PERFORMANCE MEASURES OF ROAD CROSSING STRUCTURES FROM RELATIVE MOVEMENT RATES OF LARGE MAMMALS

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Performance Measures of Road Crossing Structures from Relative Movement Rates of Large Mammals

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In recent decades, there has been an increase of engineering projects that seek to mitigate the barrier effect roads impose on wildlife by installing wildlife crossing structures that promote permeability of the road corridor. The 41 fish and wildlife crossing structures installed along a 90km stretch of US Highway 93 on the Flathead Indian Reservation in western Montana, represent one of the most extensive of such projects in North America. As mitigation efforts are increasingly considered and implemented in road construction projects, the need to assess these structures' effectiveness grows. This study is the first to compare observations of animal movement rates at structures to expected frequencies estimated from observations using the same sampling methodology, within the same time-step, and in contiguously adjacent habitat. I investigated performance measures of wildlife use for 15 congruent crossing structures installed on US Highway 93 on the Flathead Indian Reservation between Evaro and Polson, Montana for one field season between April and November 2015. Across all structures studies, large mammals were 2.6 times more likely to use crossing structures. As groups, deer and carnivores were 2.7 and 1.7 times as likely to use structures on average, respectively. Despite significantly positive corridor-wide performance, differentials for individual crossing structures varied considerably from -1.15 to 6.46 average movements per day. This highlights the importance of using many congruent structures as replicates to determine performance measures. This study illustrates an efficient and rigorous methodology for rapidly assessing the performance of wildlife crossing structures that can be applied to mitigation projects at any scale.

1. Introduction

As human populations grow and expand, transportation infrastructure connects disparate human communities while simultaneously disconnecting wildlife populations. At over 6.5 million km in length within the United States alone (USDOT 2014) and a forecast of 25 million km globally by 2050 (Dulac 2013), the road system is easily the most extensive, direct impact humans have on the ecosystem (Forman 2003). Forman (1998) described the relationship between the road system and the environment as two giants in an uncomfortable embrace—with the road network superimposed upon preexisting, ecological dynamics of the land. Roads and their associated impacts affect wildlife in myriad ways. Roads create direct habitat loss; induce avoidance behavior by wildlife; lead to direct mortality; subdivide populations; alter landscape scale spatial patterns, inhibiting wildlife movement; and provide a vector for the introduction of invasive species, poaching, and further development; to name only a few effects (Forman & Alexander 1998; Trobulak & Frissell 2000; Forman et al. 2003; Coffin 2007).

Although most roads in the U.S. were built in an era prior to ecological understanding of their impacts (Forman 1998), in recent decades the threat of roads to wildlife populations has been increasingly addressed through the inclusion of animal crossing features into road planning projects (Glista et al. 2009; Grilo et al. 2010; Kociolek et al. 2015). Unfortunately, wildlife and ecosystem concerns typically do not enter road planning projects until very late in the process when budgets are already stretched and physical or design limitations may already be in place (Cramer & Bissonette 2007). Projects, therefore, tend to bias mitigation toward traditional transportation priorities, such as efficiency and safety (for instance, by reducing the presence of wildlife on roads and wildlife-vehicle collisions) rather than ecological or environmental priorities.

The reconstruction of US Highway 93 (US93) in western Montana is an exemplar of wildlife mitigation efforts that incorporated ecological values into the earliest stages of planning (Kroll 2015). In designing the new highway, planners endeavored to protect the "integrity and character" of the landscape, "premised on the idea that the road is a visitor and that it should…be respectful of the land and Sense of Place" of the Confederated Salish and Kootenai Tribes' culture (Marshik et al. 2001: 248). This included a goal to mitigate habitat fragmentation and restore connectivity of wildlife species that are considered both natural and cultural resources for the Tribes (Marshik et al. 2001; Hardy et al. 2007). Between 2005 and 2010, 41 fish and wildlife crossing structures and approximately 28.0 km (17.4 miles) of wildlife exclusion fencing (along 14.0 km of road) were installed on a 90 km (56 mile) stretch of US 93 from Evaro to Polson, Montana (Huijser et al. 2015).

Roads do not only affect the land directly beneath them—their impact bleeds out from the road itself as direct alterations result in secondary and tertiary effects. This area encumbered by this dispersed impact is called the "road effect zone" (Forman 1999). The road effect zone can be quite expansive for large mammals at the population scale with up to 38% reductions in animal abundance as far away as 17 km from road infrastructure (Benitez-Lopez et al. 2010). The road effect zone contracts when considered at the scale of individual animal behavior, however. It has been shown that mule deer exhibit road avoidance primarily within 200m of roads and in open cover (Rost and Bailey 1979). White-tail deer, in contrast, exhibit very little road avoidance (Carbaugh et al. 1975). In general, ungulate species exhibit avoidance at very local scale (Dyer et al. 2001, Papouchis et al. 2001, Sawyer et al. 2007, Keller and Bender 2007, Meisingset et al 2013). While the road effect zone may completely exclude some animals, it is clear that many develop at least a limited tolerance. Crossing structures like those installed in the US 93 reconstruction are primarily intended for those tolerant animals found within the road effect zone in close enough proximity to benefit from uses of such measures.

The structures vary considerably in design and allow animals to pass under (i.e. underpasses, culverts, over-span bridges, etc.) or over (i.e. "animal bridges") the road corridor (Huijser et al. 2008 and Glista et al. 2009 provide good overviews of structure designs used globally). A few large projects employing crossing structures intended to ameliorate the effect of roads on wildlife have been completed (e.g. Canada (Clevenger et al. 2002), Florida (Foster & Humphrey 1995), and Arizona (Dodd et al. 2007)) or planned (Washington (WSDOT 2008)) in the North America; however, the US93 project from Hamilton to Polson, is one of the most extensive to date. Despite the increased adoption and implementation of mitigation measures and considerable monetary investments, performance standards for the majority of crossing structure designs have not been investigated. This makes US 93 an important venue to improve our understanding.

In this study, I asked the following questions:

- Are underpasses designed for large mammals used at similar rates as random points in the immediately surrounding habitat? And,
- How does this vary by species or clade?

A number of methods have been used to assess the effectiveness of road mitigation measures and moves have been made to standardize these methods (van der Grift and van der Ree 2015). Specifically on the US 93 corridor, studies have monitored reduction in wildlife-vehicle collision, crossing rates (Huijser et al. 2015) and acceptance rates (Purdum 2013) at many of the project's structures. These studies are valuable; however, none directly assess the extent a structure contributes to wildlife movement through the structure in relation to animals' unobstructed movements in the surrounding habitat. Studies from other projects have addressed this question through before-after or control-treatment designs to establish expected crossing frequencies. Huijser et al. (2008) point out that for these studies to be informative, they must account for spatial (between treatment and control sites) and temporal (between before and after) variability, for instance, population size, traffic volumes, etc. that may confound comparisons. Previous studies have employed abundance estimates (from, for instance, DNA, tracking beds, cameras, scat counts, observational transects, radio telemetry, etc.) to interpolate expected crossing rates (van der Ree et al. 2007). These methods can be spurious because detection rates and confidence in estimators vary, especially across time and across species.

Van der Grift and van der Ree (2015) suggest that control plots should be established well outside of the road effect zone in order to establish comparison to pre-road conditions. In the case of this study, the primary goal was to investigate how crossing rates compare to movements in habitat within the road effect zone, not to pre-road conditions; so, I chose to survey the roadside area that included the road effect zone. The animals that approach the structures are already road effect tolerant, are most likely to cross through the structures, and generally represent species that we are most concerned with. A strength of this study is the use of the same detection methods in the same time step to both measure observed crossing rates and estimate expected crossing frequencies from adjacent reference plots.

2. Methods

I monitored 15 wildlife crossing structures along US Highway 93 on the Flathead Indiana Reservation in western Montana (Figure 1). This 90.6 km (56.3 mi) section of highway from Evaro to Polson, MT was slated for reconstruction in 2000 and to date includes 41 wildlife crossing structures of various designs from small box culverts to a vegetated overpass, as well as disjointed wildlife fencing (Huijser et al. 2015).

The road runs north-south through the Flathead Valley, along the base of the 2,993 m (9.828 ft) Mission Range and Rattlesnake Range which bound the valley to the east and southeast. Flathead Lake lies at the northern terminus of the road section and the Rattlesnake Divide Mountain Range to the south. The road runs through a heterogeneous landscape comprised of shrub, grassland, wetland habitats and agricultural lands in the valley bottom and forest habitat dominated by Ponderosa pine (*Pinus ponderosa*) near the Evaro area (see Supplemental Materials A). The road bifurcates a large wetland complex in the Ninepipes area that has not yet been reconstructed to include wildlife crossing structures.

This section of highway receives an average of 7,059 vehicles per day (MDT 2014). The roadway design includes both divided and undivided, 4 and 3 lane highway and accommodates a maximum speed limit of 70 miles per hour (113 kmh), reducing to 25-45 mph (40-72 kmh) in towns.

In order to assess the effectiveness of the road project's goal to decrease fragmentation, wildlife presence and behavior was monitored between March and

November 2015 and observed crossing rates were compared to expected rates to calculate performance measures for species (Hardy et al. 2004; van der Grift 2013).

Fifteen structures representing the most common design: elliptical corrugated metal underpasses with entrances approximately 7.32m wide by 5.55m high (width range = 6.86m to 7.95m, height range = 3.65m to 5.55m) and 25.6m long (length range = 14.6m to 40 m), were monitored (Table 1). All structures include concrete retaining walls that extend out from the structure at approximately 35 degree angle to the road and extend to approximately 10m. Trail cameras (HyperFire PC900 Reconyx™; Holmen, WI) were placed at the structure and in the adjacent habitat approximately 1m from the ground (Figure 2). This model of camera emits no visible flash; provides for infrared illumination up to a distance of 50ft; utilizes an appropriate sense range, trigger speed, and recovery time for capturing medium and large mammals; and operates within weather ranges typical of the field site. A point 10m from the cameras was demarcated with a stake, and only animals and their associated group that crossed within 10m were considered for analysis. The entrances to the structures are generally slightly shorter than 10m. In order to maintain consistent measurements, I moved the camera out from the entrance along the angled retaining wall until a 10m viewing distance parallel was reached (usually 1-2m from the entrance). A stake was placed at the 10m distance along the opposite retaining wall and records were analyzed exactly as those in the surrounding. This standardized the observational range between structure entrances and control plots and limited observations to those well within the camera's detection range.

I defined a structure's success at mitigating the road barrier, as observing equal movement rates at the structure and in the surrounding environment (see Figure 3). In other words, an animal should be just as likely to move past a random point in the habitat as through a crossing structure. At structures associated with sufficient lengths of wildlife exclusion fencing, animals are limited to movements in the surrounding (movement type a in Fig. 3) or crossing through the structure (movement type b in Fig. 3). Animals at sites without sufficient exclusion fencing also have the opportunity to cross the road at-grade (movement type c in Fig. 3). If the proportion of animal movements in the surrounding habitat is greater than those observed at the structure ($b-(a+c) < 0$), the structure is not completely successful in encouraging animal passage. In this case, some animals are either choosing to cross at grade or choosing not to cross the road. In the best case, animals will chose to preferentially use the crossing structure rather than crossing at grade or avoiding the road corridor ($b-(a+c) > 0$). A null model study design was employed to test the hypothesis that movements at crossing structures did not significantly differ from expected (calculated from control plots) (Hardy et al. 2004).

Van der Grift et al. (2013) and Huijser et al. (2008) point out the potential for confounding variables to vitiate the inferences made from such studies. The current study attenuated this problem by a.) selecting control plots immediately adjacent to and corresponding to the structure being tested to minimize landscape variability, b.) monitoring control plots and structure in the same time-step to minimize temporal variability, and c.) selecting structures with very similar designs to limit variability of physical attributes. This is the first study using remote cameras to compare observations of animal use at structures to expected frequencies estimated from observations using the same sampling methodology, within the same time-step, and in contiguously adjacent habitat.

