilo et al. 2008). Human use can encompass many different types of anthropogenic presence, including pedestrians, cyclists, motorized vehicles (automobiles and off-road vehicles such as snowmobiles and all-terrain vehicles (ATVs)), as well as trains.

For multi-use passages, one study found no significant effect of recreational human co-use on crossing structure use by small and medium mammals and roe deer (*Capreolus capreolus*), so long as certain structural requirements were met, including a large width of structure and the presence of screening between wildlife and human paths (van der Ree and van der Grift 2015). However, another study found that human co-use of multi-use passages deterred use by carnivores such as badgers (*Meles meles*) and genets (*Genetta genetta*) (Grilo et al. 2008). For large mammals such as black bear, grizzly bear, cougar, wolf, and ungulates, it has been observed that recreational human co-use of multi-use passages acts as a severe hindrance to mammal presence (Clevenger and Waltho 2000). For other mammals, such as wildcat (*Felis silvestris*) and red fox (*Vulpes vulpes*), human presence in the form of trains had no significant effect on mammal passage (Rodriguez et al. 1997). Often, these findings cannot be generalized across species since animal sensitivity to traffic noise and human presence varies considerably. Research on existing crossing structures is sparse, and a better understanding of the relationships between their use by wildlife and the factors that may encourage or discourage use is needed for effective mitigation of habitat fragmentation by roads.

Here, we (1) assessed the use of existing crossing structures by wildlife, and (2) explored the influence of human activity levels on the use of existing crossing structures by wildlife. Specifically, we addressed the following questions:

a) Which species are using the structures and how often?

b) How do the ratios of successful crossing through the structure (full crossings) and aversion to the structure (aversions) differ between species?

c) How much does the use of existing crossing structures by wildlife and humans vary during the course of the day?

d) How does the daily frequency of use by wildlife relate to the daily frequency of human activity?

Methods

Study area

Our research focused on eight existing (human-use) crossing structures in the Appalachians of southern Quebec, Canada, more specifically in the Northern Green Mountain linkage. Extending across 83 million acres from Northern Massachusetts, USA, to the north of the Gaspe Peninsula in Quebec, Canada, the Northern Appalachian-Acadian ecoregion retains the largest expanse of intact forest in the contiguous United States (Anderson et al. 2006). Within this ecoregion, the Northern Green Mountain linkage straddles northern Vermont and southern Quebec (Staying Connected Initiative 2018) and is home to numerous wide-ranging mammals including black bear, moose, bobcat (*Lynx rufus*), coyote (*Canis latrans*), fisher (*Pekania pennanti*), as well as American marten (*Martes americana*), North American river otter (*Lontra canadensis*), and American mink (*Neovison vison*) (Gratton and Bryant 2012). The Northern Appalachian-Acadian ecoregion remains one of the most forested yet vulnerable ecoregions in Eastern North America, due to a lack of protected natural areas and the proximity of human infrastructure to undeveloped areas (Trombulak et al. 2008). While large carnivores such as the wolf and cougar have been extirpated from the ecoregion, there remain many wildlife species within the area that are listed as needing immediate conservation action, including woodland caribou (*Rangifer tarandus*) and maritime shrew (*Sorex maritimensis*) (Anderson et al. 2006).

A section of the four-lane Highway 10 East bisects the Northern Green Mountain linkage and fragments the northern Estrie and Monteregie regions from the Sutton Mountain range to the south (Daguet 2015). This high-traffic highway exposes populations to high levels of mortality while also acting as a potential barrier to those species presenting road avoidance behaviour (Jaeger et al. 2005). Each year, an average of 89 white-tailed deer, 7 moose, and 1.5 black bear have been reported to be killed in WVCs along Highway 10 East (i.e., the section between km 68 and 143) in the Appalachians of southern Quebec, in addition to over 69 collisions with medium-sized mammals such as coyote, red fox, and porcupine (*Erethizon dorsatum*) (Ministère des Transports du Québec, unpublished data). These high yearly mortality events, especially of large mammals, cause great economic damage (Bissonette et al. 2008) and can result in loss of human lives. At the time of this study, there were no WVC mitigation measures in place along Highway 10 East, other than some warning signs advising drivers of deer presence in the area.

Eight existing crossing structures were selected for monitoring within the Northern Green Mountain linkage along a 75 km stretch of Highway 10 East between the towns of Granby (km 68) and Sherbrooke (km 143) (Fig. 1). The study sites are numbered 1, 2, and 4 through 9; Site 3, a road underpass, was not included in this study due to time constraints for data analysis (due to extremely high human use). The site numbering was left as originally assigned to allow for future analysis of the sites and comparisons to the findings from this study. A variety of underpass types were selected for this study, including train underpasses, a gravel road byway, and water culverts (Fig. 2). The study sites are located on average 4.4 kilometres from one another, with a maximum distance of 11 kilometres between two adjacent study sites and a minimum distance of less than one kilometre.

The first monitored train underpass, site 1, is located 22.4 metres from the forest edge (calculated as the mean distance to forest from both openings) and has a height of

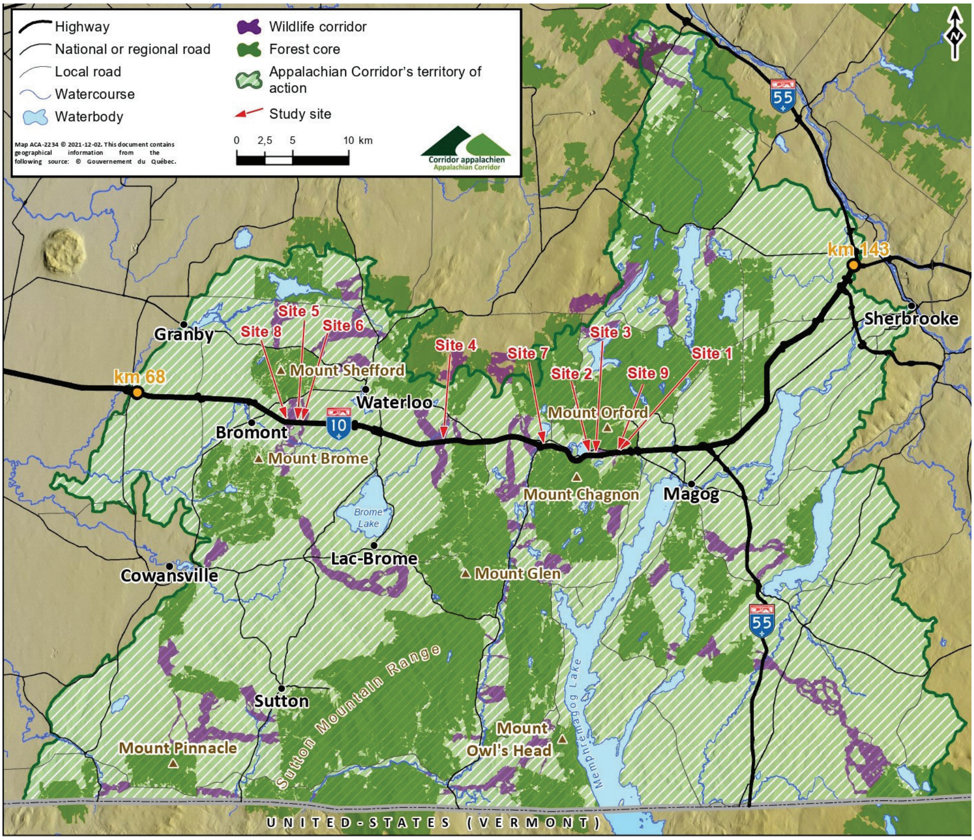

Figure 1. Predicted wildlife corridors in the Appalachians of southern Quebec based on GIS modeling of landscape connectivity, habitat validation on the ground, and mammal tracking. Large unfragmented forest blocks of more than 10 km^2 are shown in dark green. Following preliminary results from the multivariate analysis by Salvant (2017), several sections of Highway 10 East were selected to monitor human and mammal activity at a total of nine suitable multi-use underpasses (i.e., sites 1–9, although site 3 was not considered in this paper due to time constraints for data analysis). Adapted from Rapport sur l'identification des corridors fauniques de part et d'autre de l'autoroute 10 - Phase II (Daguet 2015).

8.0 metres and a width of 12.0 metres (Table 1). The underpass is 67.2 metres long and covered with a coarse gravel substrate, with one train track running through the center. The underpass is in proximity to a main road (Route 112, several hundred metres), a gas pipeline with open vegetation (less than a dozen metres), and a residential lot with a mowed lawn and artificial lake. The second monitored train underpass, site 4, is located 17.5 kilometres west of site 1 and 14.0 metres from the forest edge. The underpass has a height of 15.0 metres, a width of 25.0 metres and a length of 61.9 metres. Site 4 is covered with a mix of gravel substrate and vegetation within the underpass with one train track running through the center. Site 4 has the highest openness ratio (calculated as height × width / length) of all structures at 6.06 metres, while site 1 has


Site 1
Site 2
Site 4
Site 5
Site 6
Site 7
Site 8
Site 9

Figure 2. Photos of all eight existing underpasses observed in this study, none of which are dedicated wildlife passages. Sites 1 and 4 are train underpasses. Site 5 is a gravel road underpass. Sites 2 and 6 through 9 are water culverts (photos: Michelle Anderson and Daniella LoScerbo).

an openness ratio of 1.43 metres, the third highest of all monitored crossing structures. The train underpass is located far from any main road or residential development and the high openness ratio allows for natural light within the underpass.

The gravel road underpass, site 5, is located 29.1 metres from the forest edge and has a height of 7.0 metres and a width of 16.0 metres. The underpass is 41.9 metres long with an openness ratio of 2.67 metres, the second highest of the monitored underpasses. The road is a low-use gravel byway with two 1.0-metre-wide vegetated drainage ditches running along each side of the road.

The water culvert at site 2 is a circular concrete water culvert with a height of 1.8 metres, a width of 1.8 metres, and is 76.9 metres in length (resulting in an openness ratio of 0.04 metres, the lowest of all monitored underpasses). The culvert is located 4.8 metres from the forest edge. The box water culvert located at site 6 is made of concrete with a height of 2.6 metres, a width of 6.8 metres, and is 48.4 metres in length (resulting in an openness ratio of 0.37 metres). The culvert is located 11.0 metres from the forest edge and from September to June, water fills the culvert completely. During the summer months of July to August, the water within the culvert will dry partially, exposing a dry path on either side of the steam. The circular concrete water culvert at site 7 has a height of 1.9 metres, a width of 2.3 metres, and is 60.8 metres in length (resulting in an openness ratio of 0.07 metres). The culvert is located 11.0 metres from the forest edge. From September to June, water fills the culvert completely. During the summer months of July to August, the stream within the culvert runs dry. The box water culvert at site 8 is a concrete culvert with a height of 1.8 metres, a width of 2.3 metres, and is 50.5 metres in length (resulting in an openness ratio of 0.08 metres). The culvert is located 10.0 metres from the forest edge and is filled with water year-round (no dry path). The final water culvert, at site 9, is a circular concrete water culvert with a height of 4.0 metres, a width of 4.2 metres, and is 94.3 metres in length (the longest of all studied underpasses). The structure has an openness ratio of 0.18 metres and is adjacent to the forest edge. The culvert is filled with water year-round with no dry path. More information about the structure height, width, and length of each underpass, as well as substrate type and the presence of water, is given in Table 1.

