DEPARTMENT OF BIOLOGICAL AND
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EFFECTIVITY OF ROAD AND RAILWAY CROSSING STRUCTURES FOR WILD MAMMALS

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Photos by EnviroPlanning AB. Ungulates at various crossing sites, captured using camera traps.

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ABSTRACT

Roads and railways act as barriers in the landscape, preventing wildlife from moving freely. This has negative demographic and genetic effects which can cause declines in animal abundances and species richness. Crossing structures, theoretically, mitigates these effects by allowing animals to cross roads and railways safely. However, animals do not use all structures to the same extent. In this study I investigate how effective different crossing structures are for large and medium-sized mammals, and how that effectivity is influenced by the dimension, the type of structure and by human co-use.

Eighteen crossing structures were monitored using camera traps and effectivity was estimated using an index based on animal activity in a crossing structure compared to animal activity outside the same structure. The results showed that for both moose and roe deer, there was a strong tendency toward overpasses being more effective than underpasses. In contrast to previous studies, the width of the structures had a minor impact only on the effectivity for roe deer. Human use correlated with effectivity in contradictory ways for different species, negatively for roe deer and hare but positively for moose.

Future studies should focus on direct comparisons between overpasses and underpasses and finding minimum size requirements for both types since this is important for management decisions.

Keywords: Crossing structure, wildlife, connectivity, moose, roe deer, camera trap

SAMMANFATTNING

Vägar och järnvägar utgör barriärer i landskapet som hindrar vilda djur från att röra sig fritt. Detta medför negativa demografiska och genetiska konsekvenser som kan orsaka minskade tätheter av djur samt förlust av artrikedom. Passager över och under vägar och järnvägar kan, i teorin, lindra dessa effekter genom att låta djur passera på ett säkert sätt. Vilda djur använder dock inte alla passagemöjligheter i samma utsträckning. I den har studien undersöker jag hur effektiva olika passager är för stora och medelstora däggdjur, med fokus på älg och rådjur, samt hur passagernas dimensioner, typen av passage och mängden mänsklig aktivitet kan påverka effektiviteten.

Arton passager övervakades med hjälp av kamerafällor och effektiviteten uppskattades med hjälp av ett index baserat på mängden djuraktivitet i passagen jämfört med djuraktiviteten utanför. Resultaten visade på en stark tendens av att passager över infrastrukturen kan vara mer effektiva än passager under för både älg och rådjur var. Till skillnad från tidigare studier hade passagernas bredd en svag inverkan endast på effektiviteten för rådjur. Mänsklig aktivitet korrelerade med effektiviteten på skilda sätt för olika arter, negativ korrelation för rådjur och hare men positiv för älg.

Fortsatt forskning bör fokusera på direkta jämförelsen mellan broar och tunnlar och att finna minsta tillräckliga bredd för båda typerna av passage, eftersom detta är av stor vikt vid beslut om lämpliga åtgärder.

1 INTRODUCTION

Roads and railways cover almost 500 000 hectares, about 1%, of the land area in Sweden (Statistics Sweden 2015), forming a network that connects all areas inhabited or used by humans. As roads and railways extend through natural habitats, they cause negative ecological effects that are multifaceted. Among the most pronounced negative effects on wildlife are increased fragmentation and mortality. Crossing structures over and under roads and railways can mitigate these effects but only if animals will use them. This work will focus on how different factors, such as size and human activity, can impact the effectivity of crossing structures.

1.1 Ecological Effects of Fragmentation

When changes in land use occur, whether by the construction of infrastructure or other human use, one result is often increased fragmentation of natural habitats. Fragmentation is not the same thing as habitat loss. Even though the two concepts are strongly linked in practice, they can and should be distinguished (Fahrig 2003). Habitat loss is the reduction in total amount of natural habitat while fragmentation is the partitioning of natural habitats into smaller patches. Habitat loss is the single largest threat to biodiversity, however, fragmentation per se is the cause of an array of complex ecological effects that should not be overlooked (With 1997). While roads and railways also cause habitat loss and habitat degradation, fragmentation is a significant contributing factor to the negative ecological effects (Spellerberg 1998, Bekker and Iuell 2003). Therefore, the following sections will focus on the effects of fragmentation per se on biodiversity and abundance of species but will also describe more generally why roads and railways cause problems for wild animals.