Control plots were established in the habitat immediately adjacent to the structure by randomly selecting points at least 50m apart within a 300m by 300m area centered at the structure (following previous methodology by Purdum (2013))(see Figure 2). The 300m boundary reflects the minimum daily active radius of the most common species of concern, white-tailed deer (Dusek et al. 1989). The sampling unit (herein referred to as movements per day) was calculated by averaging the number of movements recorded across a subset of cameras (i.e. only cameras at structure entrances, only cameras from control plots, or only cameras from control plots on one side of the road) and dividing by the number of days that the cameras recorded at the site and the number of cameras in each subset by location (see equation)

$$\sum_{i=1}^{d} \frac{Movements_i}{d * c}$$

d = full 24-hour days recorded
c = fully functioning cameras at site

A movement was defined as any animal recorded within 10m of the camera, separated by at least 5 minutes from the next observation. Allen (2011) found that, in the same study area, for groups of the three most common species (white-tailed deer, mule deer, and bear), either all or none of the groups crossed through road crossing points. Therefore, for obvious groups of animal observed at control sites, all animals in the group were recorded as individual movements if at least one animal crossed within 10m, even if the others did not. This calibrates movements in the control plots to animal movements at the structure where the retaining wall forces all animals in the group to enter within the 10m distance and eliminates a bias toward success in performance measures.

A minimum expected crossing rate was established using methodology similar to van der Grift et al. (2013) and defined as the mean observed movements per day at the control plots. This rate provides an estimate of movements of type *a* (and *c* where structures associate with fencing) from Figure 3. Comparison of expected crossing rates and observed crossing rates at the structure (movement type *b* in Fig. 3) yielded a performance measure for each species or species group (Table 2).

As an ancillary test to determine how much influence avoidance of the road effect zone had on the movement patterns observed within the 300 corridor, I plotted the average daily movements recorded by each camera at control plots against the distance from centerline of the road and fit a linear model of the relationship (Figure 4).

For many sites, habitat and other variables that may impact animal behavior differ between sides of the road at the same site. Therefore, I conducted further analysis using two-sided paired t-tests computed to compare observations from control plots on either side of the road to the structure independently to investigate the potential that side-specific habitat preferences may influence overall performance measures for a given structure (Table 3).

The presence of wildlife exclusion fencing and fencing length is also variable between sites and could have an impact on animals' use of the crossing structures (Huijser et al. 2016). To examine the effects of fencing on wildlife movement rates, I tested for correlation between the distance to the nearest alternative crossing opportunity and movement differentials between the structure and control plots (Figure 5). At structures associated with exclusion fence, I defined the nearest crossing opportunity as either the nearest fence end or the nearest alternative crossing structure, depending on which was closer. For structures without fences at which animals can cross at-grade, I defined the distance to the nearest alternative as 0m.

A final, overall performance measure of all structures surveyed corridor-wide was conducted for large mammals, deer and carnivores subsets using boostrapping procedures (Efron & Tibshirani 1993), resampling sites and then days at each structure with replacement over 100,000 iterations to compute the mean movements per day at the structure and in the control plot. Bias-corrected and accelerated boostrap 95% confidence intervals were further calculated. Performance measures for individual species (white-tailed deer, mule deer, black bear, coyote, and bobcat) were computed using identical procedures, but with 10,000 iterations. Only structures at which at least 3 observations of the species or group in question occurred were used in the corridor-wide assessment.

All statistical analyses were conducted using R version 3.2.3 (R Core Team 2015). Hypothesis tests using two-sided paired tests of movements per day were calculated for each site. Residual plots and Q-Q Normal plots of the residuals were plotted to assess the normality of the distribution of the paired differences. For analysis of subsets of data in which normality of the distribution was questionable (for instance, when subsetting by species or side of the road), Wilcoxon exact two-sided rank tests were calculated using package "exactRankTests" in R (Hothorn and Hornik 2015). Prior to any analysis, collinearity between days was tested using autocorrelation analysis.

3. Results

During the study, each of 15 structures and adjacent habitat were observed for a median of 14 days (range = 12 to 20). Only movements occurring on days in which cameras recorded full, 24-hour periods and from cameras that recorded for the full tenure at the site were considered in the analysis.

Each unique movement record was aggregated by species and summed for each day. A wide variety of wild species (excluding human, domestic pets, and livestock) were observed, including white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), black bear (*Ursus americanus*), moose (*Alces alces*), elk (*Cervus canadensis*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), raccoon (*Procyon lotor*), striped skunk (*Mephitis mephitis*), American badger (*Taxidea taxus*), mountain cottontail rabbit (*Sylvilagus nuttallii*), red squirrel (*Tamiasciurus hudsonicus*), bat (sp. unknown), ring-necked pheasant (*Phasianus colchicus*), turkey (*Meleagris gallopavo*), grouse (sp. unknown), magpie (*Pica hudsonia*), great blue heron (*Ardea herodias*), western meadowlark (*Sturnella neglecta*), starling (*Sturnus vulgaris*), red-tailed hawk (*Buteo jamaicensis*), Canada goose (*Branta canadensis*), and great-horned owl (*Strix nebulosa*) (Table 4). Two mountain lions (*Puma concolor*) observations were recorded; however, they were not included in the analysis as they fell on partial days or from malfunctioning cameras.

Wild species were grouped by guild for further analysis. Groupings included Large Mammals (white-tailed deer, mule deer, moose, elk, black bear, coyote, bobcat, raccoon, badger, and striped skunk), Carnivores (order Carnivora—black bear, coyote, bobcat, raccoon, badger, and striped skunk), and Deer (white-tailed and mule deer). An ungulate group (including both deer species, moose, and elk) was considered, but because moose and elk comprise only less than 1% of total ungulate observations and deer are the main species of concern for the Department of Transportation, only deer species were analyzed (Table 4).

A total of 2926 wild animal movements were recorded (at the structures and control plots), with large mammal movements comprising 2798 (95.6%) (Table 4). Deer (white-tailed and mule deer) comprised 94.0% of large mammal observations, while carnivores comprised 5.9% and other ungulates (moose and elk) comprised 0.1%. Of the total movements recorded, 886 (30.3%) were observed at crossing structures and 2040 (69.7%) were observed at control sites. The number of total movements recorded varied among the sites (mean = 193, max = 381, min = 34). The number of movements per day also varied among sites (mean = 1.22, SD = .84, max = 2.47, min = 0.23).

I performed a two-sided paired t-test on the daily differential between movements per day at the structure and corresponding control plots to test the hypothesis that daily movements at the structure did not significantly differ from expected values at control sites. The average differential use by large mammals varied among structures (mean = 1.26, SD = 2.15, max = 6.45, min = -0.14), but at the majority of structures (11 of 15) large mammals showed positive performance differentials (Table 2, Figure 6.1). Most structures (n = 8, 53.3%) did not exhibit differential use by large mammals that significantly deviated from zero. Many structures (n = 6, 40%) did exhibit strong ($p < .001$) to moderately strong ($p < .05$) evidence to suggest that large mammals tend to move through the crossing structures more frequently than observed in the surrounding habitat.

When partitioned by guild, deer exhibited a positive performance differential for most structures (10 of 15)(Table 2, Figure 6.2). Results of hypothesis tests show that deer exhibit a significant, negative use differential for only one structure (Structure 12), and significant, positive values for 5 structures (Structures 2, 6, 13, 14, 15). Result for the remaining nine structures did not provide evidence to suggest that use differentials differ from zero (Table 2).

Average daily differential use of structures by carnivores was closer to zero and varied less (mean = 0.04, SD=1.3, max= 0.40, min= -0.09)(Table2, Figure 6.3). Two sites, structures 1 and 13, were excluded from the carnivore analysis due to a lack of carnivore observations (n=0 and n=1, respectively). Hypothesis testing for two structures (number 11 and 14) suggests evidence (p=.01) that carnivores use the structure less than the surrounding habitat, while only one structure (number 5) shows evidence for positive differential use at the structure (Table 2). Most structures (n=10, 76.9%) did not show evidence that carnivore movement differentials differed from zero.

Corridor-wide, large mammals showed a significant propensity to use the structures and were 2.55 times more likely to move through the structures than at a random point in the surrounding environment (Table 6). I further subset animals by groups and species, only including structures at which the species or group occurred during the sampling period. Deer, as a group, exhibited similar performance ratios to large mammals and were 2.72 times more likely to use the structure. Carnivores utilized the structures 1.67 times as often as expected. Performance ratios for White-tailed deer were similar to the Deer group at 2.58, however, Mule deer showed an impressive 20.37 times greater likelihood to use the structures than expected. All individual carnivore species exhibited performance ratios of close to zero (<0.001).

Figure 4 shows the relationship of the road effect zone on movement rates recorded at individual cameras within control plots. I found no evidence of correlation between the rate of large mammal movements observed at each camera placement and its distance from the road. A linear regression line fitted to the overall data exhibits very little evidence of an effect of distance from the road with an increase of just 0.02 movements per day for every 100m increase in distance (R^2=0.018, p=0.11). When considering only camera locations with greater than 50% canopy cover, there is a negative relationship between distance from the road and movements observed, with a decrease of 0.02 movements per day for every 100m increased away from the road (R^2=.010, p=.43). Camera locations with less than 50% canopy cover showed a statistically significant increase as intuitively expected, but of only 0.01 movements per day for every 100m increase in distance (R^2=.126, p=.001).

Figure 5 shows the relationship of the movement differential between the structure and control plots for each site for both deer and carnivores when presented with increasing distances to the nearest crossing opportunity. Deer showed no evidence of a relationship between the distance to the nearest alternative crossing opportunity and differential movement rates (R^2=0.029, p=0.55). Carnivores exhibited evidence (R^2=0.61, p=0.002) of a positive relationship, with an increased differential of just 0.04 for every 100m increase in distance to nearest alternative.

4. Discussion

The lack of strong evidence for a road-effect gradient within the 300m distance surveyed indicates that the population of large mammals considered in this study did not avoid the road in the distance sampled. Visual and auditory stimuli have been linked with animals' avoidance of roads (Foreman and Alexander 1998), however the scale at which noise contributes to behavioral responses is inconsistent (Iglesias et al. 2012). Therefore, in more open habitats in which noise travels farther and in which lines of sight are longer, the road-effect zone should protract. So, it is intuitive that I found a positive association between the distance from roads and average daily movements recorded in open habitats (< 50% cover) and no evidence for a significant association in closed habitats (> 50% cover) (Figure 5). The association in open habitats, although statistically significant, is weak and biologically insignificant.

Wildlife crossings can provide conservation value in many ways and at many scales, however determining the conservation value of a given project depends on the intended purpose of the crossing structure (Clevenger and Waltho 2005). In the case of the US 93 project, mitigation efforts had two goals: 1.) minimize wildlife-vehicle collisions, and 2.) minimize habitat fragmentations, especially by allowing alternatives to at-grade crossings (Marshik et al. 2001; Hardy et al 2007; Huijser et al. 2015).

Overall, as a group and across all sites, large mammals were about 2.55 times more likely to move through the crossing structure than the surrounding environment with an average positive differential of 0.1 movements per day (se=0.08)(Table 6.). This suggests that the structures are fulfilling at least one of their intended purposes: to decrease fragmentation due to road barrier effects by promoting movement through the structures; however, it should be considered that this "corridor-wide" analysis only applies to road lengths that include underpasses, which are only a fraction of the total road length. Analysis considering individual structures also lends evidence of success, with only one structure, number 12, exhibiting a significantly negative movement differential for large mammals (Table 2).

By pooling movements per day, respectively, of each of the most common species (white-tailed deer, mule deer, black bear, coyote, and bobcat) across all sites at which that species occurred, I was able to see corridor-wide associations between movements at the structures for each species. With the exception of coyote, all species exhibited a positive average association with the structures compared to control plots. Corridor-wide, both deer species were more likely to move through the structure than control plots. Mule deer showed the strongest positive value, and were 20.37 times more likely to move through the structure than through the control plots with 0.12 more movements per day at the structure on average (se=0.19), while white-tailed deer were only 2.58 times more likely (Table 6). Mule deer's affinity for moving through US93 structures is surprising in light of studies that have shown mule deer to exhibit low acceptance rates at structure entrances compared to white-tailed deer (Gagnon et al. 2011; Purdum 2013). This might indicate that mule deer are more likely to use the structure to cross the road, but are more reticent of structures overall. Some of the discrepancy may also be accounted for by the variability in structure design examined in these studies and a difference in the approach distance used to calculate acceptance rates (Purdum 2014). Purdum (2014) surveyed a wide range of structure designs in his analysis including an over-span bridge and a vegetated overpass which correlated highly with white-tail deer acceptance rates. Lack of an exit-view and length of the structure correlated negatively with mule deer acceptance rates (Purdum 2014). Gagnon et al. (2011) studied structures that were on average 4 times longer than those studied on US 93. Limiting my study to relatively short structures and reducing structural variation which excluded structures highly preferred by white-tail deer, may account for the relatively high differential for mule compared to white-tail deer. It should also be noted that Mule deer only occurred at 5 structures, which is a small sample for this type of analysis. Two of the three most common carnivore species (black bear and bobcat) also exhibited a positive association for moving through the structure versus control plots, while coyote showed a slightly negative association (Table 6). None of the carnivore ratios differ substantially from zero; however, this may be due to low observation rates for these species in general, and a longer study period might illuminate trends more adequately.