Camera trapping

Each monitored crossing structure was equipped with four Reconyx Hyperfire HC600 infrared motion-detection camera traps, which provided continuous observation of the study sites for a minimum of 461 days (site 5) and a maximum of 778 days (sites 1, 2, and 4). The two train underpasses (sites 1 and 4) were monitored continuously from October 2016 to November 2018. The road underpass (site 5) was monitored continuously from October 2016 to December 2017. The camera traps at site 5 were removed from the field in December 2017 due to theft of one of the four cameras at the site, prompting the removal of the remaining cameras by the research team. The five water culverts were monitored continuously from October 2016 to November 2018 (site 2 for a total of 778 continuous observation days), October 2016 to June 2018 (site

Table 1. Structural characteristics of eight monitored underpasses (Fig. 2) below Highway 10 East in Quebec, Canada. Distance to forest is the average taken from the two entrances of the structures.

Site	Type	Road km	GPS Coordinates	Height (m)	Width (m)	Length (m)	Openness (m)	Substrate type	Water presence	Dist. to forest (m)
1	Train	112.5	-72.228503°E, 45.291720°N	8.0	12.0	67.2	1.43	Gravel	No	22.4
2	Culvert	105.5	-72.253064°E, 45.282949°N	1.8	1.8	76.9	0.04	Concrete	Yes	4.8
4	Train	95	-72.428521°E, 45.302273°N	15.0	25.0	61.9	6.06	Vegetation, gravel	No	14.0
5	Road[a]	83.5	-72.593076°E, 45.319216°N	7.0	16.0	41.9	2.67	Vegetation, gravel	Yes	29.1
6	Culvert[b]	84	-72.589380°E, 45.319051°N	2.6	6.8	48.4	0.37	Concrete	Yes	11.0
7	Culvert[b]	106	-72.314650°E, 45.297190°N	1.9	2.3	60.8	0.07	Concrete	Yes	11.0
8	Culvert	82	-72.607100°E, 45.319600°N	1.8	2.3	50.5	0.08	Concrete	Yes	10.0
9	Culvert	112.5	-72.230790°E, 45.291150°N	4.0	4.2	94.3	0.18	Concrete	Yes	0.0

[a] Site 5 is a gravel road with vegetation and two 1 m wide drainage ditches running along each side of the road. [b] From September-June, water fills culvert width completely. In the summer months of July-August, the stream dries partially (site 6) and completely (site 7), expanding the dry path width through the culvert.

6 for a total of 619 continuous observation days), and July 2017 to November 2018 (sites 7, 8, and 9 for a total of 493, 498, and 493 continuous observation days, respectively). The camera traps at site 6 were removed from the study site in June 2018 due to vandalism. The camera traps at water culvert sites 7, 8 and 9 were installed in July 2017, following the installation of cameras at the other study sites in October 2016, to increase the number of crossing structures monitored for the study.

Over the past decade, there has been a significant increase in research using camera traps as a non-invasive method to study the presence and behaviour of wildlife (Wearn and Glover-Kapfer 2019). Camera traps allow for continuous data collection during the day and night with minimal environmental and wildlife disturbance, as well as low labour costs (Henschel and Ray 2003; Rowcliffe et al. 2008). However, some studies suggest that animals can detect the location of camera traps through auditory localisation acuity, which occurs when an animal is alerted to the presence of a camera due to the high-frequency sound emitted as the camera captures an image (Meek et al. 2016). While this can potentially result in avoidance behaviour toward the area in which the camera is located, overall, cameras remain an efficient and widely used method of wildlife monitoring.

For this study, two camera traps were installed at each of the northern and southern extremities of the underpasses, one facing outward and one facing inward (Fig. 3). We installed the cameras to the walls of the structures approximately four feet above the ground and positioned them horizontally at a slight downward angle, to maximize detection of small-, medium-, and large-sized mammals. The cameras were installed in metal lockboxes to prevent theft, and laminated cards were placed next to the cameras to inform readers of the research project and to deter vandalism. Triggered by movement or heat signatures within their detection ranges, the outer-facing cameras detected approaches by wildlife and humans in proximity of the underpass openings. The inner-facing cameras were used to confirm whether an animal crossed through the full length of the underpass and exited at the opposite opening from which it entered (termed a full crossing), or whether an animal doubled back inside the structure and exited through the opening from which it had entered (termed an aversion). All camera traps collected data simultaneously and were programmed to continuously take a sequence of five photographs when triggered, until the movement or heat signature was no longer within the detection range of the camera. The research team visited the study sites monthly to replace SD cards and camera batteries, as well as to reorient any cameras that may have shifted since the last maintenance visit. The research team wore gloves when manipulating the cameras to prevent odor transfer. No lures or bait were used to attract mammals near the study sites. We use standardized camera trapping terminology consistently for reporting results in this paper (Meek et al. 2014; Wearn and Glover-Kapfer 2017).

Photo analysis

Each photo depicting an animal was assessed for the following: date, time, temperature, species, number of animals in the group, and direction of movement. The sequence of

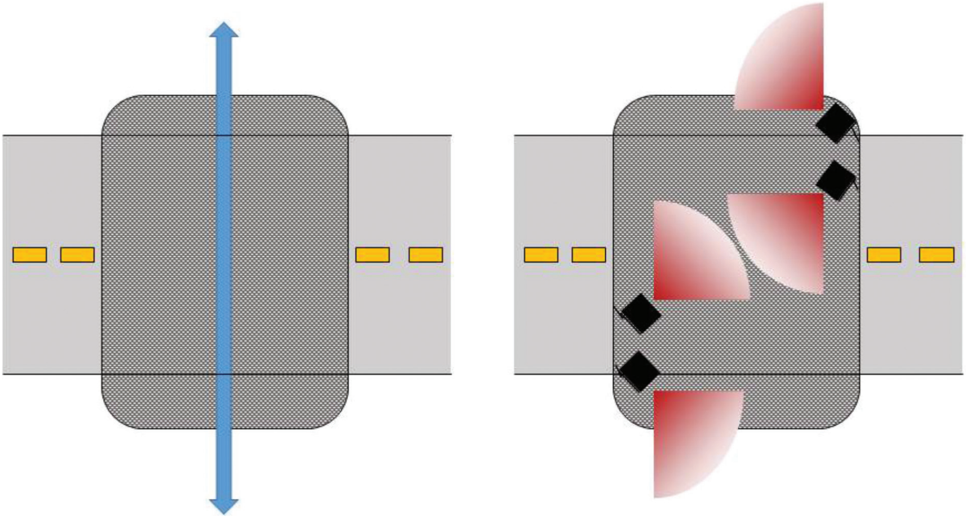

Figure 3. Display of layout for monitoring of human and animal activity by cameras in eight underpasses below Highway 10 East. The grey crosshatched rectangles indicate the underpass structure. The blue arrow suggests the theoretical path of movement through the underpass to cross below the highway. The four black boxes represent the *Reconyx Hyperfire HC600* motion and infrared detection cameras. The range of detection for each camera extends to roughly 60 feet and is represented by the red arcs.

photos that captured an animal near the entrance of or within a crossing structure was used to confirm the presence of a certain species. In the event that multiple individuals of the same species were observed in one sequence of photos, we considered the observation event as having multiple detections of the same species. When an animal or group of animals was detected by more than one camera trap simultaneously at a study site, we considered it as one observation event. If the animal was observed by any combination of camera traps showing that it successfully crossed through the underpass, this was deemed a full-crossing event. If the animal was observed to turn around, or pass near the underpass without entering, this event was termed an aversion. When the outcome of a wildlife observation was uncertain, the event was termed unknown. We calculated the crossing-success ratio for each species per study site as follows:

Crossing-success ratio = (Full crossings / Confirmed detections)

Confirmed detections are equal to the sum of confirmed full crossings and confirmed aversions. The detections for which the outcome is not confirmed (unknown) are not considered in this equation as it is uncertain how many of them were full crossings or aversions. Any events of the same species that occurred more than 5 minutes apart were considered independent observation events (to allow for sufficient time to pass through the structure).

Human activities observed at the study sites were classified into four categories, namely train, automobile/road vehicle, ATV (including snowmobile), and non-motorized activity (cyclist, pedestrian, horseback rider, etc.). All human activity was assessed for the following: direction of movement, date, time, and duration of each event. The visits by the research team (for replacement of SD cards and camera batteries) were included in the tally of human activity at each site.

We calculated the Shannon Diversity Index (H) of each crossing structure to characterize the species diversity observed at each study site, as follows:

$$H = - \Sigma\, p_i \cdot ln(p_i),$$

where p_i indicates the proportion of the entire community made up by species i. The Shannon Diversity Index accounts for both abundance and evenness of the species present within a community (Shannon and Wiener 1963). We calculated the Shannon Diversity Index for each monitored crossing structure for all mammals observed (termed overall diversity index) and for all mammals confirmed to have successfully crossed through the structure (termed full-crossing diversity index), resulting in two diversity values for each crossing structure.

Mammal classification

Wildlife species often perceive humans as predators and will display avoidance behaviour toward areas that experience high human activity, which in turn can generate population-level consequences (Frid and Dill 2002; Preisser et al. 2005; Ellenberg et al. 2006). To explore the relationship between the use of existing crossing structures by wildlife and the presence of humans at our study sites, we chose to classify the mammal species into groups that exhibit different levels of human co-use, which may reflect different levels of tolerance to humans (Samia et al. 2015). To do so, we grouped all observation days (24 hours) across all study sites based on the number of human activities per day. All observation days that showed no human activity were placed in one group; days that showed one human activity were placed in another group; and so on. We then standardized each group to represent a period of 50 days, following the recommendation of maximal smoothing histograms by Terrell and Scott (1985). Since our study sites experienced mostly low daily rates of human activity, we averaged down for the groups with low daily human activity. For groups that had less than 50 overall observation days for a particular human activity level (i.e., days with high human activity), we combined these days with days that showed similar daily human activities to produce standardized groups of 50 observation days. In total, 20 daily human activity groups were formed (Table A1 in Appendix 1).

The wildlife activities and associated full crossings within each daily human activity group were then examined for visible trends in the data. Mammal species with at least 10 detections throughout the study were classified into five categories based on their level of correlation with the aforementioned groups of daily human activity. Mammal species that were never observed fully crossing through an underpass above four daily human activities were classified into the "very low or no human co-use" category (Table 2). Species that were observed fully crossing through the structures at least once above the level of four daily human activities, while the number of full crossings above this level was very low compared to the total number of full crossings, were classified in the "low" human co-use category. The "moderate" human co-use category includes species with a negative correlation between increasing levels of human activities and the number of full crossings. The "high" human co-use category includes species that were observed having no relationship between the level of daily human activity and the number of full crossings. Finally, species that displayed a positive correlation between full crossings and increasing daily human activity levels were classified into the "very high" human co-use category.

Table 2. Mammal species classifications based on observed human co-use levels.

Level of human co-use	Criteria	Species names
Very low or none	No full crossings above 4 human activities per day	Mouse spp., muskrat, North American porcupine, rat spp., squirrel spp.
Low	Very low number of full crossings above 4 human activities per day compared to the total number of full crossings	American mink, bobcat, snowshoe hare
Moderate	The average number of full crossings for 50 days decreases with the increase in the number of daily human activities	Red fox, white-tailed deer
High	The average number of full crossings for 50 days stays the same with the increase in the number of daily human activities	Coyote, domestic cat, groundhog
Very high	The average number of full crossings for 50 days increases with the increase in the number of daily human activities	Racoon

We conducted Kendall's Tau tests (using Excel 2016) for species with the highest detection rates across the study to explore the correlation between the species' presence with human activity at the study sites. We calculated the Tau-values for these species for all detections and for all confirmed full crossings, resulting in two Tau-values for each species. Kendall's Tau is a non-parametric test used to understand the strength of the relationship between two variables. More specifically, the Kendall Tau-*a* test is used when there are no ties in the data and the Kendall Tau-*b* test is used to correct for ties in the data (Laurencelle 2009). The tests provide both a Tau-value to determine the direction of the relationship (positive or negative) and a *p*-value. We did not conduct a Kendall's Tau test on any species in the "very low or none" co-use classification as there were not enough data (detections) for these species to reflect statistical significance.