1.1.1 The Problem: Avoidance, Roadkill and Fencing

According to island biogeography theory, the smaller and more isolated an island is the less biodiverse it will be (Macarthur and Wilson 1967). Fragmentation, whether it is by roads, urbanisation, or other intensive land use, reduces the size of natural habitat patches, increases isolation between patches and increases the amount of habitat edge. The level of isolation between habitat patches is not only determined by the physical distance to other habitat patches but also a species ability to safely traverse the non-habitat areas (Ricketts 2001). Although the physical distance between patches divided by roads and railways may seem inconsequential, the effect on the ability of wild animals to move between them may be substantial. There are several behavioural and physical reasons why roads and railways may cause strong isolation and other negative ecological effects:

a) Avoidance

Some species avoid roads and railways and are therefore unlikely to attempt to cross them (Jaeger, Bowman et al. 2005). Deterring effects can, for example, be caused by noise, pollutants, or light from traffic. For such species, the effect of isolation is strong, but the effective habitat loss caused by roads and railways can also be substantial. Although responses vary between species, abundance of mammalian species has been shown to decrease up to 17 kilometres away from roads (Benitez-Lopez, Alkemade et al. 2010).

b) Mortality

Wild animals that are not deterred by roads or railways may readily enter onto them. However, this increases their risk of being hit and injured or killed by traffic. Some animals may even be attracted to roads, e.g. for basking (Grilo, Bissonette et al. 2011). A considerable number of wild mammals are killed by traffic. It has been estimated that up to 20% of European badger (*Meles meles*) populations in some areas are killed by traffic each year (Clarke, White et al. 1998). Furthermore, in 2019, at least 39 Eurasian lynx (*Lynx lynx*), 5000 moose (*Alces*

alces) and more than 40 000 roe deer (*Capreolus capreolus*) were involved in wildlife-vehicle accidents in Sweden alone (Nationella viltolycksrådet 2019). Traffic is probably a major cause of mortality for many non-avoidant species and this is likely to contribute to reduced animal densities and ultimately species loss (Forman and Alexander 1998, Lode 2000).

a) Physical barriers

Since animal-vehicle accidents are costly and dangerous for both humans and animals, fencing is sometimes used to keep larger mammals from entering onto major roads and railways. Fencing can reduce animal-vehicle accidents by 54-83% (Rytwinski, Soanes et al. 2016). However, fences also creates physical barriers to movement, increasing the isolation between habitat patches (Seiler, Cederlund et al. 2003, Jakes, Jones et al. 2018). Other physical barriers to animals include steep roadside verges and midline fences (Barrientos, Ascensao et al. 2019).

The ecological effects of roads and railways vary depending on the species and the road/railway type, including factors such as traffic volume, surface material and width (Jaeger, Bowman et al. 2005). The research on the ecological effects of transportation infrastructure has focused mostly on roads. The ecological effects of railways and trains are not as well-known, but these also cause disturbance, increased isolation and increased mortality. However, the magnitude of effects may be different from that of roads (Dorsey, Olsson et al. 2015) and, in addition, some complications are unique to railways such as electrocution and rail entrapment.

1.1.2 The Effect: Reduced Persistence of Species

Increased isolation, increased habitat edge and reduction in patch size have been shown to negatively affect species richness, species persistence, community composition and migration rate (Haddad, Brudvig et al. 2015).

Thus, fragmentation causes the onset of a gradual loss of species (Saunders, Hobbs et al. 1991, Tilman, May et al. 1994). One study showed that effects of fragmentation may still increase 20 years after the fragmentation event has occurred (Saunders, Hobbs et al. 1991). Effects are thought to develop slower in larger habitat patches and quicker in small ones (Haddad, Brudvig et al. 2015).

On the landscape scale, fragmentation can increase biodiversity (Fahrig 2003). This is naturally the case, in the short term, since fragmentation creates new habitat niches and increases landscape heterogeneity. For example, the introduction of a railway into an otherwise unfragmented forest habitat will create railway verges and forest edge habitats that can be colonised by species not previously inhabiting the area. Despite this, landscape scale diversity and abundance of pre-existing species (before fragmentation) and specific taxa have been shown to decline (Saunders, Hobbs et al. 1991, Fahrig and Rytwinski 2009).

Fragmentation by roads, in particular, has been shown to negatively affect abundance and persistence of species of birds, amphibians, reptiles and mammals (Fahrig and Rytwinski 2009).

1.1.3 The Root Cause: Genetic and Demographic Change

When small subpopulations become isolated, their genetic make-up can become differentiated from one another and genetic diversity can be lost through genetic drift or inbreeding (Allendorf and Luikart 2006). Inbreeding within a population typically leads to inbreeding depression – reduced viability of the population due to loss of heterozygosity. Inbreeding depression may have a greater effect than demographic change on the persistence of some species inhabiting fragmented landscapes (Saccheri, Kuussaari et al. 1998).

Fragmentation by roads have been shown to reduce genetic diversity and cause genetic differentiation of subpopulations (Holderegger and Di Giulio 2010). However, long-term effect on population persistence has not been demonstrated. Roads and railways are typically not complete barriers to movement and it is expected that the exchange of 1-10 individuals per generation is enough to maintain heterozygosity within subpopulations (Mills and Allendorf 1996).

The primary cause for reduced persistence and abundance may instead be demographic change. Persistence of a population in the landscape ultimately depends on its birth and death rate (Fahrig 2002). Roads and railways that fragment the landscape may limit access to vital resources and habitats. Death rates are also likely to increase due to unsuitability of the non-habitat area and habitat edges, e.g. because of increased predation, parasitism or, in the case of roads and railways, deaths by traffic (Ries, Fletcher et al. 2004). Mating is less likely to occur in a fragmented landscape due to reduced encounter rates (Wosniack, Santos et al. 2014), which will also lower the birth rate.