Numerous studies have shown that large mammals, when presented with a linear barrier of variable resistance, will travel to find optimum sites to cross (e.g. Whittington 2004; Clevenger and Waltho 2005; Meisingset et al. 2013). Meisingset et al. (2013) found that the habitat type adjacent to a road influences crossing rates, with red deer crossing more frequently at flat, forested habitat than in rugged terrain or pastures. At some sites along the US 93 project corridor, habitat within the 300m control plot boundaries varied substantially between sides of the highway. For instance, in the Ravalli Curves section of the highway (sites number 5, 6, and 7) the west side of the road is characterized by flat, often wet, wooded and grassy riparian habitat, while the east side is characterized by steep, dry, pastures and brushy vegetation. Also, habitat in the Post Creek area (sites number 13 and 14) is characterized by grasslands and streamside habitat on the west side of the road and developed agricultural fields on the eastern side.

If habitat preferences lead animals to move about more frequently on one side of the highway, but much less frequently or along only a few defined trails on the opposite side, the negative differential in movement from one side of the highway could cancel out the positive differential from the other (or the reverse). In addition to habitat leading up to a structure, the entrance of the structure itself can influence animal movement. For instance, Gagnon et al. (2011) and Purdum (2013) both found that the ability to see through a crossing structure to the exit influenced acceptance rates. Along the length of the project corridor, animals have multiple options for crossing the road because fencing sections are not contiguous or absent, or where long sections of fencing is present, structures are close enough for animals to easily reach a nearby structure. When animals are presented with multiple crossing options within their daily active radii, they may exhibit assortative selection for given directionality. For instance, if habitat leading up to a structure entrance or structural attributes at the entrance are more favorable on one side than the opposite, animals may exhibit a crossing preference for only one direction and instead opt for a more favorable alternative crossing point to return.

In order to test if the effect of habitat on one side of the road was masking a significant overall pattern, I conducted hypothesis tests for movements independently for each side of the road compared to those at the structure (Table 5). By evaluating movement rates of each side independently, it is clear that in some cases, frequency of animal use varies with respect to habitat or structure variables on a particular side of the road; however, the sign of the association matched for both sides in every case. Thus, there does not seem to be a strong effect of side-specific features driving animal movement patterns for the structure included in this study.

It has been suggested that the use of tunnels by predators may prevent use of the same tunnels by prey species (Little et al. 2002; Mata et al. 2015). Purdum (2013) found that, along the US93 corridor, bobcat, black bear, and coyote tended to use the same structures. If the presence of predators negatively affects prey species, we would expect to see an inverse usage rate between carnivores and deer at an individual structure, which to some extent does seem to hold true, especially for close structures in which animals can easily choose to use a separate structure. Structures number 5 and 6 are adjacent and only

965m apart with wildlife exclusion fencing running almost continuously between (Figure 6.2 and 6.3). At structure 5 where carnivore use is highest, deer use is relatively low, whereas at structure 6 deer use is relatively very high while carnivore use is low (Figure 6.2 and 6.3). In contrast, structures number 14 and 15 are also very close, just 305m apart. Deer use at structures 14 and 15 remained constant despite large variability in carnivore use (Figures 6.2 and 6.3). Studies with longer observational windows should be conducted at these sites to test if use of predators influences deer crossing decisions.

More data should be collected and multivariate analysis needs to be conducted to determine what elements of crossing design or habitat features associated with the installation location of the structures promotes greatest permeability. In the case of the US 93 project, animals have multiple options for crossing the road because fencing sections are not contiguous or absent (Huijser et al. 2016). Where long sections of fencing has been installed, structures are close enough for animals to easily reach a nearby structure. When animals are presented with multiple crossing options within their daily active radii, they may exhibit selection for given directionality. Further studies using telemetry or visual tagging and camera traps needs to be conducted on similar sections of road with high densities of crossing structures and demonstrable side-specific crossing rates.

I tested the most obvious factor, distance to nearest alternative crossing structure and found no correlation for large mammals as a whole (Figure 4). When analyzed by clade, carnivores showed a statistically significant relationship with increased fencing barriers while deer showed no significant relationship (Figure 4). These results do not necessarily indicate that deer have no relationship to fencing. Fences were installed in locations along the corridor with known, high on-road mortality rates and were not included in areas where project planners thought they would be unnecessary for effective mitigation (Hardy et al. 2003; Huijser et al. 2015). Therefore, fence locations are already associated with locations at which habitat or road features promote the use of alternative crossings, and the corollary, fences are absent from locations where habitat and road features discourage crossings. Therefore, the intentional placement of fencing certainly confounds any association.

There are many benefits to the study design employed in this thesis. Using the same sampling method in the same time-step between the structure and control plots, and using relative rates, controlled for many potentially confounding variables like daily fluctuations in animal movement, temporal variations across different days or even years for historic data. Sampling across the putative road effect gradient for 300m immediately adjacent to the road controlled for habitat variation between control plots and the structure site. Also, the use of cameras provided much more definitive observations compared with tracking beds, pellet counts, and other remote sampling methods used in other road ecology studies. Finally, the shear abundance of structures in the US 93 corridor allowed for sampling of many, almost identically designed structures. To my knowledge, no other study has sampled so many congruent structures. Unlike other studies that sampled various structure designs and non-cotemporaneous sampling periods, this study provides more robust data for future multivariate analysis to consider the effect of habitat, fence length, and other variables of interest.

Due to the limited survey time at each site, this study is limited in extending inference across years and seasons. Replication of the study in subsequent years would provide stronger inference for trends across time.

Observation rates for carnivore species and especially cryptic carnivores like bobcats and mountain lions were considerably low. Future studies at sites with demonstrated carnivore presence for longer intervals would need to be conducted for more robust analysis of trends in carnivore use. The observation rates from this study could be used to inform a power analysis to determine the most effective sampling interval for future studies.

Acknowledgements:

The unprecedented, high density of wildlife crossing structures on the Flathead Reservation provided an incomparable study system for this project. Therefore, I am sincerely grateful to the Confederated Salish and Kootenai Tribes (CSKT) for permission to conduct research on tribal lands, to the Montana Department of Transportation for permission to conduct research at the structures and in the highway right of way corridor, and to the many private landowners who allowed me to access their lands to install wildlife cameras.

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My partner, Bayla Arietta, earned a very special thanks for her patience in my absence during field work and for serving me meals during too many all-night data entry sessions. Finally, I thank my father who inspired in me an unabashed awe and lifelong curiosity in the natural world; and who, if he were still here, would have been incredibly proud of this project.

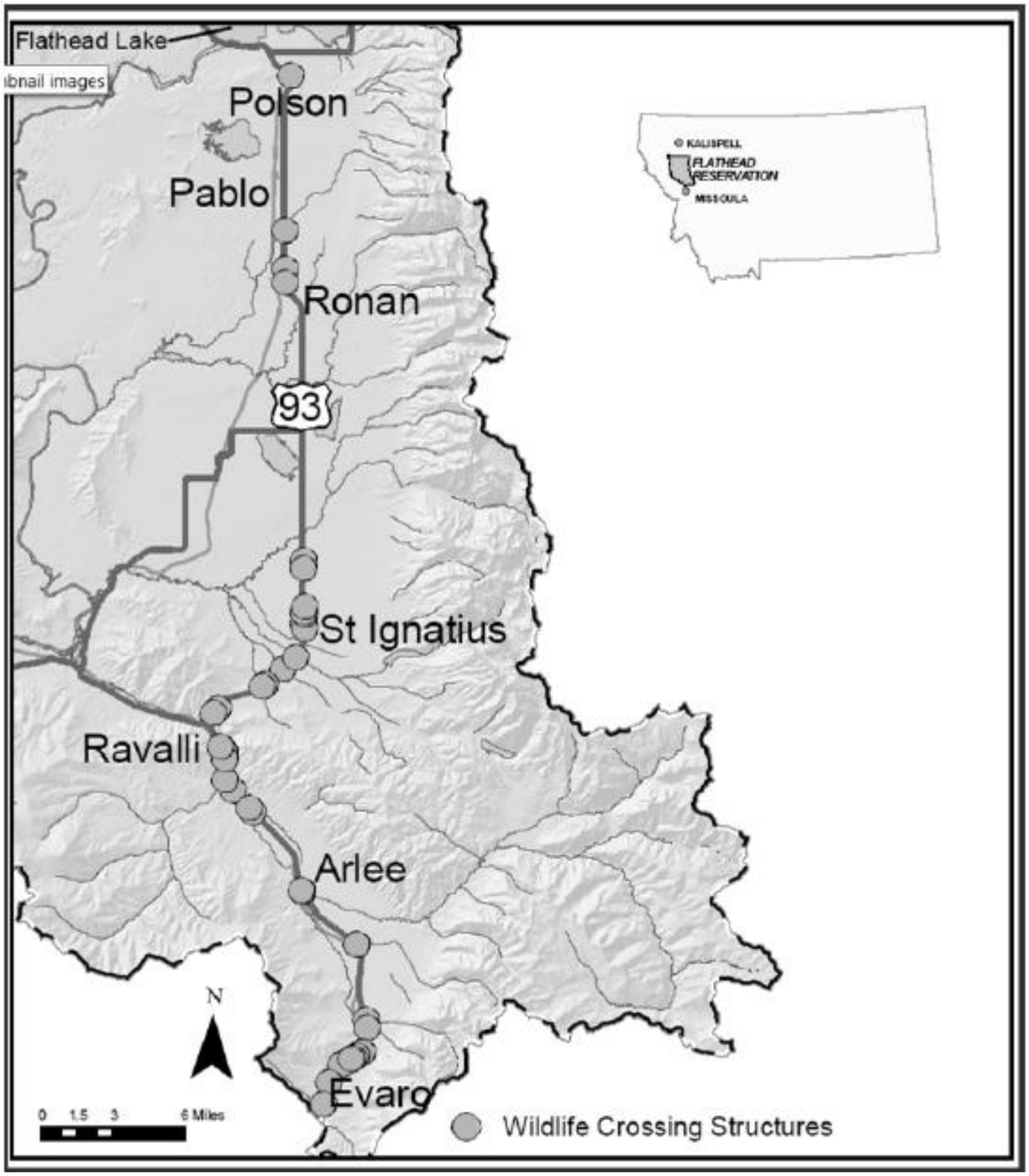


Figure 1. Map of the Flathead Indiana Reservation in western Montana showing major highways including US93 and the location of 41 fish and wildlife crossing structures.

Table 1. Physical attributes of elliptical, corrugated metal wildlife crossing structures surveyed on US 93 through the Flathead Indian Reservation, Montana.