Results

Which species are using the structures?

Mammal movement at eight existing crossing structures was documented between 461 (site 5) and 778 (sites 1, 2, and 4) continuous observation days (total sampling effort of this study was 19,592 camera trap days), encompassing over 1.3 million photos (Fig. 4) and 3459 mammal detections across 23 species, including black bear, bobcat, coyote, moose, raccoon (*Procyon lotor*), red fox, and white-tailed deer (Table 3). Other non-focal animals observed included various bird species, including wild turkey (*Meleagris gallopavo*), great blue heron (*Ardea herodias*), American crow (*Corvus brachyrhynchos*), duck species, as well as turtle species. Across all study sites, nine animal detections were not identified by species due to low photo resolution (termed unknown species in Table 3).

How do the ratios of successful crossing through the structure (full crossings) and aversion to the structure (aversions) differ between species?

Of the total number of mammal detections, 1832 were confirmed as successful crossings through the monitored underpasses (full crossing), 1285 exhibited aversion behavior toward the structures (aversion), and 342 outcomes could not be confirmed (unknown). This results in an overall crossing success ratio of 58.8% across all mammal detections. Raccoon, white-tailed deer, and red foxes were the predominant users across all structures and were the only three species observed at all eight study sites. Among the three species recorded at all eight study sites, raccoons had the highest crossing success ratio at 85% (1212 full crossings over 1423 confirmed detections), followed by red foxes (47%, 196 full crossings over 420 confirmed detections) and white-tailed deer (24%, 222 full crossings over 910 confirmed detections). However, regarding the type of crossing structure, of the 564 white-tailed deer detections recorded at the water culverts (sites 2 and 6–9), only 16 were confirmed as successful crossings through the structures, an overall culvert success ratio of only 3% (16 full crossings over 553 confirmed detections).

The eight crossing structures observed in this study vary greatly in structural characteristics, human activity, and animal activity. To illustrate potential patterns of human-animal co-use across these diverse sites, the following sections detail human and animal activity by crossing structure type.

Train underpasses

The railroad at site 1 was visited by American mink, bobcat, coyote, groundhog (*Marmota monax*), moose, raccoon, red fox, and white-tailed deer for a total presence of 236 mammal detections. Red foxes (100) and white-tailed deer (97) showed the highest presence at site 1. Notably, all raccoons (46) detected at site 1 crossed through the underpass, similarly for bobcat (2) and coyote (2). White-tailed deer were the least likely to cross through this structure at 51% (47 full crossings over 93 confirmed detections). There was an average of 3.4 daily human activities at site 1, mainly consisting of trains, maintenance vehicles, and monthly research team activity. Site 1 had the third-highest overall diversity index (1.32) and third-highest overall full crossing ratio (79%) of all study sites, resulting in a full crossing diversity index of 1.37, the second highest of all crossing structures.

The railroad at site 4 was visited by bobcat, coyote, domestic cat (*Felis catus*), fisher, groundhog, raccoon, red fox, weasel (*Mustela ermine*), and white-tailed deer. White-tailed deer (221) and raccoon (32) had the highest presence at site 4. All bobcat (20) observed at the site used the crossing structure within the month of February 2017. While the red fox was the dominant species observed at the train underpass at site

Table 3. Total numbers of individuals detected at each existing underpass for mammal species (confirmed detections + unknowns). A confirmed detection is an instance where an animal was detected at the structure and either crossed through the structure (full crossing) or avoided the structure (aversion); the number of detections for which an animal was detected at a structure, but the outcome is not known (unknown) is given after the + sign. The number in brackets represents the percentage of full crossings out of the confirmed detections. Daily human activity is the average calculated from the total (24-hour) days observed at each site and includes trains, automobiles and other road vehicles, ATVs (including snowmobiles), pedestrian, cyclists, equestrian riders, as well as the research crew visiting sites for maintenance.

Species	Total number of mammals detected at existing underpasses (% of full crossing)							
	Train underpass		Road underpass	Culvert				
	1	4	5	2	6	7	8	9
Neovison vison (American mink)	1 (100%)	-	-	4 (75%) + 29	4 (0%)	26 (81%) + 1	1 (0%) + 1	11 (18%)
Ursus americanus (Black Bear)	-	-	-	1 (100%)	1 (100%)	-	-	-
Lynx rufus (Bobcat)	2 (100%)	20 (100%)	2 (50%)	2 (100%)	1 (0%)	-	-	2 (0%)
Tamias striatus (Chipmunk)	-	-	-	-	-	- + 1	-	-
Canis latrans (Coyote)	2 (100%)	1 (100%)	4 (100%)	-	-	-	3 (0%)	2 (0%) + 6
Felis catus (Domestic Cat)	-	10 (90%)	19 (89%) + 2	-	1 (0%)	-	-	-
Pekania pennanti (Fisher)	-	1 (100%)	-	1 (0%) + 1	-	-	-	-
Marmota monax (Groundhog)	10 (90%)	11 (91%) + 4	9 (22%)	3 (100%)	2 (0%)	4 (75%)	2 (0%)	-
Alces alces (Moose)	3 (100%)	-	-	-	1 (0%)	1 (0%)	-	-
Mus spp. (Mouse spp.)	-	-	-	-	- + 1	14 (29%) + 8	3 (0%)	-
Ondatra zibethicus (Muskrat)	-	-	-	-	-	17 (82%) + 9	-	-
Castor canadensis (North American beaver)	-	-	-	1 (100%)	-	-	-	-
Erethizon dorsatum (North American porcupine)	-	-	1 (100%)	-	-	16 (88%)	-	-
Lontra canadensis (North American river otter)	-	-	-	1 (100%)	-	5 (100%)	- + 1	-
Procyon lotor (Raccoon)	47 (100%)	30 (73%) + 2	602 (96%) + 48	141 (88%) + 20	201 (88%) + 59	284 (88%) + 5	29 (52%) + 15	89 (0%) + 10
Rattus spp. (Rat spp.)	-	-	-	-	-	20 (100%)	-	-
Vulpes vulpes (Red fox)	90 (93%) + 10	5 (80%) + 1	3 (67%) + 1	3 (0%)	2 (0%)	298 (36%) + 23	1 (0%)	18 (0%)
Rodentia (Rodent)	-	-	-	9 (0%)	-	-	-	-
Sciurus spp. (Squirrel spp.)	-	-	-	3 (100%)	-	77 (13%) + 4	-	1 (0%)
Mephitis mephitis (Striped skunk)	-	-	-	-	-	4 (100%)	-	-
Lepus americanus (Snowshoe hare)	-	-	-	6 (0%)	-	1 (0%)	3 (33%)	4 (50%)
Mustela erminea (Weasel)	-	1 (100%)	-	1 (100%)	-	-	-	-

Species	Total number of mammals detected at existing underpasses (% of full crossing)							
	Train underpass		Road underpass	Culvert				
	1	4	5	2	6	7	8	9
Odocoileus virginianus (White-tailed deer)	93 (51%) + 4	181 (77%) + 40	82 (24%) + 24	106 (0%) + 2	109 (12%) + 5	60 (3%) + 2	216 (0%) + 2	62 (0%)
Unknown	1 (100%)	-	2 (0%) + 1	2 (50%)	-	1 (0%)	2 (0%)	-
All mammals	249 (79%) + 14	260 (80%) + 47	724 (86%) + 76	284 (49%) + 52	322 (59%) + 65	828 (55%) + 53	260 (7%) + 19	189 (2%) + 16
Overall diversity index	1.32	1.04	0.66	1.37	0.81	1.70	0.74	1.36
Full-crossing diversity index	1.37	0.99	0.37	0.59	0.28	1.44	0.24	0.69
Daily human activity	3.4	2.6	33.9	0.1	1.3	0.2	1.1	0.1
Total days observed (site-based camera-trap days)	778	778	461	778	619	493	498	493
Total sampling effort (site-based camera-trap days x number of cameras)	3,112	3,112	1,844	3,112	2,476	1,972	1,992	1,972

Figure 4. Select photos of mammals at various monitored structures. In photo (**A**), a red fox (*Vulpes vulpes*) walked along the railroad at site 1 with prey in its mouth. A bobcat (*Lynx rufus*) was detected crossing through a water culvert at site 2 (**B**). A black bear (*Ursus americanus*) successfully crossed through a water culvert (site 2) during summer months when the water level was lowest and a dry path was present (**C**). In photo (**D**), a white-tailed deer (*Odocoileus virginianus*) and its fawn were observed outside a water culvert (site 6).

1, only six red fox detections were recorded at site 4. However, site 4 had the second highest overall crossing-success ratio across observed species of all underpasses at 80%. The overall diversity index for site 4 (1.04) was slightly lower than for site 1 (1.32) even though site 4 was visited by a higher number of mammal species (9 and 8, respectively). This is due to the number of white-tailed deer (221) observed visiting the site, which made up 72% of wildlife detected around or within the railroad underpass. Site 4 also saw a lower full-crossing diversity index (0.99) compared to site 1 (1.37), due to the smaller number of species that crossed through the structure. The average daily human activity at site 4 was 2.6 per day, once again consisting primarily of trains, maintenance vehicles, and monthly research team activity.

Road underpass

The gravel road at site 5 was visited by bobcat, coyote, domestic cat, groundhog, North American porcupine, raccoon, red fox, and white-tailed deer. Site 5 was the second-most visited study site (following site 7) with 800 mammal detections, consisting mostly of raccoon (650), white-tailed deer (106), and domestic cat (21). The overall full crossing success ratio across all mammal species for site 5 was 86%, i.e., the highest of all structures, largely due to raccoon with a crossing-success ratio of 96%. Although visited by eight mammal species throughout the course of the study, this structure had the lowest diversity index of all monitored underpasses ($H = 0.66$) due to the disproportionate number of raccoons. The high proportion of raccoon (578 of 623 total full crossings) resulted in the third-lowest full-crossing diversity index (0.37) of all structures studied. Moreover, site 5 had the highest observed daily human activity at 33.9, consisting primarily of vehicle traffic driving through the underpass.

Water culvert underpasses

Site 2 - circular water culvert: At site 2, 334 mammal detections from 14 confirmed species (and two unknown) were recorded at the structure, consisting mainly of raccoon (161) and white-tailed deer (108). The only North American beaver (*Castor canadensis*) detected was confirmed to have crossed through this culvert, alongside one of the only two detected black bears in the study. Notably, all 106 confirmed detections of white-tailed deer resulted in avoidance behaviour toward the structure, as did all observed red fox (3), rodent species (9), and snowshoe hare (*Lepus americanus*, 6). High mink activity was observed during the month of March 2016 (25 detections of 33 detections in total). The overall diversity index for site 2 was 1.37 but the full-crossing diversity index was only 0.59. Site 2 showed the lowest daily human activity level of all monitored structures at 0.1 per day, alongside site 9, which consisted mainly of monthly research team activity.

Site 6 - box water culvert: At site 6, ten mammalian species were detected, consisting mainly of raccoons (260) and white-tailed deer (114). While both species were observed crossing through the structure, white-tailed deer displayed a crossing-success ratio of only 12%. Raccoons had an overall crossing success ratio of 88%, and one of the only two black bears observed during the study crossed through this structure. Site 6 had the third lowest overall diversity index (0.81) and the second lowest full-crossing diversity index (0.28). Average daily human activity level for site 6 was 1.3 per day, consisting mainly of ATVs and monthly research team activity.

Site 7 - circular water culvert: Site 7 exhibited the highest number of mammal detections (881) across fifteen mammal species, including red foxes (321), raccoons (289), and white-tailed deer (62), resulting in the highest overall diversity index (1.70) and the highest full-crossing diversity index (1.44). While raccoons were observed to have a high crossing-success ratio of 88%, other species exhibited avoidance behaviour toward the structure, including white-tailed deer (3%), squirrel species (13%), and red fox (36%). However, all detections of striped skunk (*Mephitis mephitis*, 4), rat species (20), and North American river otter (5) were confirmed as crossing through the structure. Daily human activity level at site 7 was the second lowest of all monitored structures at 0.2 per day, consisting primarily of monthly research team activity.

Site 8 - box water culvert: Site 8 had 289 mammal detections across nine confirmed species and an overall crossing-success ratio of only 7%. White-tailed deer (218) and raccoons (44) dominated mammal activity at site 8. Only two species were observed to successfully cross through the structure, namely raccoons (52%) and snowshoe hares (33%). The full-crossing diversity index at the site was 0.24, lower than the overall diversity index of 0.74. Site 8 was observed to have an average daily human activity level of 1.1 per day, which consisted mainly of ATVs and monthly research team activity.

Site 9 - circular water culvert: Site 9 had the lowest crossing-success ratio (2%) of all underpasses and the lowest average daily human activity level (0.1 per day), alongside site 2. Only two of the eight species observed were confirmed to have crossed through the structure, namely two American mink (18%) swam through the structure in May 2018 and two snowshoe hares (50%) travelled through the structure in January 2018, when the water was frozen over. This water culvert had an overall diversity index of 1.36 (the third highest of all structures) and a full-crossing diversity index of 0.69. No humans, apart from the research team, were observed at the site.

How much does the use of existing crossing structures by wildlife and humans vary during the course of the day?

Average daily human activity at the study sites varied between 0.1 and 33.9 events per day, with a maximum of 114 observation events at site 5 on October 23, 2017. Across all study sites, human activity levels were highest during the daytime hours (between 6:00 a.m. and 8:00 p.m.) and peak daily human activity levels were reached in the early evenings, at roughly 5:00 p.m. (Fig. 5). Contrarily to human activity, average daily mammal activity levels were highest during nocturnal hours (between 8:00 p.m. and 7:00 a.m.) with peak activity levels reached between 1:00 a.m. and 7:00 a.m. We chose to classify raccoon observations apart from other mammal species, as they were observed much more often than any other species and also exhibited a much higher overall crossing-success ratio (85%, 1212 full crossings over 1423 confirmed detections). Raccoons were almost exclusively detected during crepuscular and nocturnal hours (between 6:00 p.m. and 7:00 a.m.) with peak activity levels between 4:00 a.m. and 7:00 a.m. Full crossings across all mammal species (excluding raccoon) were highest during crepuscular hours.

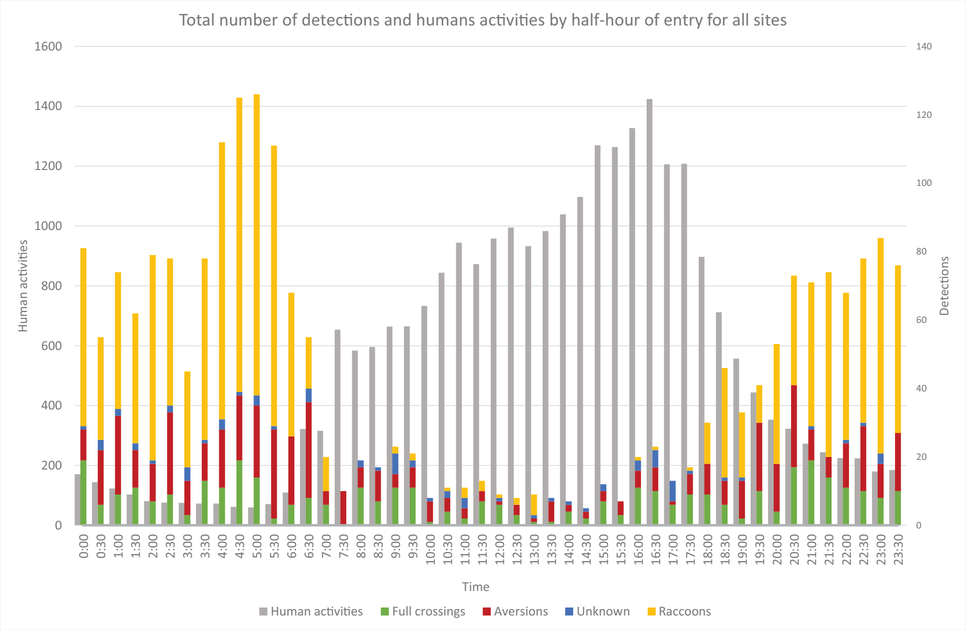

Figure 5. The total number of human and mammal detections by half-hour across all study sites. The results for raccoon (*Procyon lotor*) were removed from the other mammal species to prevent a skew due to the high numbers of raccoons observed throughout the study. Grey bars indicate human observations. Green bars indicate confirmed full crossings for mammal species and red bars indicate confirmed aversions for mammal species (excluding raccoon). Blue bars indicate mammal observations for which the outcome is unknown (excluding raccoon). Yellow bars indicate raccoon detections.

How does the daily frequency of use by wildlife relate to the daily frequency of human activity?

To relate wildlife activity in underpasses to human activity levels, we compared the total numbers of detections for each species across 50 days (Tables A1–A3) with the associated daily human activity across all sites (Fig. 6).

Very low or no human co-use

Mouse species, muskrat (*Ondatra zibethicus*), North American porcupine, rat species, and squirrel species displayed very low or no human co-use at the existing underpasses (Table 2). All species in this group, excluding squirrel species, were never observed successfully crossing through a structure on days when human activity occurred. Squirrel species were not observed successfully crossing through a structure on days with more than four human activities.

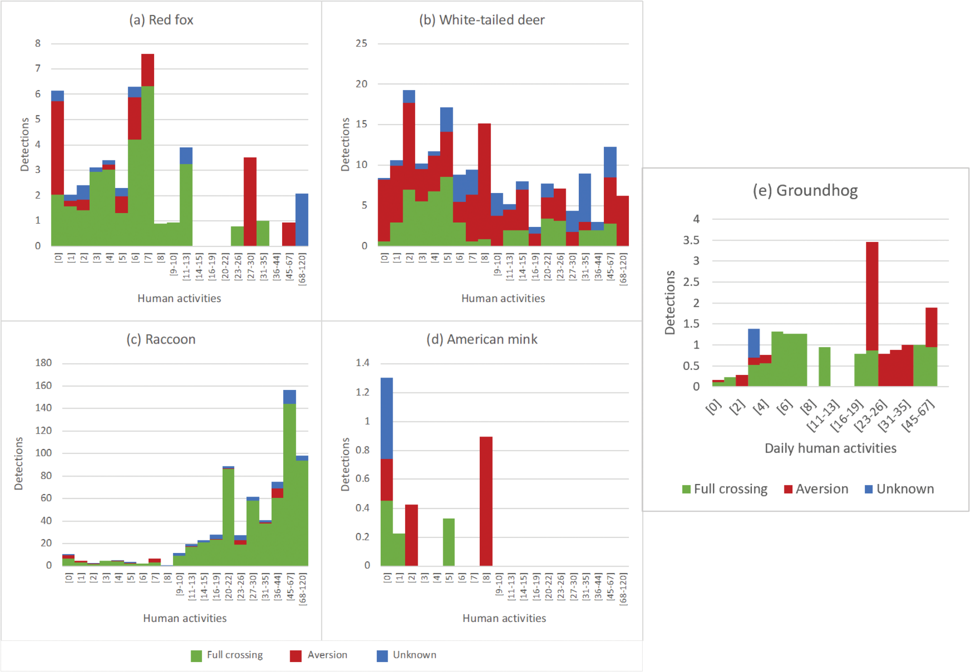

Figure 6. The average number of detections of (**a**) red fox, (**b**) white-tailed deer, (**c**) raccoon, (**d**) American mink, and (**e**) groundhog over 50 days by daily human activity levels. Green bars indicate confirmed full crossings, red bars indicate confirmed aversions, and blue bars indicate detections for which the outcome was unknown.

Low human co-use

American minks were observed crossing through the structures on 26 occasions on days with no human activity and only once on a day with five human activities (Fig. 6). Snowshoe hares were observed on 14 occasions throughout the study and only one detection occurred on a day with more than four human activities. Bobcats, the final species in the classification, were observed only three times on days with more than 4 human activities (out of 29 detections). We conducted a Kendall's Tau-*b* test on American mink for both full crossings and total observation events to explore the relationship with human presence. For full crossings, we obtained a Tau-value of -0.253 (p = 0.0154) and for total observation events, we obtained a Tau-value of -0.345 (p = 0.007) (Table 4), indicating a negative correlation between American mink's use of the existing crossing structures and human presence.

Moderate human co-use

Species in this class included white-tailed deer and red fox (Fig. 6). The majority of full crossings for red fox were observed on days with fewer than 14 human activities. On

Table 4. Results obtained from the Kendall's Tau tests (*a* and *b*) performed on raccoon, white-tailed deer, red fox, American mink, and groundhog to measure the correlation between human presence at the study sites and full crossings by wildlife, as well as number of detections.

Species	Full crossings			Total detections		
	Test	Tau-value	*p*-value	Test	Tau-value	*p*-value
Raccoon	Tau-*a*	0.642	7.55×10^{-5}	Tau-*a*	0.674	3.28×10^{-5}
White-tailed deer	Tau-*b*	-0.236	0.150	Tau-*a*	-0.389	0.016
Red fox	Tau-*b*	-0.492	0.002	Tau-*b*	-0.298	0.068
American mink	Tau-*b*	-0.253	0.015	Tau-*b*	-0.345	0.007
Groundhog	Tau-*b*	-0.064	0.686	Tau-*b*	0.128	0.434

days with 14 or more human activities, there were on average no more than 3.5 red fox detections and no more than one full crossing per 50 days. White-tailed deer were most often observed crossing through the structures on days with less than seven human activities but were nonetheless also observed crossing on days with up to 67 human activities.

We conducted Kendall's Tau-*a* and Tau-*b* tests for white-tailed deer and red fox for full crossings and total detections. For white-tailed deer, we conducted a tau-*b* test for full crossings (to correct for ties) and a tau-*a* test for total detections (no ties). We obtained a Tau-value of -0.236 (p = 0.150) for full crossings (non-significant) and a Tau-value of -0.389 (p = 0.016) for total observation events, suggesting a negative correlation for total observation events. For red fox, we conducted a Tau-*b* test on both datasets and obtained a Tau-value of -0.492 (p = 0.002) for full crossings, and for total detections we obtained a Tau-value of -0.289 (p = 0.068, i.e., marginally significant).

High human co-use

Coyote, domestic cat, and groundhog showed similar patterns of underpass use independent of human activity level. The full crossings by groundhog remained relatively stable across all daily human activity levels, with no more than 1.5 full crossings on average over 50 days, regardless of human activity level (Fig. 6). The observations for coyote and domestic cat showed similar trends, with observations remaining relatively stable across all daily human activity levels. Kendall's Tau-*b* test for groundhog resulted in a Tau-value of -0.064 (p = 0.686) for full crossings and a Tau-value of 0.128 (p = 0.434) for total detections. Both results are non-significant and do not indicate a relationship between groundhog use of the existing structures and human presence.