Site Name	Site Code	Struct. Num.	Width (m)	Height (m)	Length (m)	Fencing	Year Constructed
North Evaro	NEV	1	7.75	5.10	25.8	N	2010
Finley Creek #1	FC1	2	7.95	5.55	32.0	Y	2010
Finely Creek #2	FC2	3	7.95	5.55	21.9	Y	2010
Finely Creek #3	FC3	4	7.75	5.10	24.7	Y	2010
Ravalli Curves #1	RC1	5	6.86	4.78	22.0	Y	2006
Ravalli Curves #2	RC2	6	6.86	4.78	25.6	Y	2006
Copper Creek	COPC	7	7.75	5.10	18.3	Y	2006
Ravalli Hills #1	RH1	8	7.30	5.20	39.0	Y	2007
Ravalli Hills #2	RH2	9	7.30	5.20	31.2	Y	2007
Pistol Creek #1	PIC1	10	7.30	5.20	40.0	N	2007
Pistol Creek #2	PIC2	11	7.30	5.20	40.0	N	2007
Sabine Creek	SABC	12	7.32	3.65	14.6	Y	2007
Post Creek #1	POC1	13	7.32	4.75	28.8	Y	2007
Post Creek #2	POC2	14	7.32	4.75	22.0	Y	2007
Post Creek #3	POC3	15	7.32	3.90	19.5	Y	2007

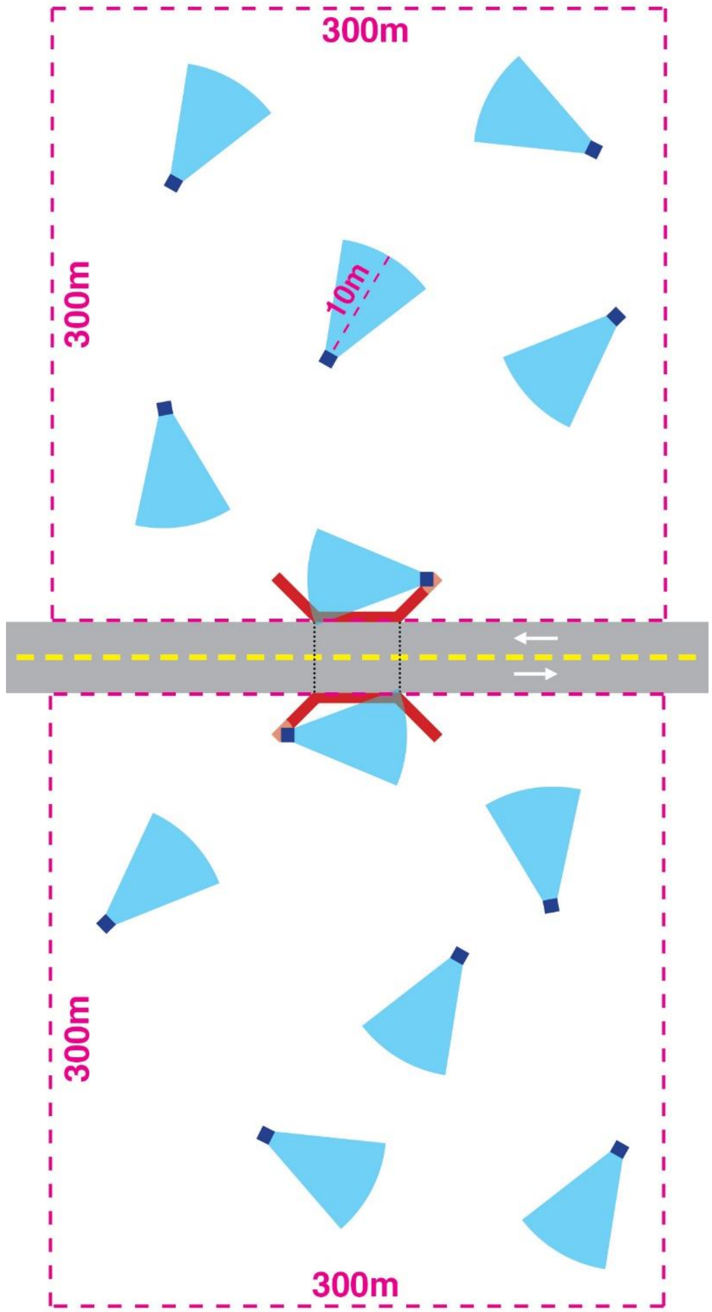


Figure 2. Camera placements in relation to a highway wildlife crossing structure.*

Twelve HyperFire PC900 Reconyx™ trail cameras (dark squares indicate cameras, light blue indicates approximate 40 degree sampling window) were installed at each site for approximately two weeks. Two cameras were installed at the structure to capture animal movements entering and leaving in the structure. Ten cameras were placed in control plots with five cameras installed at random points at least 50m apart within a 300m square area adjacent to each side of the structure. Cameras were installed approximately 3m from the ground and a marker was installed to demarcate a 10m viewing distance commensurate with the viewing distance of the cameras at the structure entrance. At the structure entrances narrower than 10m, the camera was moved outward along the retaining wall (solid red lines) until a 10m distance parallel to the road between the camera and opposite retaining wall could be attained to match all view distances.

* Figure is not drawn to scale.

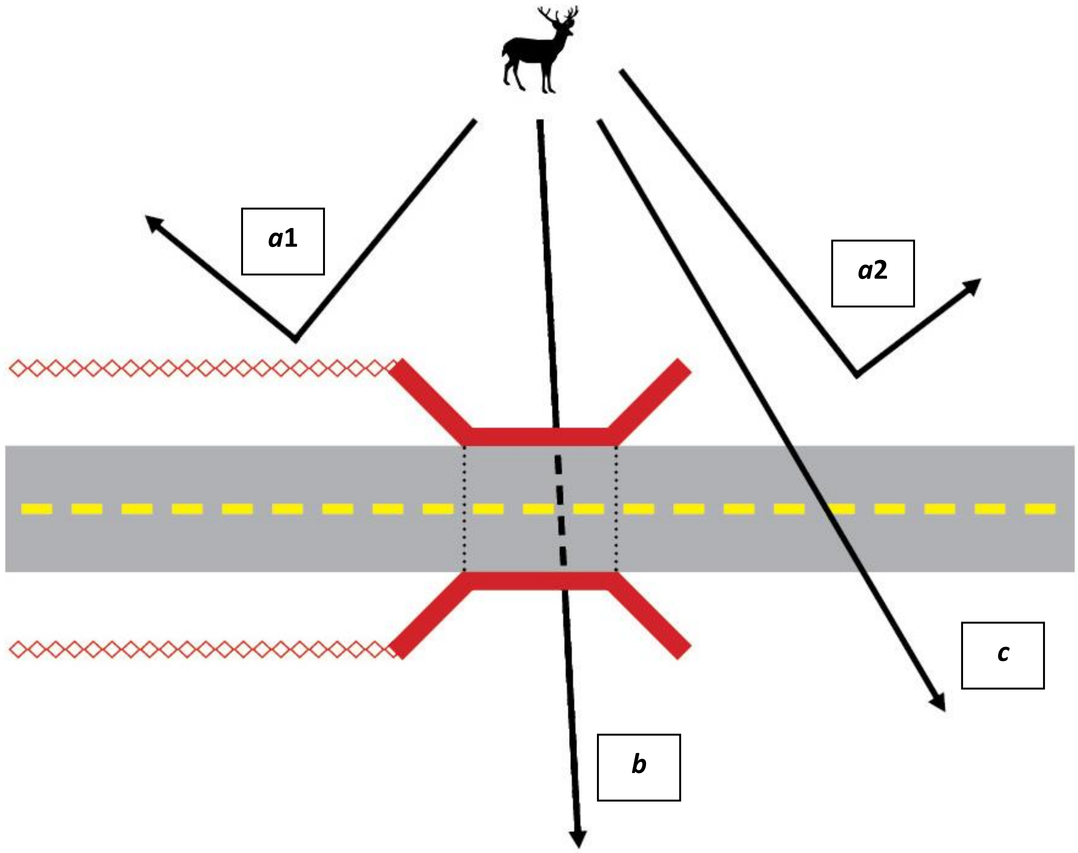


Figure 3. Animal movements in relation to a road with a wildlife crossing underpass and partial wildlife exclusion fencing.

When encountering a road barrier, animals can react in three basic ways: the animal may choose not to cross the barrier due to exclusion fencing (red crosshatches)(*a*1) or negative behavioral response (*a*2), the animal may cross through the structure (*b*), or the animal may cross at an alternative location (*c*)(either at-grade as shown or through a different nearby crossing structure).

Table 2. Average daily differential use of structures versus surrounding habitat for large mammals, deer, and carnivores.

		Large Mammals			Deer			Carnivores		
Site	Structure Number	Average Difference	SE	P-value	Average Difference	SE	P-value	Average Difference	SE	P-value
NEV	**1**	0.29	0.47	0.484	0.30	0.47	0.484	NA	NA	NA
FC1	**2**	5.68	0.79	0.001	5.65	0.83	0.001	0.04	0.07	0.533
FC2	**3**	-0.41	0.35	0.823	-0.47	0.31	0.852	0.02	0.09	0.813
FC3	**4**	0.54	0.39	0.374	0.50	0.39	0.373	0.05	0.04	0.219
RC1	**5**	1.60	0.55	0.050	1.20	0.51	0.173	0.40	0.14	0.008
RC2	**6**	6.46	2.06	0.006	6.56	2.02	0.006	-0.07	0.07	0.294
COPC	**7**	0.02	0.15	0.357	-0.15	0.07	0.317	0.17	0.13	0.175
RH1	**8**	0.94	0.36	0.107	0.89	0.37	0.220	0.05	0.08	0.497
RH2	**9**	-0.15	0.18	0.144	-0.08	0.16	0.273	-0.07	0.05	0.111
PIC1	**10**	-0.21	0.16	0.893	-0.22	0.15	0.593	-0.02	0.06	0.691
PIC2	**11**	0.04	0.30	0.156	0.13	0.30	0.496	-0.09	0.03	0.005
SABC	**12**	-1.15	0.29	0.033	-1.09	0.29	0.039	-0.05	0.04	0.205
POC1	**13**	0.15	0.61	0.005	0.16	0.61	0.005	NA	NA	NA
POC2	**14**	2.39	1.02	0.035	2.44	1.02	0.033	-0.06	0.02	0.013
POC3	**15**	2.46	0.92	0.006	2.26	0.94	0.007	-0.03	0.02	0.104
Mean		**1.24**			**1.21**			**0.03**		
s		**2.20**			**2.21**			**0.12**		

*Highlighted cells indicate statistical significance at the P<.05 level.

Table 3. Daily average differential use of structures versus surrounding habitat by large mammals, deer, and carnivores by side of road*

		Large Mammal				Deer				Carnivores			
		East		West		East		West		East		West	
Site	#	Diff.	*p*	Diff.	*p*	Diff.	*p*	Diff.	*p*	Diff.	*p*	Diff.	*p*
NEV	1	0.03	0.484	0.56	0.285	0.03	0.484	0.57	0.180	NA	NA	NA	NA
FC1	2	3.81	0.001	0.00	0.001	5.35	0.001	5.95	0.001	0.03	1.000	0.06	0.655
FC2	3	0.05	0.823	-0.90	0.054	-0.01	0.852	-0.94	0.021	0.08	0.680	-0.04	0.622
FC3	4	0.44	0.374	0.67	0.063	0.41	0.373	0.62	0.061	0.03	0.655	0.08	0.157
RC1	5	1.44	0.050	1.76	0.001	1.00	0.173	1.40	0.002	0.44	0.007	0.36	0.016
RC2	6	7.25	0.006	5.84	0.030	7.21	0.006	6.03	0.006	0.04	0.336	-0.15	0.125
COPC	7	0.13	0.357	-0.10	0.575	-0.08	0.317	-0.22	0.066	0.22	0.066	0.12	0.324
RH1	8	0.75	0.107	1.09	0.004	0.64	0.220	1.09	0.005	0.11	0.180	0.01	0.916
RH2	9	-0.31	0.144	0.01	0.492	-0.27	0.273	0.11	0.655	-0.04	0.317	-0.10	0.059
PIC1	10	-0.05	0.893	-0.42	0.032	-0.06	0.593	-0.42	0.037	-0.02	0.593	-0.02	0.785
PIC2	11	0.10	0.156	-0.02	0.235	0.22	0.496	0.05	0.498	-0.12	0.015	-0.12	0.038
SABC	12	-1.09	0.033	-1.20	0.003	-1.06	0.039	-1.12	0.003	-0.03	0.157	-0.08	0.180
POC1	13	1.94	0.005	-0.92	0.152	1.96	0.005	-0.92	0.152	NA	NA	NA	NA
POC2	14	2.54	0.035	2.27	0.048	2.64	0.033	2.29	0.048	-0.11	0.034	-0.01	0.317
POC3	15	3.13	0.006	1.79	0.096	2.94	0.007	1.58	0.300	-0.04	0.083	-0.01	0.317

*Cells highlighted in light grey indicate statistical significance at the P<.05 level. Cells highlighted in dark grey indicate nearly significant values.