Very high human co-use

Raccoon was the only species exhibiting a positive correlation between full crossings and high daily human activities (Fig. 6). Almost half of all observed raccoons' full crossings occurred at the gravel road underpass at site 5 (47.6%), which is the site that displayed by far the highest average daily human activity (33.9 per day) across all study sites. Additionally, raccoons represented 92.5% of all full crossings at site 5. Kendall's Tau-*a* test (since there were no ties) resulted in a Tau-value of 0.642 ($p = 7.55 \times 10^{-5}$) for full crossings and a Tau-value of 0.674 ($p = 3.28 \times 10^{-5}$) for total detections, indicating a clear positive correlation between raccoon use of the structures and human presence at the study sites.

Species that were observed less than 10 times throughout the study and therefore were not considered in the classification of human co-use included black bear, chipmunk (*Tamias striatus*), fisher, moose, North American beaver, North American river otter, striped skunk, and weasel. Of these, only fisher, moose, and weasel were observed crossing through a structure on a day with more than two human activities.

Discussion

Use of existing crossing structures by wildlife: Species distribution and frequencies of use

In an effort to estimate the permeability of Highway 10 East to wildlife, we found that 21 mammalian species used at least one of the eight observed underpasses at least once to cross under the highway, and a few species frequented some of the underpasses on a regular basis, namely raccoon, red fox, and white-tailed deer.

Train underpasses

Railroad underpasses show promise in facilitating mammal crossing, with considerable rates of full crossings detected for a diverse range of species within this study. Notably, medium- and large-sized mammals known to frequently cause VWCs along Highway 10 East in the region were detected at train underpass structures, including moose, white-tailed deer, bobcat, coyote, and raccoon. Remarkably, each of the three moose detected at a railroad underpass (site 1), which is darker and more coarsely gravelled than site 4, were confirmed to have fully crossed through the structure. Similar patterns were observed for American minks, bobcats, coyotes, and raccoons, for which all detections resulted in confirmed full crossings at the darker train underpass (site 1). Additionally, all bobcat detections (20) that occurred at the train overpass which exhibited more natural light, in addition to having vegetation and a soil substrate on either side of the train tracks (site 4), were confirmed to have successfully crossed through the structure. Of those bobcat detections, 15 occurred during the same month (February 2017), which suggests one or a few individuals may have revisited the train underpass throughout the month. Similarly, the brighter, more vegetated train underpass facilitated a larger number of white-tailed deer detections, with the species accounting for 72% of the total wildlife detected around or within the railroad underpass at site 4. In contrast, at the darker, more coarsely gravelled train underpass (site 1), white-tailed deer detections made up only 37% of total wildlife detections. These differences in wildlife use of the railroad underpasses suggest that species behaviour may be influenced by the structural and environmental differences between the underpasses. This notion has been confirmed in earlier studies, which have determined that high openness ratios (short in length, as well as high and wide) facilitate higher rates of usage by grizzly bears (*Ursus americanus*), wolves, and deer (Clevenger and Waltho 2005), and that natural substrates throughout crossing structures encourage full crossings by wildlife by connecting habitat (Yanes et al. 1995).

Human activity remained relatively similar in both underpasses, consisting mostly of trains and monthly visits by the research crew. This leads us to believe that the significant variation in crossing-success ratios at both train underpasses may be due to the height and width differences, i.e., the openness ratio of the structures (1.43 m at site 1 and 6.06 m at site 4) and substrate differences between the structures.

Road underpass

The unpaved road underpass had the greatest frequency of mammal use, where on average nearly two wildlife individuals crossed per day. However, this result was driven by raccoons, a species of low concern to conservation organizations or transport and wildlife authorities. A significant number of white-tailed deer (108 individuals) also visited the site, perhaps due to the large openness ratio of the structure and the presence of vegetation along the sides of the road. However, only 24% of detected white-tailed deer were observed crossing through the structure, suggesting avoidance behaviour to certain characteristics of the gravel road underpass, possibly the presence of vehicles and nearby cottages. Our observations and the very low full-crossing diversity index (0.37) suggest that road underpasses are suitable for co-use by raccoons and white-tailed deer but are unlikely to be used by other species.

Water culverts

Numerous species were detected using water culverts to cross below the highway: black bear, raccoon, white-tailed deer, American mink, river otter, striped skunk, snowshoe hare, red fox, and rodent species. Moose, fisher, and chipmunk were detected at culvert sites, but were never observed crossing through successfully. Water culverts are much less frequented by humans than both train and road underpasses but have structural features that can limit wildlife use. Deer were only observed crossing through the culvert with the highest openness ratio (site 6), and only during the summer seasons, when water levels were lowest. Flooded conditions of culverts likely impeded use by mammals, namely white-tailed deer. Reports of ungulate use of culverts are rare, as most research points to their strict aversion of enclosed spaces with low openness (Foster and Humphrey 1995; Clevenger and Waltho 2005; Kintsch and Cramer 2011). Alternatively, high water levels can facilitate crossings for some mammal species such as American mink, which was detected swimming through the water culvert at site 9 in late spring. In winter, ice formations at water culverts can also affect crossing success. Snowshoe hares were detected using the water culvert at site 9 in winter when the water was fully frozen over. For much of each winter season, snow and ice pile-up obstructed the entrances to one culvert (site 2) almost entirely, leaving only a small opening for access to the structure. Minimal wildlife full crossings were detected during the winter months at this site compared to the other non-obstructed culverts. Interestingly, this obstructed culvert became a winter burrow for an American mink during the winter months of 2016, highlighting the multiple ways that water culverts can serve both humans and animals.

While various species were detected using culverts to cross below the highway, our findings indicate that water culverts are frequented considerably less often than the other studied structures, namely a gravel road underpass and two railroad underpasses. Research conducted on the same highway at nearby water culverts of smaller size (with heights less than 1.8 metres and widths less than 1.8 metres, including one rectangular culvert with a height of 3.0 metres and a width of 6.0 metres) concluded that the culverts were used considerably less than one could expect for designated wildlife passages (Brunen et al. 2020). The study found that out of 20 species observed in the vicinity of the culverts, only about half of the species were detected making a full crossing, and only two species known to be tolerant to water, namely raccoons and American minks, were observed crossing through the culverts with regularity (Brunen et al. 2020). These results may be in part due to the significant structural and environmental differences between the structure types, including the smaller openness ratio of the studied water culverts, the concrete substrate, and the presence of water. Water culverts are a common structural component of highway systems, and our findings support previous work documenting their use by some mammal species; however, water culverts also show limited use compared to larger, more open structures. The potential for water culvert use by wildlife to be improved based on modifications, maintenance, and structural design is an important topic for future work, e.g., retrofitting with ledges to allow small- and medium-sized mammals to use culverts without having to enter the water (Trocmé and Righetti 2012).

Species of special interest

A number of species are of particular interest for conservation purposes, due to large home ranges which bear significance to inform land conservation prioritization at a local or regional scale, where habitat fragmentation, functional ecological connectivity, and adaptation to climate change are key elements of interest (Koehler and Pierce 2003). Several species of interest were detected throughout the course of our study, including black bear (2), bobcat (29), coyote (12), and moose (5), all of which were observed crossing through one or several structures. A recent study in the same region exclusively on water culverts also detected black bear and bobcat near the openings of the structures, but no entries were observed (Brunen et al. 2020), likely due to the significantly smaller size of monitored culverts compared to the size of structures monitored in our study. However, these observations are noteworthy as they indicate the species' presence near the highway, and, in our case, their ability and willingness to enter and cross through some of the existing structures. All species of special interest have naturally low population densities within the region and large home ranges, believed to be a function of food distribution and abundance (Leptich and Gilbert 1989; Koehler and Pierce 2003). Urbanization and habitat fragmentation have significant adverse impacts on wildlife species, especially mammalian carnivores, in large part due to their habitat size and preferences (Riley et al. 2003). Monitoring the effects of habitat fragmentation and investing in mitigation measures (including fencing and wildlife passages) could facilitate the movement of these species and decrease the number of WVCs within the region (Rytwinski et al. 2016).

Species rarely detected

Among species we might have expected to detect more frequently, fisher (2) is especially noteworthy due to its conservation interest. Fisher presence in the region is frequently confirmed both by trapping records and winter tracking information that is collected by trained volunteers and coordinated by various local or regional conservation organizations (including Appalachian Corridor, Conservation des vallons de la Serpentine, and Ruiter Valley Land Trust). Also of note, snowshoe hare is a favoured prey of several of the mammalian carnivores detected in the region, including coyote and bobcat (Patterson et al.1998; Matlack and Evans 1992). The snowshoe hare is frequently encountered in the region yet its presence at the crossing structures was relatively low (14) compared to other detected prey species, including squirrels (77) and groundhogs (41). Although information from winter tracking efforts confirmed fisher and snowshoe hare presence in the region, and along specific sections to the north or south of Highway 10 East, it would be beneficial to consider more systematic surveys within the region. We believe that surveys encompassing natural habitats abutting the monitored crossing structures and running along both the northern and southern boundaries of the road may provide valuable information on species distribution in the study area and possible causes of the limited detection of several mammal species at the study sites.

Co-use of existing crossing structures by wildlife and humans

Very low or no human co-use

While our study did not differentiate between squirrel species, red squirrels (*Sciurus vulgaris*) are rarely observed using crossing structures that experience human activity. Research in Spain found that only days with less than one human event allowed for crossings by red squirrels and rats (Mata et al. 2005). Another study evaluated wildlife use of a wildlife-designated structure and two existing crossing structures and found that red squirrels were observed crossing only through the wildlife-designated structure (Yushin et al. 2020). The results from both studies coincide with what we have observed at our crossing structures, namely that squirrel species have a very low human co-use level and were not observed crossing through a structure on days with over four human activities.

Low human co-use

In our study, American minks and snowshoe hares rarely utilized the crossing structures when daily human activity levels were above four, suggesting a low co-use to human activity. Research has shown that European hares (*Lepus europaeus*) have been observed using multi-use crossing structures three hours after use by humans (van der Ree and van der Grift 2015). Small mammals, including Eurasian hares (*Lepus capensis*) and mustelid species, pass through wildlife culverts in Poland significantly less often during months that incurred high levels of human activity (May and October) (Wazna et al. 2020). These studies indicate aversion to crossing structures for hare and mustelid species when daily human activity levels are high. Contrarily, one study conducted on woolly hares (*Lepus oiostolus*) found that human presence did not influence their use of existing crossing structures (Wang et al. 2018). However, this lack of correlation may be due to the limited range of human activity detected at the crossing structures, which mainly consisted only of occasional highway maintenance crew visits to the sites.

We found a negative correlation between American mink full crossings and human presence and a strong negative correlation between total observation events and human presence (Table 4). Out of the 78 American mink detections throughout the study period, 77 of them occurred at one of five water culvert sites, which are the structure type that exhibited the lowest overall daily human activity levels (between 0.1 and 1.3 per day). These findings suggest that American mink are less likely to be observed near crossing structures that experience more than an average of one human activity per day.

Moderate human co-use

Red foxes showed a negative correlation between successful full crossings and increasing daily human activity at the study sites. Our statistical results about red foxes suggest a negative correlation for full crossings and a marginally significant negative correlation for total detections (Table 4). Many studies have found little to no correlation between full crossings by red foxes and human presence at wildlife passages and existing crossing structures (Rodriguez et al. 1996; Mata et al. 2005; Grilo et al. 2008; Yushin et al. 2020). However, one study found a negative correlation between wildlife use and human use of wildlife passages for all species observed, which included red foxes (Wazna et al. 2020), which supports our categorization of moderate human co-use for red foxes at our study sites.