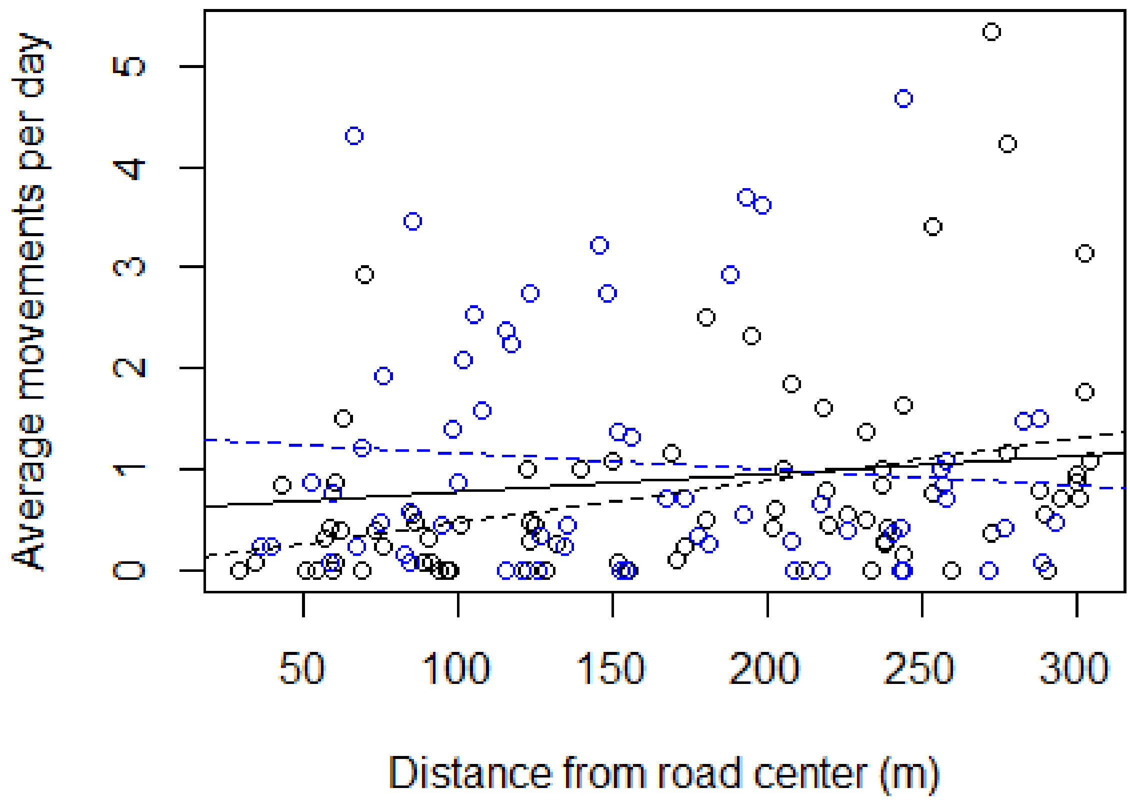


Figure 4. Effect of distance and percent cover on observed movement rates per day of wildlife at control plots along highway US93.

A simple linear model was calculated to predict average movements per day of large mammals based on distance to road center. Blue indicates plots with greater than 50% cover and black indicates those with less than 50% cover. A regression equation for plots with greater than 50% cover (blue dotted line) was found (n=63, p=0.43, R^2=0.001) to show no evidence of a significant relationship. A regression equation for plots with less than 50% cover (black dotted line) was found (n=78, p=.001, R^2=0.126) to show evidence that average movements per day increase by 0.004 for each additional 1 meter distance from the road center. The solid black line is a fitted linear model for all plots (n=142, p=0.11, R^2=0.018) which did not show evidence of a significant relationship.

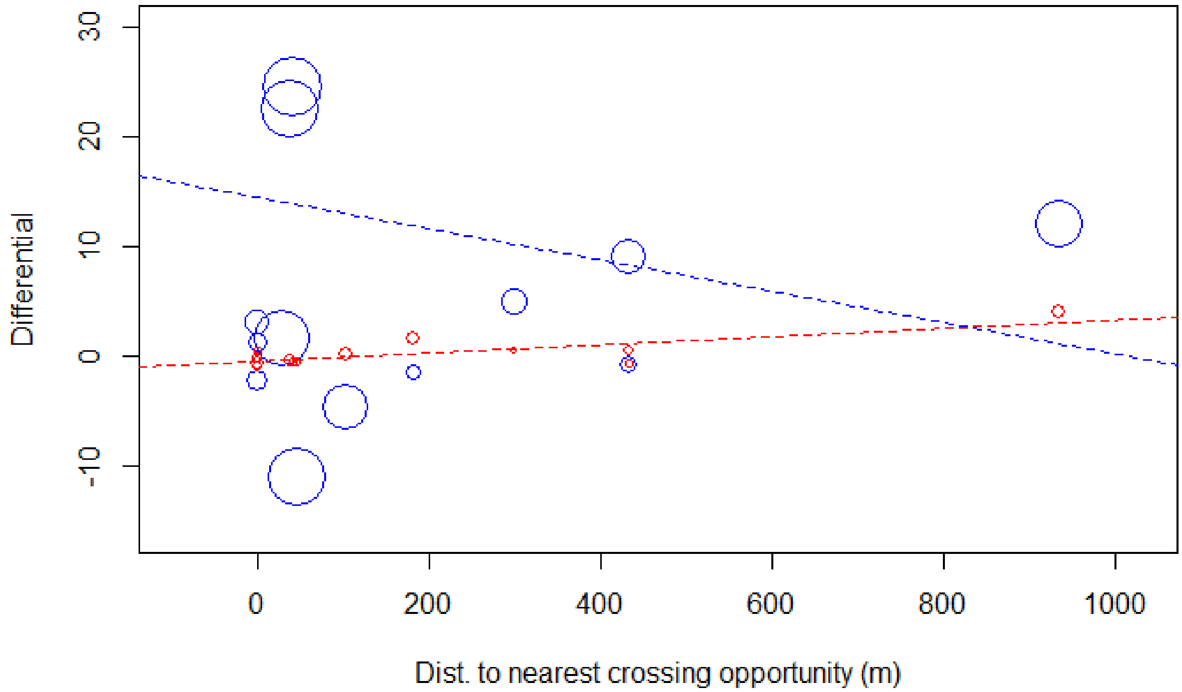


Figure 5. Relationship between average daily movement rate differentials at wildlife crossing structures to distance to nearest alternative crossing opportunity.

Area of circles represents average total movements recorded per day at each site. Blue points represent deer species and red points represent carnivores. The dotted blue lines represent an unweighted, fitted linear models for deer (n=15, p=0.55, R^2=0.03) and shows no evidence of a significant relationship. The red dotted line represents carnivores (n=13, p=0.002, R^2=0.61) and shows significant evidence that differential values for average daily movements (structure minus control plots) increases by 3.7×10^{-4} for every additional increase of 1 meter to the distance to the nearest alternative crossing structure.

Table 4. Total observations and group percentages of animal movements at both structure and control plots along US93 within the Flathead Indiana Reservation, Montana for April through November 2015

Species	Number of Observations	Percent of Wild Animal Observation	Percent of Large Mammal Observations	Percent of Deer Observations	Percent of Carnivore Observations
White-tailed deer (*Odocoileus virginianus*)	2047	70.0%	73.2%	77.8%	
Mule deer (*Odocoileus hemionus*)	576	19.7%	20.6%	21.9%	
Deer sp. (sp. unknown)	7	0.2%	0.3%	0.3%	
Moose (*Alces alces*)	2	0.1%	0.1%		
Elk (*Cervus canadensis*)	1	0.0%	0.0%		
Black bear (*Ursus americanus*)	57	1.9%	2.0%		34.5%
Bear sp. (sp. uknown)	1	0.0%	0.0%		0.6%
Coyote (*Canis latrans*)	86	2.9%	3.1%		52.1%
Bobcat (*Lynx rufus*)	6	0.2%	0.2%		3.6%
Raccoon (*Procyon lotor*)	10	0.3%	0.4%		6.1%
Skunk (*Mephitis mephitis*)	4	0.1%	0.1%		2.4%
American badger (*Taxidea taxus*)	1	0.0%	0.0%		0.6%
Mountain cotton-tail rabbit (*Sylvilagus nuttallii*)	23	0.8%			
Red squirrel (*Tamiasciurus hudsonicus*)	3	0.1%			
Bat (sp. unknown)	2	0.1%			
Ring-necked pheasant (*Phasianus colchicus*)	47	1.6%			
Turkey (*Meleagris gallopavo*)	13	0.4%			
Grouse (sp. unknown)	1	0.0%			
Magpie (*Pica hudsonia*)	10	0.3%			
Great Blue Heron (*Ardea herodias*)	1	0.0%			
Western meadowlark	1	0.0%			

(*Sturnella neglecta*)					
Starling	15	0.5%			
(*Sturnus vulgaris*)					
Red-tailed hawk	1	0.0%			
(*Buteo jamaicensis*)					
Canada goose	2	0.1%			
(*Branta canadensis*)					
Great-horned owl	1	0.0%			
(*Strix nebulosa*)					
Bird sp.	8	0.3%			
(sp. unknown)					
Data Collector	63				
Human	54				
Cow	1783				
Dog	31				
Cat	31				
Total Obs.	**4888**	**2926**	**2798**	**2630**	**165**
(Percent of wild animal observations)		**(100%)**	**(95.6%)**	**(89.9%)**	**(5.6%)**

Table 5.1. Differential movements rates of deer species by structure*

		Structure – Both Sides	Structure – East		Structure - West	
Site	#	Differential	Differential	*p*	Differential	*p*
NEV	1	0.30	0.03	0.484	0.57	0.180
FC1	2	5.65	5.35	0.001	5.95	0.001
FC2	3	-0.47	-0.01	0.852	-0.94	0.021
FC3	4	0.50	0.41	0.373	0.62	0.061
RC1	5	1.20	1.00	0.173	1.40	0.002
RC2	6	6.56	7.21	0.006	6.03	0.006
COPC	7	-0.15	-0.08	0.317	-0.22	0.066
RH1	8	0.89	0.64	0.220	1.09	0.005
RH2	9	-0.08	-0.27	0.273	0.11	0.655
PIC1	10	-0.22	-0.06	0.593	-0.42	0.037
PIC2	11	0.13	0.22	0.496	0.05	0.498
SABC	12	-1.09	-1.06	0.039	-1.12	0.003
POC1	13	0.16	1.96	0.005	-0.92	0.152
POC2	14	2.44	2.64	0.033	2.29	0.048
POC3	15	2.26	2.94	0.007	1.58	0.300

Table 5.2. Differential movement rates for carnivore species by structure*

		Structure – Both Sides	Structure – East		Structure – West	
Site	#	Differential	Differential	*p*	Differential	*p*
NEV	1	NA	NA	NA	NA	NA
FC1	2	0.04	0.03	1.000	0.06	0.655
FC2	3	0.02	0.08	0.680	-0.04	0.622
FC3	4	0.05	0.03	0.655	0.08	0.157
RC1	5	0.40	0.44	0.007	0.36	0.016
RC2	6	-0.07	0.04	0.336	-0.15	0.125
COPC	7	0.17	0.22	0.066	0.12	0.324
RH1	8	0.05	0.11	0.180	0.01	0.916
RH2	9	-0.07	-0.04	0.317	-0.10	0.059
PIC1	10	-0.02	-0.02	0.593	-0.02	0.785
PIC2	11	-0.09	-0.12	0.015	-0.12	0.038
SABC	12	-0.05	-0.03	0.157	-0.08	0.180
POC1	13	NA	NA	NA	NA	NA
POC2	14	-0.06	-0.11	0.034	-0.01	0.317
POC3	15	-0.03	-0.04	0.083	-0.01	0.317

*Cells highlighted in light grey indicate statistical significance at the P<.05 level. Cells highlighted in dark grey indicate nearly significant values.

Figure 6. Differential (structure minus control) use of crossing sites by large mammals (1), deer (2), and carnivores (3) by site.

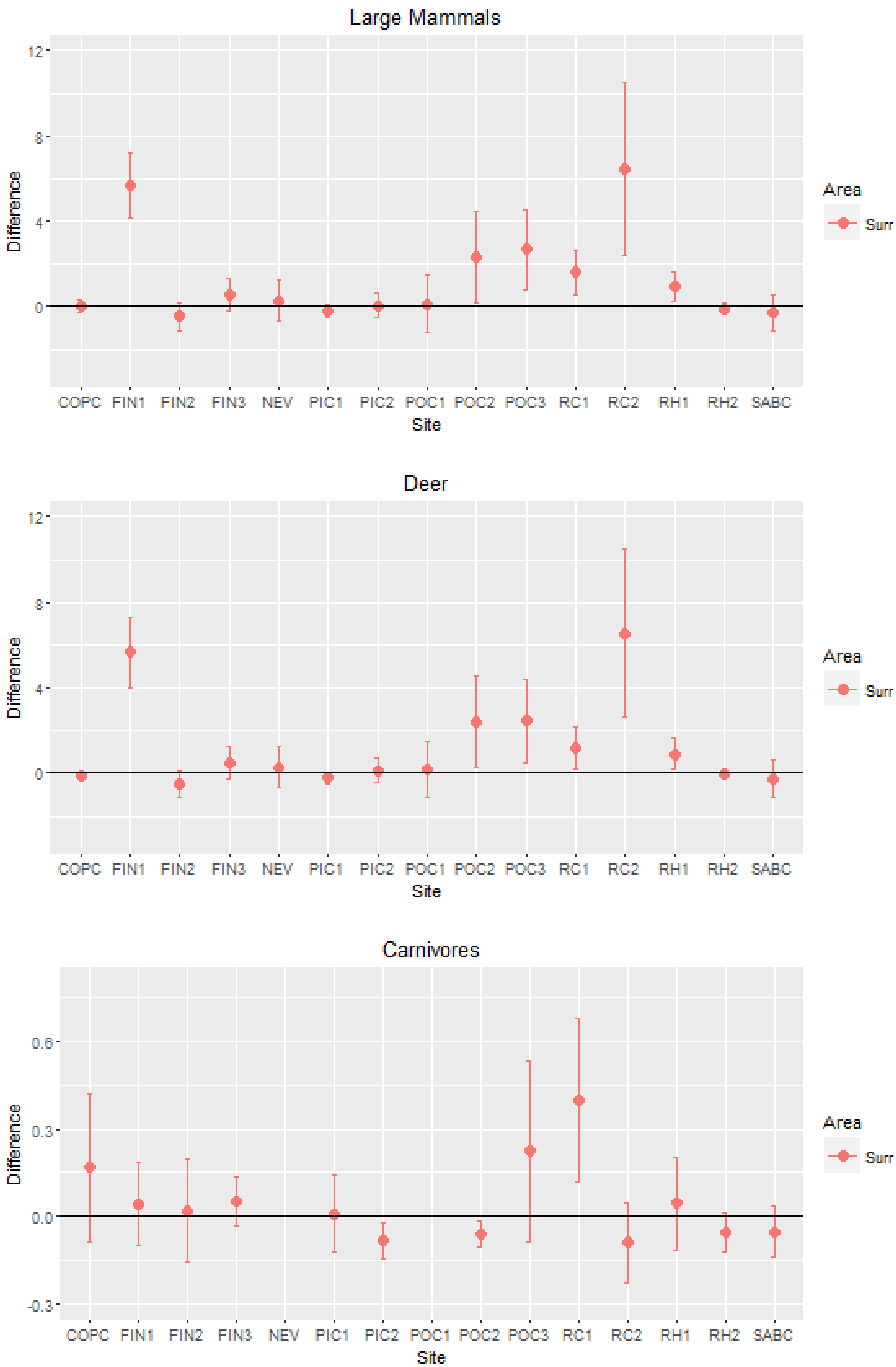


Table 6.- Corridor-wide (pooled across all structures where species or group is present) movement differentials and performance ratios.

Species	n	differential	SE	ratio
Large Mammals	15	0.092	0.083	2.550
Deer	15	0.090	0.082	2.727
Carnivores	14	0.001	0.004	1.667
White-tailed deer	13	0.056	0.072	2.581
Mule deer	5	0.127	0.188	20.368
Black bear	8	0.004	0.005	0.000
Coyote	12	-0.001	0.004	0.000
Bobcat	5	0.0003	0.0017	0.0000

In this analysis, an individual unit (n) is a unique site at which each species or group occurs.

*Cells highlighted in light grey indicate statistical significance at the $P<.05$ level. Cells highlighted in dark grey indicate nearly significant values.

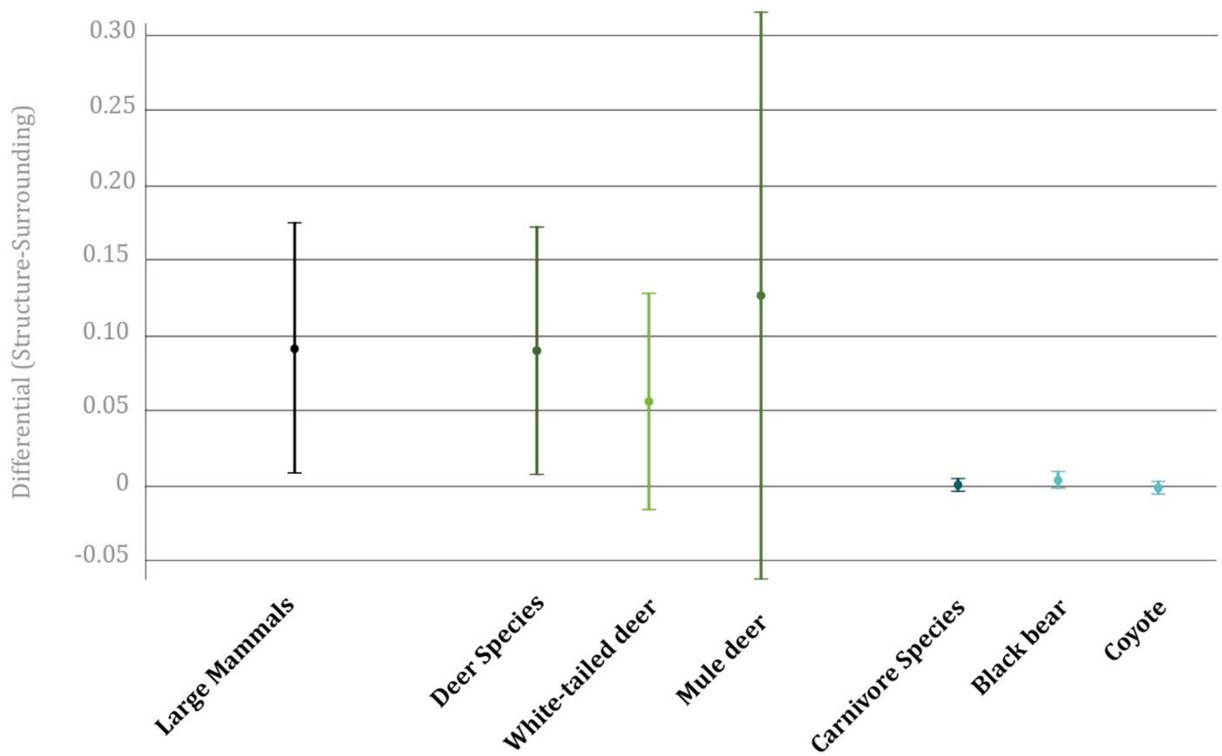


Figure 7. – Corridor-wide (pooled across all structures where species or group is present) movement differentials by species or group. Bars indicate 95% confidence intervals.

Literature Cited:

Allen TDH. 2011. The use of wildlife underpasses and the barrier effect of wildlife guards for deer and black bear [master's thesis]. Montana State University, Bozeman, MT: 71p.

Benítez-López A, Alkemade R, Verweij PA. 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biological Conservation **142**: 1307-1316.

Carbaugh B, Vaughan JP, Bellis ED, Graves HB. 1975. Distribution and activity of white-tailed deer along an interstate highway. The Journal of Wildlife Management **39**(4): 570-581.

Clevenger AP, Chruszcz B, Gunson KE. 2002. Roads and wildlife in the Canadian Rocky Mountain Parks—movements, mortality, and mitigation. Final report to Parks Canada, Banff, Alberta, Canada.

Clevenger AP and Waltho N. 2005. Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. Biological Conservation **121**: 453-464.

Coffin AW. 2007. From roadkill to road ecology: a review of the ecological effects of roads. Journal of Transportation Geography **15**: 396-406.

Cramer PC and Bissonette J. 2007. Integrating wildlife crossings in transportation plans and projects in North America. Pages 328-334 Irwin CL, Nelson D, and McDermott KP, editors. Proceedings of the 2007 International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC.

Dodd NL, Gagnon JW, Manzo AL, Schweinsburg RE. 2007. Video surveillance to assess highway underpass use by elk in Arizona. Journal of Wildlife Management **71**(2): 637-645.

Dulac J. 2013. Global land transport infrastructure requirements: estimating road and railway infrastructure and costs to 2050. International Energy Agency, Paris, France. Available from https://www.iea.org/publications/freepublications/publication/TransportInfrastructureInsights_FINAL_WEB.pdf

Dusek GL, MacKie RJ, Herriges Jr. JD, Compton BB. 1989. Population ecology of white-tailed deer along the Lower Yellowstone River. Wildlife Monographs **104**: 3-68.

Dyer SJ, O'Neill JP, Wasel SM, Boutin S. 2001. Avoidance of industrial development by woodland caribou. The Journal of Wildlife Management **65**(3): 531-542.

Efron B and Tibishirani R. 1993. An introduction to the bootstrap. Chapman & Hall, New York.

Forman RTT. 1999. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology **14**(1): 31-35.

Forman RTT. 1998. Road ecology: a solution for the giant embracing us. Landscape Ecology **13**: iii-v.

Forman RTT and Alexander LE. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics **29**: 207-231.

Forman RTT, Sperling D, Bissonette JA, Clevenger AP, Cutshall CD, Dale VH, Fahrig L, France R, Goldman CR, Heanue K, Jones JA, Swanson FJ, Turrentine T, Winter TC. 2003. Road Ecology: science and solutions. Island Press, Washington, D.C.

Foster ML and Humphrey SR. 1995. Use of highway underpasses by Florida panthers and other wildlife. Wildlife Society Bulletin **23**(1): 95-100.

Gagnon JW, Dodd NL, Ogren KS, Schweinsburg RE. 2011. Factors associated with use of wildlife underpasses and importance of long-term monitoring. The Journal of Wildlife Management **75**: 1477-1487.

Glista DJ, DeVault TL, DeWoody JA. 2009. A review of mitigation measures for reducing wildlife mortality on roadways. Landscape and Urban Planning **91**: 1-7.

Grilo C, Bissonette JA, Cramer PC. 2010. Mitigation measures to reduce impacts on biodiversity. Pages 73-114 in Jones SR, editor. Highways: construction, management, and maintenance. Nova Science Publishers, Hauppauge, NY.

Hardy A, Clevenger AP, Huijser MP, Graham N. 2004. An overview of methods and approaches for evaluating the effectiveness of wildlife crossing structures: emphasizing the science in applied science. Pages 319-330 in Irwin CL, Garrett P, and McDermott KP, editors. Proceedings of the 2001 International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC.

Hardy AR, Fuller J, Huijser MP, Kociolek A, Evans M. 2007. Evaluation of wildlife crossing structures and fencing on US Highway 93 Evaro to Polson – Phase I: preconstruction data collection and finalization of evaluation plan final report. FHWA/MT-06-008/1744-2. Montana Department of Transportation, Helen MT. Available from http://www.mdt.mt.gov/research/projects/env/wildlife_crossing.shtml

Hothorn T and Hornik K. 2015. exactRankTests: exact distributions for rank and permutation tests. R package version 0.8-28. Available from http://CRAN.R-project.org/package=exactRankTests.

Huijser MP, Fairbank E, Camel-Means W. 2015. US 93 North post-construction wildlife-vehicle collision and wildlife crossing monitoring and research on the Flathead Indian Reservation between Evaro and Polson, Montana annual report 2014. Western Transportation Institute, College of Engineering, Montana State University, Bozeman, MT. Available from http://www.mdt.mt.gov/other/webdata/external/research/docs/research_proj/wildlife_crossing/phaseii/annual_2014.pdf

Huijser MP, Fairbank E, Camel-Means W, Graham J, Watson V, Basting P, Becker D. 2016. Effectiveness of short sections of wildlife fencing and crossing structures along highways in reducing wildlife-vehicle collisions and providing safe crossing opportunities for large mammals. Biological Conservation **197**: 61-68.