Our observation that white-tailed deer are less likely to approach crossing structures that exhibit higher human activity levels agrees with other studies. While we did not analyze the times of day at which individual species utilized the crossing structures (other than raccoon in Fig. 5), Barrueto et al. (2014) reported that white-tailed deer are prone to crossing through crossing structures more often during crepuscular and nocturnal hours, whereas daily human activity levels are high during daytime hours. Similarly, van der Ree and van der Grift (2015) found that deer species would cross through crossing structures on average three hours after human presence for sites with high daily human activity levels. Other research also found that the total number of full crossings for roe deer (*Capreolus capreolus*) and white-tailed deer was negatively correlated with an increase in human activity (Bhardwaj et al. 2020; Wazna et al. 2020).

Our statistical results on white-tailed deer and human presence do not suggest a relationship between full crossings and human presence but do show a negative relationship between total detections and human presence. While our results align with other studies (Bhardwaj et al. 2020; Wazna et al. 2020), many factors are likely to influence use of existing crossing structures by white-tailed deer (as well as for other species). Ungulate use of culverts is rare due to aversion behaviour toward spaces and structures with low openness (Foster and Humphrey 1995; Clevenger and Waltho 2005; Kintsch and Cramer 2011). Although the water culverts in our study experienced the lowest average daily human activity levels across all structure types, white-tailed deer rarely crossed through the monitored water culverts, likely due to low openness and presence of water. This general aversion behaviour toward the water culverts would influence the results obtained from the Kendall's Tau tests.

High human co-use

Our study found no correlation between coyote full crossings and level of human activity at the scale of full days, but this difference compared to other studies may be due to the different evaluation timeframes used in the studies. Coyote have been known to modify their behaviour near wildlife crossing structures to avoid human presence, preferring to cross during crepuscular and nocturnal hours (Barrueto et al. 2014). Barrueto et al. (2014) also found that coyotes tend to cross later on days with high human activity.

Groundhogs were observed to use the underpasses regardless of human activity levels. One study conducted on Himalayan marmots (*Marmota himalayana*) also found no correlation between use of crossing structures and human activity levels (Wang et al. 2018). Additionally, studies have found no correlation between use of crossing structures and levels of human activities for the domestic cat (Mata et al. 2005; Yushin et al. 2020). The results from our correlation tests on groundhog and human presence support these findings, suggesting there is no clear relationship between human presence and groundhog full crossings nor total detections (Table 4). Groundhog observations at the study sites remained relatively stable across all categories of daily human activity levels.

Very high human co-use

We found a strong positive correlation between the use of existing crossing structures by raccoon and the presence of raccoon at the structures with increasing human activity levels. This correlation may be heavily influenced by raccoon use of the gravel road underpass (site 5), which had the highest observed daily human activity levels (33.9 per day) of all study sites. Additionally, site 5 is located on a small gravel municipal road that is sparsely lined with houses and cottages, which may attract raccoons to the area for scavenging purposes. A recent study by Yushin et al. (2020) found that raccoons exhibited no preference between a wildlife passage and two existing crossing structures used by humans.

Limitations and future research needs

While our observations across eight existing crossing structures provide evidence of mammal presence and use of the structures and of a species-specific influence of human use, a larger sample size of existing crossing structures will be needed to further analyze the influence of human use on mammal behaviour and movement patterns, while controlling for other variables. There have been a few studies comparing the effects of human use at large numbers of existing crossing structures (LaPoint et al. 2003; Ng et al. 2004; Grilo et al. 2008), yet their periods of observation were limited to ranges of only 4 to 40 days, or their sites were limited to low levels of human activity (Rodriguez et al. 1997). We chose to analyze fewer underpasses in exchange for a longer observation period, as we believe the seasonal and diurnal changes in human and mammal activity levels could be an important factor to consider in future statistical analyses on this dataset to assess the effectiveness of existing underpasses for mammal use.

The detectability of mammals by motion-sensor cameras has been questioned in a recent comparison of video to infrared and motion-detection cameras showing that the cameras missed 10% of medium-sized mammals visiting culverts (Jumeau et al. 2017). As we chose to employ an equal number of cameras at each site, regardless of structure size and openness, it is possible that some mammal crossings (most likely by small- and medium-sized mammals) were not detected, at least in the larger structures. For large mammals, this is less likely, as all cameras were adjusted for maximum range detection and maximal coverage of underpass width. However, at the train underpasses or the road underpass, a few large mammals may have been missed, while detection of small mammals may have been higher in the water culverts. We would encourage future studies to use a greater diversity of angles and heights to maximise detection of species of all sizes (Meek et al. 2014). Numbers of mammal detections at all sites should be considered as a minimum activity, as true passages and presence may be higher. At the circular water culvert at site 2, the placement of cameras did not allow for the detection of ATVs and pedestrians passing by the northern end of the culvert via an adjacent bridge. The tally of human activity at this site must therefore be taken as a minimum, and the results at this site are likely incomplete. Another limitation of the use of cameras is the possibility of underrepresented species due to camera avoidance behaviour. Some predators, including red fox, detect and avoid cameras due to certain stimuli (Meek et al. 2016). Since we did not include a second method of mammal detection in our study for comparison, such as print traps, we cannot determine whether wildlife exhibited avoidance behaviour toward the cameras.

It is important to note that Kendall's Tau tests only consider overall positive or negative relationships (Laurencelle 2009), but for species that exhibit higher occurrences of full crossings or detections on days with intermediate human activity levels, the results from Kendall's Tau test would not reflect this non-linear relationship.

A final limitation of this study is the lack of robust statistical analysis, due to the limited number of sites observed, and the high variability of characteristics between sites. It is difficult to include all eight research sites into one combined statistical test due to the wide range of structural differences between the structures. For example, the culvert located at site 9, which always showed presence of water, varies greatly from the train underpass located at site 1, which always had a dry path and has a much higher openness ratio. These differences are difficult to quantify and are complex to incorporate into a comprehensive statistical test, unless a large sample of structures is monitored. Such a larger analysis would also allow for a species-specific approach to identify preferences for existing crossing structures by different species if the observation period is long enough (several years) to gather sufficient data for individual species.

Conclusion

Our results provide evidence that 21 wildlife species of small-, medium-, and large-sized mammals in the study area used one or several existing crossing structures, including water culverts, train underpasses, and a gravel road byway. We found evidence that some mammal species will use underpasses with low levels of daily human activity, suggesting co-use of existing crossing structures is possible for select species. The crossing structures that are most promising in supporting a diversity of wildlife crossings by species of particular interest for conservation (moose, black bear, bobcat, coyote, fisher) and by large mammals causing the most damage or loss of lives in WVCs (i.e., including white-tailed deer) were the two train underpasses, whereas the gravel road underpass was mostly used by raccoons, with only a moderate number of crossings by white-tailed deer and very few crossings by any other species. The water culverts were the least promising as overall, they were very rarely used by these species due to structural and environmental characteristics, including their smaller size, substrate composition, frequent presence of water, and lack of vegetation.

While our study did not consider crossing structures of higher human use, such as high-use roads or highways, the strengths of our study include the length of time during which continuous monitoring took place at the structures (up to 778 days) and the placement of four camera traps at each structure (two facing inward and two facing outward), allowing us to determine whether individuals successfully crossed through the structures or displayed avoidance behaviour.

Despite the absence of an extensive statistical analysis within our study, we have gathered an extensive number of observations spanning seasons and years around the study area and we believe the following recommendations should be considered for future research and conservation efforts. Given our knowledge of habitat fragmentation and WVCs, we recommend that to increase the use of existing underpasses by mammals, fencing should be installed along Highway 10 East to guide wildlife to the structures and to decrease road mortality. Wildlife fencing is effective at reducing road mortality, whereas measures that are less expensive than fencing, such as wildlife warning signs and reflectors, are ineffective, and wildlife passages do not reduce road mortality unless fences are present (Rytwinski et al. 2016). Continued use of cameras will then be able to determine if additional species would discover and start using the structures. Mortality reduction graphs can be applied to the area to prioritize road sections for fencing (Spanowicz et al. 2020). Based on our knowledge of the study area and species observed near the crossing structures, we believe retrofitting the existing water culverts with dry ledges might encourage small- and medium-sized mammals that were rarely observed crossing through the monitored water culverts to utilize the structures (including groundhog and red fox). Additionally, while our study does not explicitly demonstrate that designated wildlife passages are needed, the construction of such wildlife passages (e.g., in priority areas with high animal activity and in mortality hotspots where existing structures are not well used by wildlife) would very likely encourage safe wildlife crossings for species, particularly the mammal species grouped into the lower levels of human-co-use in our paper (including North American porcupine, American mink, and bobcat). To better support these considerations, we recommend that further research within the area focus on a considerably larger sample size of underpasses to allow for a comparison of the influence of structural and environmental variations between existing structures.

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References

Anderson MG, Vickery B, Gorman M, Gratton L, Morrison M, Maillet J, Olivero A, Ferree C, Morse D, Kehm G, Rosalska K, Khanna S, Bernstein S (2006) The Northern Appalachian/Acadian Ecoregion: Conservation assessment status and trends: 2006. The Nature Conservancy Eastern Regional Science in collaboration with The Nature Conservancy of Canada: Atlantic and Quebec Regions. Boston, MA.

Barrueto M, Ford AT, Clevenger AP (2014) Anthropogenic effects on activity patterns of wildlife at crossing structures. Ecosphere 5(3): e27. https://doi.org/10.1890/ES13-00382.1

Bhardwaj M, Olsson M, Seiler A (2020) Ungulate use of non-wildlife underpasses. Journal of Environmental Management 273: e111095. https://doi.org/10.1016/j.jenvman.2020.111095

Bissonette JA, Kassar CA, Cook LJ (2008) Assessment of costs associated with deer-vehicle collisions: human death and injury, vehicle damage, and deer loss. Human-Wildlife Conflicts 2(1): 17–27. https://www.jstor.org/stable/24875102

Brunen B, Daguet C, Jaeger JAG (2020) What attributes are relevant for drainage culverts to serve as efficient road crossing structures for mammals? Journal of Environmental Management 268: e110423. https://doi.org/10.1016/j.jenvman.2020.110423

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

Clevenger AP, Waltho N (2005) Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. Biological Conservation 121(3): 453–464. https://doi.org/10.1016/j.biocon.2004.04.025

Daguet C (2015) Rapport sur l'identification des corridors fauniques de part et d'autre de l'autoroute 10 - Phase II. Corridor Appalachien, Eastman, Québec, 47 pp.

Dodd CK, Barichivich WJ, Smith LL (2004) Effectiveness of a barrier wall and culverts in reducing wildlife mortality on a heavily traveled highway in Florida. Biological Conservation 118(5): 619–631. https://doi.org/10.1016/j.biocon.2003.10.011

Ellenberg U, Mattern T, Seddon PJ, Jorquera GL (2006) Physiological and reproductive consequences of human disturbances in Humboldt penguins: The need for species-specific visitor management. Biological Conservation 133(1): 95–106. https://doi.org/10.1016/j.biocon.2006.05.019

Ford AT, Barrueto M, Clevenger AP (2017) Road mitigation is a demographic filter for grizzly bears. Wildlife Society Bulletin 41(4): 712–719. https://doi.org/10.1002/wsb.828

Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annual Review of Ecology and Systematics 29(1): 207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Foster ML, Humphrey SR (1995) Use of highway underpasses by Florida panthers and other wildlife. Wildlife Society Bulletin 23(1): 95–100. https://www.jstor.org/stable/3783202

Frid A, Dill L (2002) Human-caused disturbance stimuli as a form of predation risk. Ecology and Society 6(1): e11. ttps://doi.org/10.5751/ES-00404-060111

Gratton L, Bryant D (2012) Une approche intégrée à l'échelle des paysages pour préserver la connectivité. Le Naturaliste Canadien 136(2): 101–107. https://doi.org/10.7202/1009115ar

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

Henschel P, Ray J (2003) Leopards in African rainforests: Survey and monitoring techniques. Wildlife Conservation Society, Bronx, New York, 216 pp.

Jaeger JAG, Bowman J, Brennan J, Fahrig L, Bert D, Bouchard J, Charbonneau N, Frank K, Gruber B, Tluk von Toschanowitz K (2005) Predicting when animal populations are at risk from roads: An interactive model of road avoidance behavior. Ecological Modelling 185(2–4): 329–348. https://doi.org/10.1016/j.ecolmodel.2004.12.015

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

Kintsch J, Cramer PC (2011) Permeability of existing structures for terrestrial wildlife: A passage assessment system. Research Report No. WA-RD 777.1. Washington State Department of Transportation, WSDOT Research Report, Olympia, WA, 60 pp. [+ 4 app.]

Koehler GM, Pierce JD (2003) Black bear home-range sizes in Washington: Climatic, vegetative, and social influences. Journal of Mammalogy 84(1): 81–91. https://doi.org/10.1644/1545-1542(2003)084<0081:BBHRSI>2.0.CO;2

LaPoint SD, Kays RW, Ray JC (2003) Animals crossing the Northway: Are existing culverts useful? Adirondack Journal of Environmental Studies (Spring/Summer 2003): 11–17.

Laurencelle L (2009) Le tau et le tau-b de Kendall pour la corrélation de variables ordinaires simples ou catégorielles. Tutorials in Quantitative Methods for Psychology 5(2): 51–58. https://doi.org/10.20982/tqmp.05.2.p051

Leptich DJ, Gilbert JR (1989) Summer home range and habitat use by moose in Northern Maine. The Journal of Wildlife Management 53(4): 880–885. https://doi.org/10.2307/3809581

Mata C, Hervas I, Herranz J, Suarez F, Malo JE (2005) Complementary use by vertebrates of crossing structures along a fenced Spanish motorway. Biological Conservation 124(3): 397–405. https://doi.org/10.1016/j.biocon.2005.01.044

Matlack CR, Evans AJ (1992) Diet and condition of bobcats, *Lynx rufus*, in Nova Scotia during autumn and winter. Canadian Journal of Zoology 70: 1114–1119. https://doi.org/10.1139/z92-156

Meek PD, Ballard G, Claridge A, Kays R, Moseby K, O'Brien T, O'Connell A, Sanderson J, Swann DE, Tobler M, Townsend S (2014) Recommended guiding principles for reporting on camera trapping research. Biodiversity and Conservation 23(9): 2321–2343. https://doi.org/10.1007/s10531-014-0712-8

Meek PD, Ballard G, Fleming P, Falzon G (2016) Are we getting the full picture? Animal responses to camera traps and implications for predator studies. Ecology and Evolution 6(10): 3216–3225. https://doi.org/10.1002/ece3.2111

Ng SJ, Dole JW, Sauvajot RM, Riley SP, Valone TJ (2004) Use of highway undercrossings by wildlife in southern California. Biological Conservation 115(3): 499–507. https://doi.org/10.1016/S0006-3207(03)00166-6

Olsson MP, Widén P, Larkin JL (2008) Effectiveness of a highway overpass to promote landscape connectivity and movement of moose and roe deer in Sweden. Landscape and Urban Planning 85(2): 133–139. https://doi.org/10.1016/j.landurbplan.2007.10.006

Patterson BR, Benjamin LK, Messier F (1998) Prey switching and feeding habits of eastern coyotes in relation to snowshoe hare and white-tailed deer densities. Canadian Journal of Zoology 76(10): 1885–1897. https://doi.org/10.1139/z98-135

Preisser EL, Bolnick DL, Bernard MF (2005) Scared to death? The effects of intimidation and consumption in predator-prey interactions. Ecology 86(2): 501–509. https://doi.org/10.1890/04-0719

Riitters KH, Wickham JD (2003) How far to the nearest road? Frontiers in Ecology and the Environment 1(3): 125–129. https://doi.org/10.1890/1540-9295(2003)001[0125:HFTTNR]2.0.CO;2

Riley SPD, Sauvajot RM, Fuller TK, York EC, Kamradt DA, Bromley C, Wayne RK (2003) Effects of urbanization and habitat fragmentation on bobcats and coyotes in Southern California. Conservation Biology 17(2): 566–576. https://doi.org/10.1046/j.1523-1739.2003.01458.x

Rodriguez A, Crema G, Delibes M (1996) Use of non-wildlife passages across a high-speed railway by terrestrial vertebrates. Journal of Applied Ecology 33(6): 1527–1540. https://doi.org/10.2307/2404791

Rodriguez A, Crema G, Delibes M (1997) Factors affecting crossing of red foxes and wildcats through non-wildlife passages across a high-speed railway. Ecography 20(3): 287–294. https://doi.org/10.1111/j.1600-0587.1997.tb00373.x

Rowcliffe JM, Field J, Turvey ST, Carbone C (2008) Estimating animal density using camera traps without the need for individual recognition. Journal of Applied Ecology 45(4): 1228–1236. https://doi.org/10.1111/j.1365-2664.2008.01473.x

Rytwinski T, Soanes K, Jaeger JAG, Fahrig L, Findlay CS, Houlahan J, van der Ree R, van der Grift EA (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 Maître ès sciences géographiques (M.Sc.), cheminement de type cours en géodéveloppement durable. Université de Sherbrooke, Département de géomatique appliquée, Faculté des lettres et sciences humaines, 87 pp.

Samia DSM, Nakagawa S, Normura F, Rangel TF, Blumstein DT (2015) Increased tolerance to humans among disturbed wildlife. Nature Communications 6(8877): 1–8. https://doi.org/10.1038/ncomms9877

Sawaya MA, Clevenger AP, Kalinowski ST (2013) Demographic connectivity for ursid populations at wildlife crossing structures in Banff National Park. Conservation Biology 27(4): 721–730. https://doi.org/10.1111/cobi.12075

Shannon CE, Wiener W (1963) The mathematical theory of Communication. University of Illinois Press, Urbana.

Spanowicz AG, Teixeira FZ, Jaeger JAG (2020) An adaptive plan for prioritizing road sections for fencing to reduce animal mortality. Conservation Biology 34(5): 1210–1220. https://doi.org/10.1111/cobi.13502

Staying Connected Initiative (2018) Northern Greens to Canada. http://stayingconnectedinitiative.org/our-places/northern-greens-to-canada [Accessed on 25 February 2018]

Terrell GR, Scott DW (1985) Oversmoothed nonparametric density estimates. Journal of the American Statistical Association 80(398): 209–214. https://doi.org/10.1080/01621459.1985.10477163

Torres A, Jaeger JAG, Alonso JC (2016) Assessing large-scale wildlife responses to human infrastructure development. Proceedings of the National Academy of Sciences of the United States of America 113(30): 8472–8477. https://doi.org/10.1073/pnas.1522488113

Trocmé M, Righetti A (2012) Standards for fauna friendly culverts. In: Wagner PJ, Nelson D, Murray E (Eds) Proceedings of the 2011 International Conference on Ecology and Transportation (ICOET). Raleigh, NC. Center for Transportation and the Environment, North Carolina State University, 557–560.

Trombulak SC, Anderson MG, Baldwin R, Beazley K, Ray J, Reining C, Gratton L (2008) The Northern Appalachian/Acadian Ecoregion Priority Locations for Conservation Action. Two Countries, One Forest. https://conservationcorridor.org/cpb/Trombulak_et_al_2008.pdf

van der Ree R, van der Grift EA (2015) Recreational co-use of wildlife crossing structures. In: van der Ree R, Smith DJ, Grilo C (Eds) Handbook of Road Ecology. John Wiley & Sons, Oxford, 184–189. https://doi.org/10.1002/9781118568170.ch22

van der Ree R, Smith DJ, Grilo C [Eds] (2015) Handbook of Road Ecology. John Wiley & Sons, Oxford, 184–189. https://doi.org/10.1002/9781118568170.ch22

van Vuurde MR, van der Grift EA (2005) The effects of landscape attributes on the use of small wildlife underpasses by weasel (*Mustela nivalis*) and stoat (*Mustela erminea*). Lutra 48: 91–108. https://zoogdierwinkel.nl/content/lutra-48-2-2005

Wang Y, Guan L, Chen J, Kong Y (2018) Influences on mammals frequency of use of small bridges and culverts along the Qinghai-Tibet railway, China. Ecological Research 33(5): 879–887. https://doi.org/10.1007/s11284-018-1578-0

Wazna A, Kazmierczak A, Cichocki J, Bojarski J, Gabrys G (2020) Use of underpasses by animals on a fenced expressway in a suburban area in western Poland. Nature Conservation 39: 1–18. https://doi.org/10.3897/natureconservation.39.33967

Wearn OR, Glover-Kapfer P (2017) Camera-trapping for conservation: A guide to best-practices. WWF Conservation Technology Series 1(1). WWF-UK, Woking, UK, 181 pp. http://www.wwf.org.uk/sites/default/files/2019-04/CameraTraps-WWF-guidelines.pdf

Wearn OR, Glover-Kapfer P (2019) Snap happy: Camera traps are an effective sampling tool when compared with alternative methods. Royal Society Open Science 6(3): e181748. https://doi.org/10.1098/rsos.181748

Yanes M, Velasco JM, Suárez F (1995) Permeability of roads and railways to vertebrates: The importance of culverts. Biological Conservation 71(3): 217–222. https://doi.org/10.1016/0006-3207(94)00028-O

Yushin A, Noro M, Yamada Y, Maruyama R (2020) Overpasses intended for human use can be crossed by middle and large-size mammals. Landscape and Ecological Engineering 16(1): 63–68. https://doi.org/10.1007/s11355-019-00396-5

Appendix 1

Table A1. Number of detections by type, species, and level of daily human activity on average over 50 days.

Number of human activities per day	Number of days in this bin	Species		American mink *Neovison vison*	Black bear *Ursus americanus*	Bobcat *Lynx rufus*	Chipmunk *Tamias striatus*	Coyote *Canis latrans*	Domestic cat *Felis catus*	Fisher *Pekania pennanti*	Groundhog *Marmota monax*
		Type of detection	Sum of detections	78	2	29	1	18	32	3	49
[0]	2767	Full crossing		0.452	0.036	0.036	-	-	0.018	-	0.108
		Aversion		0.289	-	0.036	-	0.054	0.018	0.018	0.054
		Unknown		0.560	-	-	0.018	0.108	-	0.018	-