Huijser MP, McGowen P, Clevenger AP, Ament R. 2008. Wildlife-vehicle collision reduction study: best practices manual. Report to Congress. U.S. Department of Transportation, Federal Highway Administration, Washington, D.C. Available from https://www.environment.fhwa.dot.gov/ecosystems/wvc/index.asp?redirect

Iglesias C, Mata C, Malo JE. 2010. The influence of traffic noise on vertebrate road crossing through underpasses. Ambio **41**(2): 193-201.

Keller BJ and Bender LC. 2007. Bighorn sheep response to road-related disturbance in Rocky Mountain National Park, Colorado. The Journal of Wildlife Management **71**(7): 2329-2337.

Kociolek AV, Ament RJ, Callahan AR, Clevenger AP. 2015. Wildlife crossings: the new norm for transportation planning. Institute of Transportation Engineers Journal **85**(4): 45-47.

Kroll G. 2015. An environmental history of roadkill: road ecology and the making of the permeable highway. Environmental History **20**: 4-28.

Little SJ, Harcourt RG, Clevenger AP. 2002. Do wildlife passages act as prey-traps? Biological Conservation **107**: 135-145.

Marshik, J, Renz L, Sipes J, Becker D, Paulson D. 2001. Preserving a spirit of place: U.S. Highway 93 on the Flathead Indian Reservation. Pages 244-256 in Irwin CL, Nelson D, and McDermott KP, editors. Proceedings of the 2001 International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC.

Mata C, Bencini R, Chambers BK, Malo JE. 2015. Predator-prey interactions at wildlife crossing structures: between myth and reality. Pages 190-197 in van der Ree R, Smith DJ, Grilo C, editors. Handbook of Road Ecology. 1st Ed. Wiley, Oxford.

[MDT] Montana Department of Transportation, Traffic Data Collection and Analysis Section. 2014. Montana’s automatic traffic recorders. Available from http://www.mdt.mt.gov/publications/docs/datastats/atr/atrbook14.pdf

Meisingset EL, Loe LE, Brekkum Ø, Mysterud A. 2013. Red deer habitat selection and movements in relation to roads. The Journal of Wildlife Management **77**(1): 181-191.

Papouchis CM, Singer FJ, Sloan WB. 2001. Response of desert bighorn sheep to increased human recreations. The Journal of Wildlife Management **65**(3): 573-582.

Purdum J. 2013. Acceptance of wildlife crossing structures on US Highway 93 Missoula, Montana [master’s thesis]. University of Montana, Missoula, MT: 27p.

R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.R-project.org/.

Rost GR and Bailey JA. 1979. Distribution of mule deer and elk in relation to roads. The Journal of Wildlife Management **43**(3): 634-641.

Sawyer H, Nielson RM, Lindzey FG, Keith L, Powell JH, Abraham AA. 2007. Habitat selection of Rocky Mountain elk in a nonforested environment. The Journal of Wildlife Management **71**(3): 868-874.

Trombulak SC and Frissell CA. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology **14**(1): 18-30.

[USDOT] U.S. Department of Transportation, Bureau of Transportation Statistics. 2014. National Transportation Statistics 2014. Available from http://www.bts.gov/publications/national_transportation_statistics/.

van der Grift EA and van der Ree R. 2015. Guidelines for evaluating use of wildlife crossing structures. Pages 119-128 in van der Ree R, Smith DJ, Grilo C, editors. Handbook of Road Ecology. 1st Ed. Wiley, Oxford.

van der Grift EA, van der Ree R, Fahrig L, Findlay S, Houlahan J, Jaeger JAG, Klar N, Madriñan LF, Olson L. 2013. Evaluating the effectiveness of road mitigation measures. Biodiversity and Conservation **22**: 425-448.

van der Ree R, van der Grift E, Gulle N, Holland K, Mata C, Suarez F. 2007. Overcoming the barrier effect of roads – how effective are mitigation strategies?: an international review of the use and effectiveness of underpasses and overpasses designed to increase the permeability of roads for wildlife. Pages 423-431 in Irwin CL, Nelson D, and McDermott KP, editors. Proceedings of the 2007 International Conference on Ecology and Transportation. Center for Transportation and the Environment, North Carolina State University, Raleigh, NC.

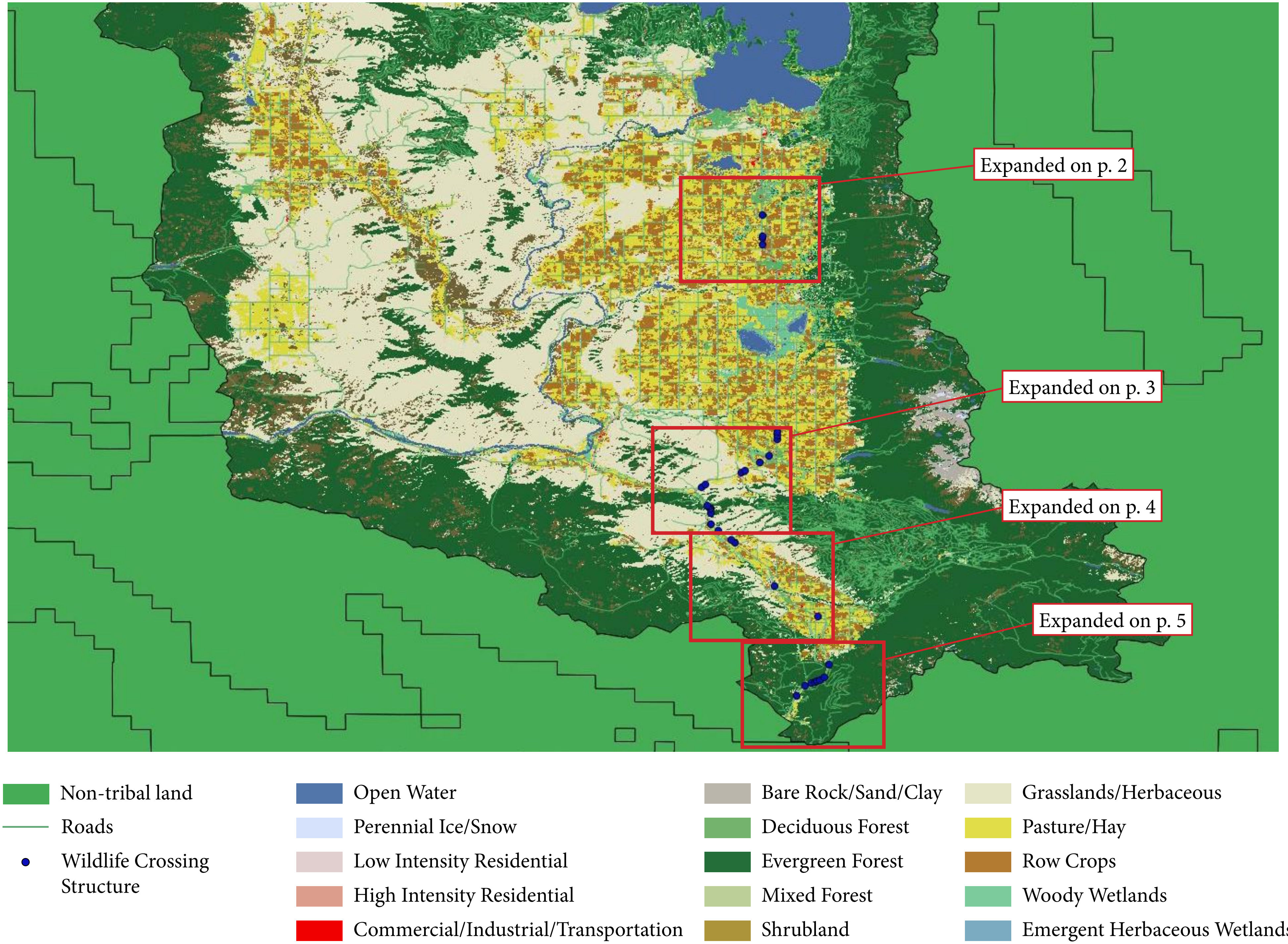
Whittington J, St. Clair CC, Mercer G. 2004. Path tortuosity and the permeability of roads and trails to movement. Ecology and Society **9**(1): Art. 4.

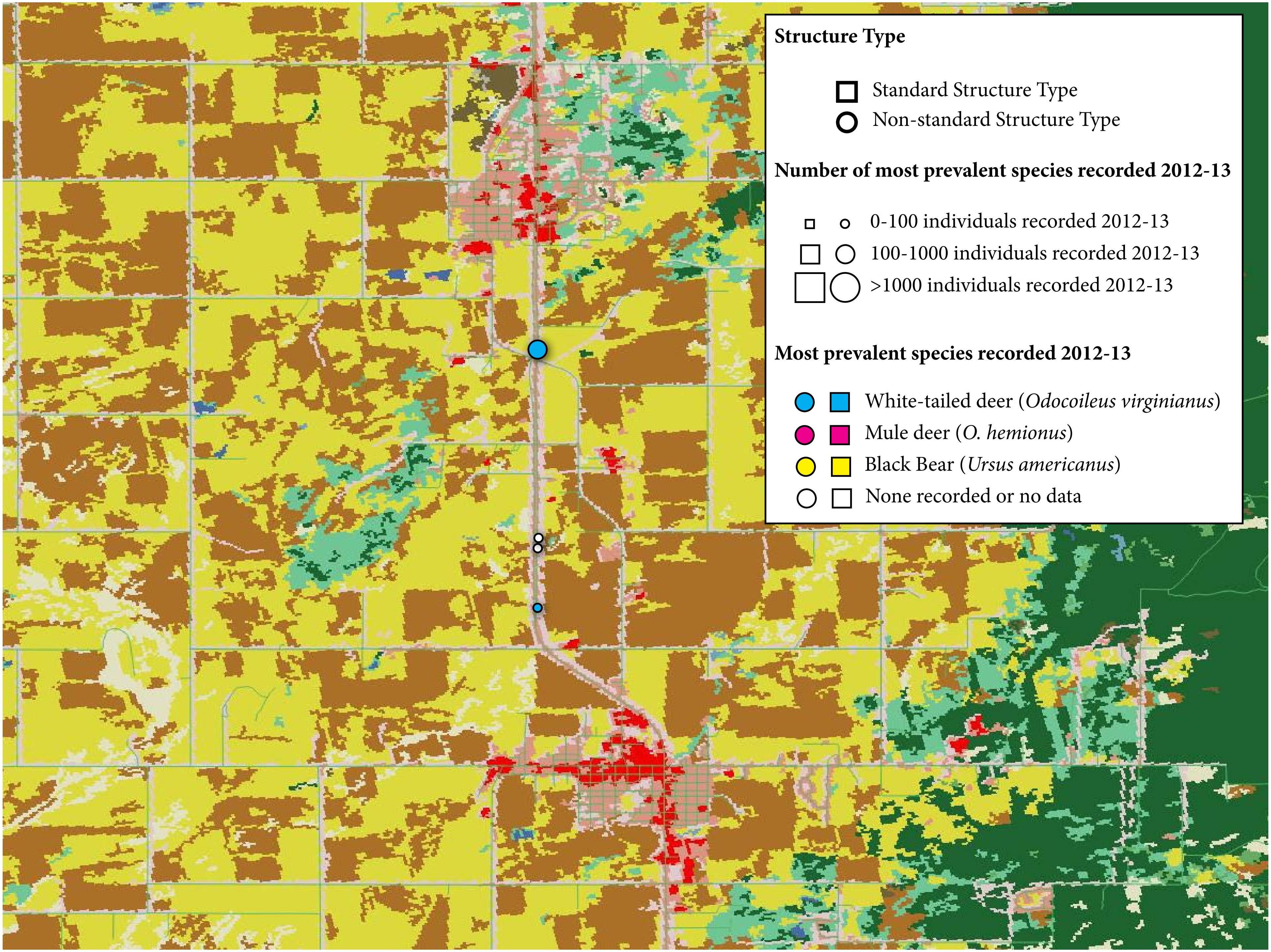
[WSDOT] Washington States Department of Transportation. 2008. I-90 Snoqualmie Pass East project final environmental impact statement. FHWA-WA-EIS-05-01-F. Available from http://www.wsdot.wa.gov/Projects/I90/SnoqualmiePassEast/Finaleis

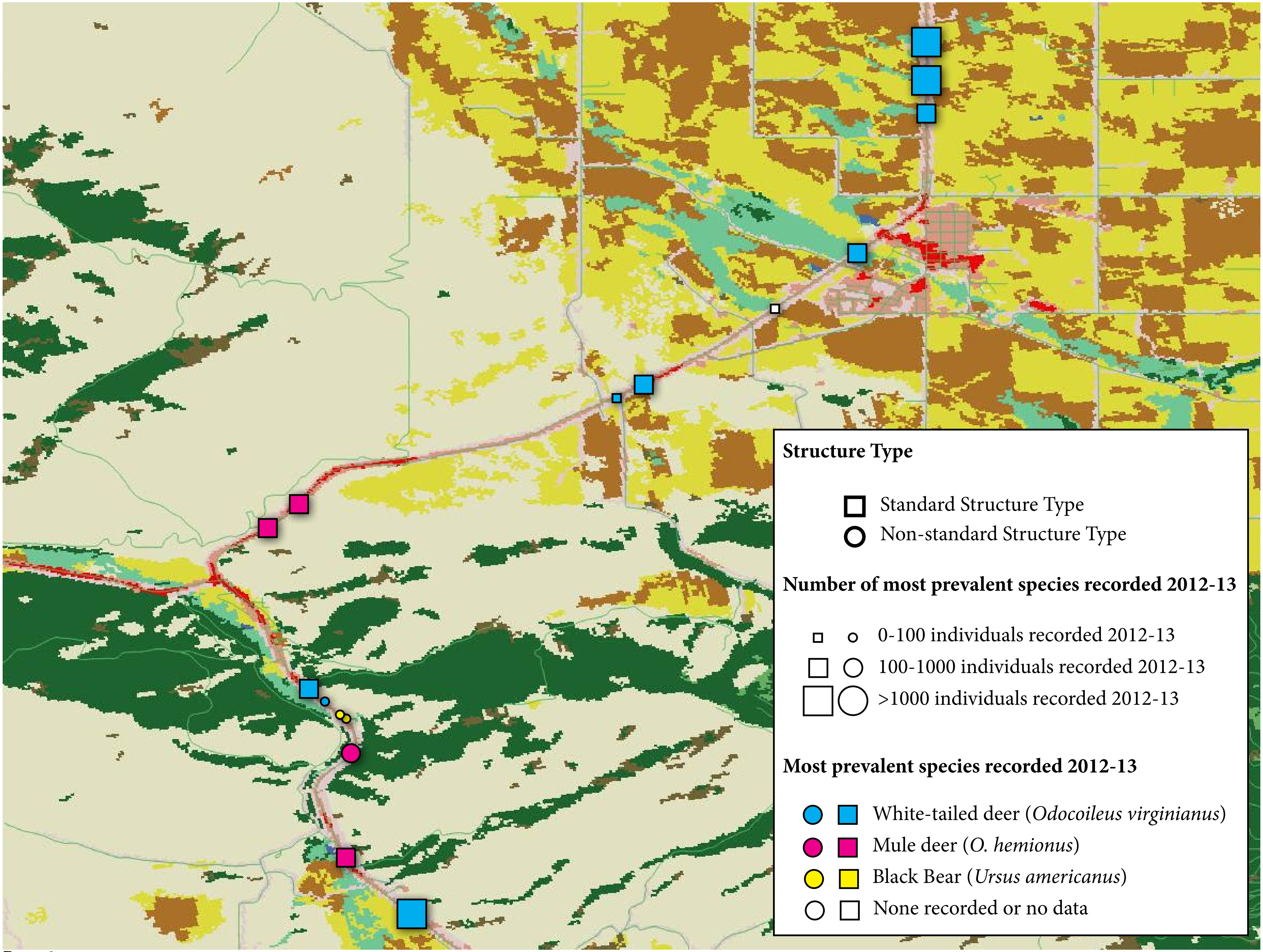
Supplementary Materials:

Land cover in road adjacent habitat and 2014 wildlife passage rates for US 93 through the Flathead Reservation

Usage of wildlife crossing structures by large mammals on the Flathead Reservation




Structure Type
Standard Structure Type
Non-standard Structure Type
Number of most prevalent species recorded 2012-13
0-100 individuals recorded 2012-13
100-1000 individuals recorded 2012-13
>1000 individuals recorded 2012-13
Most prevalent species recorded 2012-13
White-tailed deer (*Odocoileus virginianus*)
Mule deer (*O. hemionus*)
Black Bear (*Ursus americanus*)
None recorded or no data



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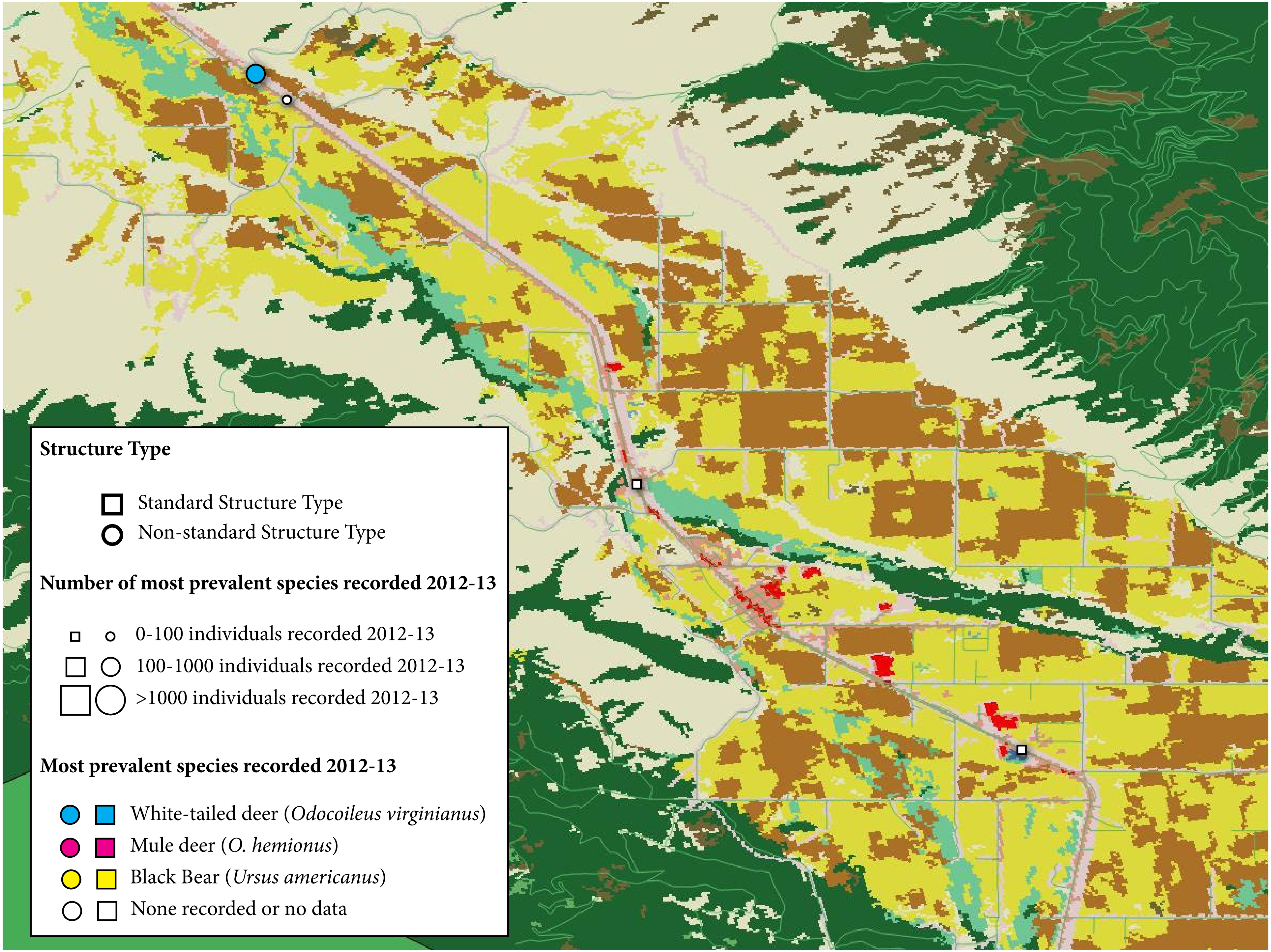

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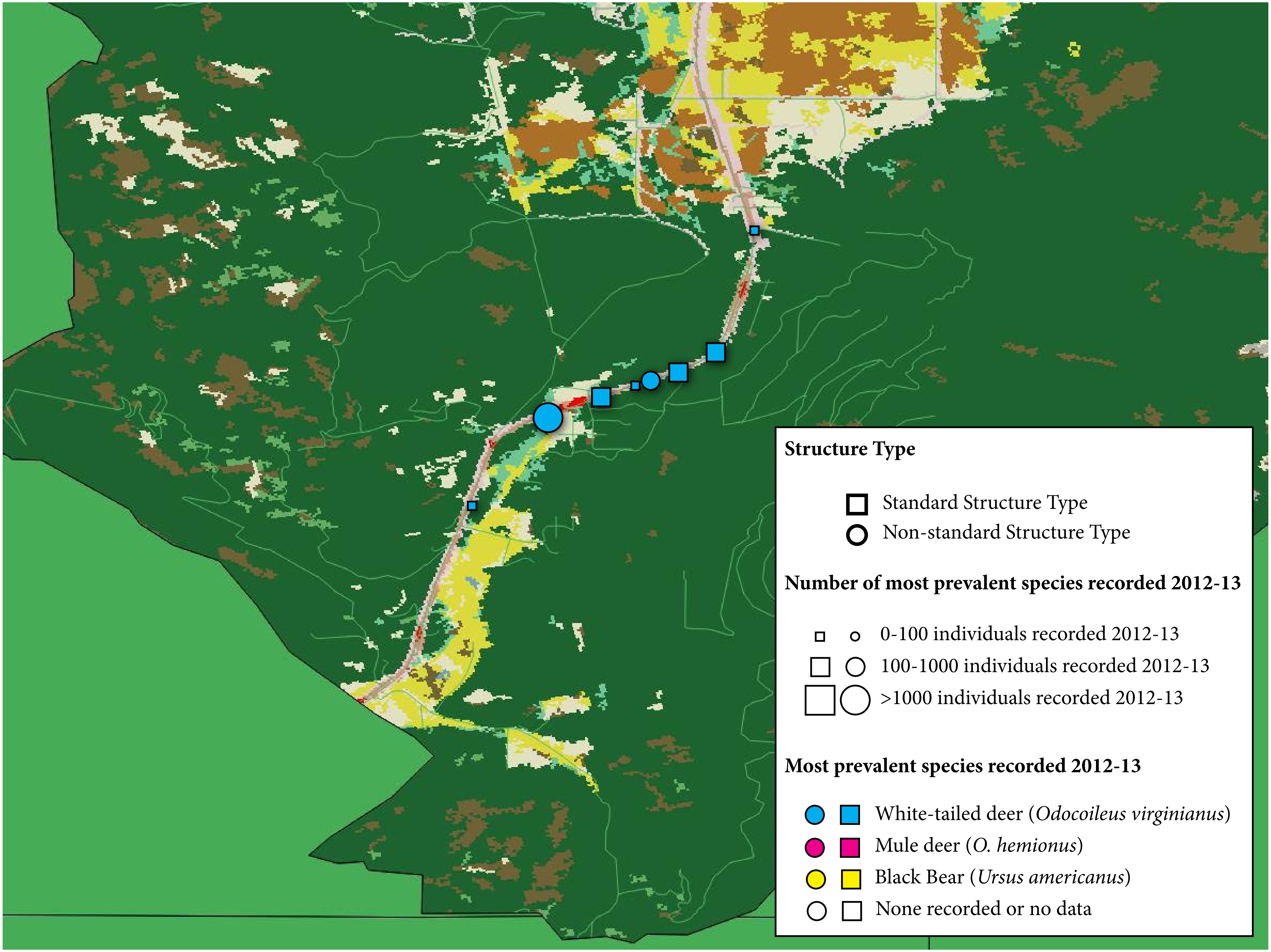
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