Number of human activities per day	**Number of days in this bin**	**Species**		**American mink *Neovison vison***	**Black bear *Ursus americanus***	**Bobcat *Lynx rufus***	**Chipmunk *Tamias striatus***	**Coyote *Canis latrans***	**Domestic cat *Felis catus***	**Fisher *Pekania pennanti***	**Groundhog *Marmota monax***
		Type of detection	Sum of detections	78	2	29	1	18	32	3	49
[1]	221	Full crossing		0.226	-	-	-	-	1.131	-	0.226
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[2]	353	Full crossing		-	-	-	-	-	0.992	-	-
		Aversion		0.425	-	-	-	-	0.142	-	0.283
		Unknown		-	-	-	-	-	-	-	-
[3]	288	Full crossing		-	-	2.083	-	-	0.174	0.174	0.521
		Aversion		-	-	2.083	-	0.174	-	-	0.174
		Unknown		-	-	-	-	-	-	-	0.694
[4]	264	Full crossing		-	-	1.515	-	0.189	-	-	0.568
		Aversion		-	-	1.515	-	0.189	-	-	0.189
		Unknown		-	-	-	-	-	-	-	-
[5]	152	Full crossing		0.329	-	-	-	0.329	1.645	-	1.316
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[6]	119	Full crossing		-	-	-	-	-	-	-	1.261
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[7]	79	Full crossing		-	-	1.266	-	0.633	1.266	-	1.266
		Aversion		-	-	1.266	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[8]	56	Full crossing		-	-	-	-	-	-	-	-
		Aversion		0.893	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	0.893	-	-
[9–10]	53	Full crossing		-	-	-	-	-	-	-	0.943
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[11–13]	77	Full crossing		-	-	-	-	-	-	-	-
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[14–15]	50	Full crossing		-	-	-	-	-	3.000	-	-
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-
[16–19]	64	Full crossing		-	-	-	-	-	-	-	0.781
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	0.781	-	-
[20–22]	58	Full crossing		-	-	-	-	0.862	-	-	0.862
		Aversion		-	-	-	-	-	-	-	2.586
		Unknown		-	-	-	-	-	-	-	-
[23–26]	63	Full crossing		-	-	-	-	-	-	-	-
		Aversion		-	-	-	-	-	-	-	0.794
		Unknown		-	-	-	-	-	-	-	-
[27–30]	57	Full crossing		-	-	-	-	0.877	-	-	-
		Aversion		-	-	-	-	-	-	-	0.877
		Unknown		-	-	-	-	-	-	-	-
[31–35]	50	Full crossing		-	-	-	-	-	-	-	-
		Aversion		-	-	-	-	-	-	-	1.000
		Unknown		-	-	-	-	-	-	-	-
[36–44]	50	Full crossing		-	-	-	-	1.000	-	-	1.000
		Aversion		-	-	-	-	-	-	-	-
		Unknown		-	-	-	-	-	-	-	-

Number of human activities per day	Number of days in this bin	Species	American mink *Neovison vison*	Black bear *Ursus americanus*	Bobcat *Lynx rufus*	Chipmunk *Tamias striatus*	Coyote *Canis latrans*	Domestic cat *Felis catus*	Fisher *Pekania pennanti*	Groundhog *Marmota monax*
		Type of detection Sum of detections	78	2	29	1	18	32	3	49
[45–67]	53	Full crossing	-	-	-	-	0.943	1.887	-	0.943
		Aversion	-	-	-	-	-	0.943	-	0.943
		Unknown	-	-	-	-	-	-	-	-
[68–120]	24	Full crossing	-	-	2.083	-	-	-	-	-
		Aversion	-	-	2.083	-	-	-	-	-
		Unknown	-	-	-	-	-	-	-	-

Table A2.

Number of human activities per day	Number of days in this bin	Species	Moose *Alces alces*	Mouse spp. *Mus* spp.	Muskrat *Ondatra zibethicus*	North American beaver *Castor canadensis*	North American porcupine *Erethizon dorsatum*	North American river otter *Lontra canadensis*	Raccoon *Procyon lotor*	Rat spp. *Rattus* spp.
		Type of detection Sum of detections	5	26	26	1	18	7	1586	20
[0]	2767	Full crossing	-	0.072	0.253	0.018	0.271	0.108	6.831	0.361
		Aversion	0.018	0.235	0.054	-	0.036	-	2.765	-
		Unknown	-	0.163	0.126	-	-	0.018	0.922	-
[1]	221	Full crossing	-	-	-	-	-	-	3.167	-
		Aversion	-	-	-	-	-	-	1.357	-
		Unknown	-	-	-	-	-	-	-	-
[2]	353	Full crossing	-	-	-	-	-	-	1.983	-
		Aversion	-	-	-	-	-	-	0.567	-
		Unknown	-	-	-	-	-	-	0.142	-
[3]	288	Full crossing	0.347	-	-	-	-	-	4.688	-
		Aversion	-	-	-	-	-	-	0.174	-
		Unknown	-	-	-	-	-	-	-	-
[4]	264	Full crossing	-	-	-	-	-	-	4.356	-
		Aversion	-	-	-	-	-	-	0.379	-
		Unknown	-	-	0.189	-	-	-	0.568	-
[5]	152	Full crossing	-	-	-	-	-	-	2.303	-
		Aversion	-	-	-	-	-	-	0.658	-
		Unknown	-	-	-	-	-	-	0.658	-
[6]	119	Full crossing	0.420	-	-	-	-	-	2.521	-
		Aversion	0.420	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	-	-
[7]	79	Full crossing	-	-	-	-	-	-	3.165	-
		Aversion	-	-	-	-	-	-	3.797	-
		Unknown	-	-	-	-	-	-	-	-
[8]	56	Full crossing	-	-	-	-	-	-	-	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	0.893	-
[9–10]	53	Full crossing	-	-	-	-	-	-	9.434	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	1.887	-
[11–13]	77	Full crossing	-	-	-	-	-	-	16.883	-
		Aversion	-	-	-	-	-	-	0.649	-
		Unknown	-	-	-	-	-	-	1.948	-
[14–15]	50	Full crossing	-	-	-	-	-	-	21.000	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	2.000	-
[16–19]	64	Full crossing	-	-	-	-	-	-	23.438	-
		Aversion	-	-	-	-	-	-	0.781	-
		Unknown	-	-	-	-	-	-	3.906	-

Number of human activities per day	Number of days in this bin	Species	Moose *Alces alces*	Mouse spp. *Mus* spp.	Muskrat *Ondatra zibethicus*	North American beaver *Castor canadensis*	North American porcupine *Erethizon dorsatum*	North American river otter *Lontra canadensis*	Raccoon *Procyon lotor*	Rat spp. *Rattus* spp.
		Type of detection Sum of detections	5	26	26	1	18	7	1586	20
[20–22]	58	Full crossing	-	-	-	-	-	-	86.207	-
		Aversion	-	-	-	-	-	-	0.862	-
		Unknown	-	-	-	-	-	-	1.724	-
[23–26]	63	Full crossing	-	-	-	-	-	-	19.048	-
		Aversion	-	-	-	-	-	-	3.968	-
		Unknown	-	-	-	-	-	-	4.762	-
[27–30]	57	Full crossing	-	-	-	-	-	-	57.895	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	3.509	-
[31–35]	50	Full crossing	-	-	-	-	-	-	38.000	-
		Aversion	-	-	-	-	-	-	1.000	-
		Unknown	-	-	-	-	-	-	2.000	-
[36–44]	50	Full crossing	-	-	-	-	-	-	61.000	-
		Aversion	-	-	-	-	-	-	8.000	-
		Unknown	-	-	-	-	-	-	6.000	-
[45–67]	53	Full crossing	-	-	-	-	-	-	144.340	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	12.264	-
[68–120]	24	Full crossing	-	-	-	-	-	-	93.750	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	4.167	-

Table A3.

Number of human activities per day	Number of days in this bin	Species	Red fox *Vulpes vulpes*	Rodent spp.	Snowshoe hare *Lepus americanus*	Squirrel spp. *Sciurus* spp.	Striped skunk *Mephitis mephitis*	Weasel *Mustela erminea*	White-tailed deer *Odocoileus virginianus*	Unknown
		Type of detection Sum of detections	461	9	14	86	4	2	1106	9
[0]	2767	Full crossing	2.024	-	0.036	0.217	0.072	0.018	0.632	0.018
		Aversion	3.704	0.163	0.145	1.175	-	-	7.553	0.072
		Unknown	0.434	-	-	0.072	-	-	0.253	-
[1]	221	Full crossing	1.584	-	-	-	-	-	2.941	-
		Aversion	0.226	-	-	-	-	-	7.014	-
		Unknown	0.226	-	-	-	-	-	0.679	-
[2]	353	Full crossing	1.416	-	-	0.142	-	-	6.941	0.142
		Aversion	0.425	-	0.283	0.142	-	-	10.765	-
		Unknown	0.567	-	-	-	-	-	1.558	-
[3]	288	Full crossing	2.951	-	-	-	-	0.174	5.556	-
		Aversion	-	-	-	-	-	-	3.993	-
		Unknown	0.174	-	-	-	-	-	0.694	-
[4]	264	Full crossing	3.030	-	-	-	-	-	6.818	-
		Aversion	0.189	-	0.189	-	-	-	4.356	-
		Unknown	0.189	-	-	-	-	-	0.568	-
[5]	152	Full crossing	1.316	-	0.329	-	-	-	8.553	-
		Aversion	0.658	-	-	-	-	-	5.592	0.329
		Unknown	0.329	-	-	-	-	-	2.961	-

Number of human activities per day	Number of days in this bin	Species	Red fox *Vulpes vulpes*	Rodent spp.	Snowshoe hare *Lepus americanus*	Squirrel spp. *Sciurus* spp.	Striped skunk *Mephitis mephitis*	Weasel *Mustela erminea*	White-tailed deer *Odocoileus virginianus*	Unknown
		Type of detection Sum of detections	461	9	14	86	4	2	1106	9
[6]	119	Full crossing	4.202	-	-	-	-	-	2.941	-
		Aversion	1.681	-	-	0.840	-	-	2.521	-
		Unknown	0.420	-	-	-	-	-	3.361	-
[7]	79	Full crossing	6.329	-	-	-	-	-	0.633	-
		Aversion	1.266	-	-	-	-	-	5.696	-
		Unknown	-	-	-	-	-	-	3.165	-
[8]	56	Full crossing	0.893	-	-	-	-	-	0.893	-
		Aversion	-	-	-	-	-	-	14.286	-
		Unknown	-	-	-	-	-	-	-	0.893
[9–10]	53	Full crossing	0.943	-	-	-	-	-	-	-
		Aversion	-	-	-	-	-	-	3.774	-
		Unknown	-	-	-	-	-	-	2.830	-
[11–13]	77	Full crossing	3.247	-	-	-	-	-	1.948	-
		Aversion	-	-	-	-	-	-	2.597	-
		Unknown	0.649	-	-	-	-	-	0.649	-
[14–15]	50	Full crossing	-	-	-	-	-	-	2.000	-
		Aversion	-	-	-	-	-	-	5.000	1.000
		Unknown	-	-	-	-	-	-	1.000	-
[16–19]	64	Full crossing	-	-	-	-	-	-	-	-
		Aversion	-	-	-	-	-	-	1.563	-
		Unknown	-	-	-	-	-	-	0.781	-
[20–22]	58	Full crossing	-	-	-	-	-	-	3.448	-
		Aversion	-	-	-	-	-	-	2.586	-
		Unknown	-	-	-	-	-	-	1.724	-
[23–26]	63	Full crossing	0.794	-	-	-	-	-	3.175	-
		Aversion	-	-	-	-	-	-	3.968	-
		Unknown	-	-	-	-	-	-	-	-
[27–30]	57	Full crossing	-	-	-	-	-	-	-	-
		Aversion	3.509	-	-	-	-	-	1.754	-
		Unknown	-	-	-	-	-	-	2.632	-
[31–35]	50	Full crossing	1.000	-	-	-	-	-	2.000	-
		Aversion	-	-	-	-	-	-	1.000	-
		Unknown	-	-	-	-	-	-	6.000	-
[36–44]	50	Full crossing	-	-	-	-	-	-	2.000	-
		Aversion	-	-	-	-	-	-	-	-
		Unknown	-	-	-	-	-	-	1.000	-
[45–67]	53	Full crossing	-	-	-	-	-	-	2.830	-
		Aversion	0.943	-	-	-	-	-	5.660	-
		Unknown	-	-	-	-	-	-	3.774	-
[68–120]	24	Full crossing	-	-	-	-	-	-	-	-
		Aversion	-	-	-	-	-	-	6.250	-
		Unknown	2.083	-	-	-	-	-	-	-