The species most sensitive to fragmentation of the landscape are those with high specialization, those that depend on seasonal migration or otherwise depend on access to large home ranges or territories, species with low population density and those which cannot disperse easily (Saunders, Hobbs et al. 1991, Tilman, May et al. 1994). Larger mammals may be particularly vulnerable since they typically have low reproductive rates and require large amounts of resources (Fahrig 2001).

1.2 Mitigation Through Crossing Structures

The fragmentation effects caused by both old and new roads and railways risk exacerbating biodiversity loss unless efficiently mitigated. Fragmentation effects may be reduced for wild animals, that are not strongly avoidant of roads and railways, if there is a sufficient number of suitable crossing opportunities. Such crossings exist in the form of tunnels and bridges for smaller roads, pedestrian and bicycle paths, rivers and streams and crossing structures explicitly built for wildlife. The construction of crossing structures under and over roads and railways was first used as a way to mitigate fragmentation effects in the 1970's (Reed, Woodard et al. 1975). Today, this mitigation strategy is being implemented worldwide, restoring connectivity for African elephant (*Loxodonta africana africana*) in Kenya (Nyaligu and Weeks 2013), for grizzly bears (*Ursus arctos horribilis*) and elk (*Cervus canadensis*) in Canada (Clevenger and Waltho 2000), for western grey kangaroo (*Macropus fuliginous*) in Australia (Chachelle, Chambers et al. 2016), for Tibetan antelope (*Pantholops hodgsonii*) and mountain weasels (*Mustela altaica*) in China (Wang, Guan et al. 2018) and for amphibians and ungulates in Europe (Olsson, Widen et al. 2008, Jarvis, Hartup et al. 2019), to mention a few. The following sections describe the purpose of a crossing structure and what factors may influence how effective a structure is in creating connectivity for wildlife.

1.2.1 Facilitating Natural Movement

A crossing structure should facilitate the natural movement patterns of wild animals. Movements of animals occurs on multiple temporal scales. Daily movement occurs within a home range or territory. For roe deer, this area ranges from around 20 hectares to over 100 hectares (Cederlund and Liberg 1995). Moose have much larger home ranges, on average 1400 hectares for cows and 2600 hectares for bulls (Cederlund and Sand 1994).

There are two types of movement occurring over greater distances: migration and dispersal. Migration occurs seasonally in order to access important resources or habitats. Moose in the north of Sweden and many amphibian species migrate seasonally (Sinsch 1990, Cederlund and Sand 1994). Dispersal is the movements from birthplace to breeding site and between breeding sites, i.e. changing home range. It can be triggered by, for example, increased competition or rivalry (Cederlund and Sand 1994).

All types of movement are important to the ecology of an animal and should be facilitated by crossing structures. Animals can only use crossing opportunities which are accessible within their movement ranges, therefore crossing structures should be available at regular intervals along barriers (Bissonette and Adair 2008).

1.2.2 Factors Influencing Effectivity

Crossing structures vary wildly in size and design depending on location and purpose, ranging from 30-centimetre-wide culverts, constructed for use by small animals, to larger bridges over 50-meters wide. Several studies have demonstrated that wild animals use some crossing structures (for example Mata, Hervas et al. 2008, Olsson, Widen et al. 2008). However, how willing, or likely animals are to use a crossing structure, i.e. the effectivity of the structure in facilitating movement, may depend on many factors.

It has been demonstrated that how much a crossing structure is used varies even for structures of the same design and dimensions (Andis, Huijser et al. 2017). This is an indication that landscape factors can influence effectivity. For example, large carnivores have been shown to be more likely to use crossing structures further from townsites (Clevenger and Waltho 2005), while effectivity for roe deer have been shown to be affected by the ratio of forest and agricultural land in the surrounding landscape as well as the distance to other crossing structures (Bhardwaj et al. submitted manuscript).

However, the design and dimensions of a crossing structure are also important. Increased width and structural openness has been shown to increase use, particularly for moose, roe deer and other ungulates (Clevenger and Waltho 2000, Bhardwaj et al. submitted manuscript). Size requirements likely depend on the body size of the animal as well as its ecology. Denning species may be more likely to use small structures than open field species (Kintsch and Cramer 2011).

Distance between the crossing structure entrances and forest cover can also affect use. Grizzly bear and elk have been shown to use underpasses where the forest edge was further from the entrance more effectively, while the opposite was true for cougars (*Puma concolor*) (Clevenger and Waltho 2005).

Human activity in or near a crossing structure has been shown to negatively affect use by roe deer, moose and large carnivores (Clevenger and Waltho 2005, Bhardwaj et al. submitted manuscript).

Traffic volume negatively affected crossing structure use by moose in one study presumably due to increase disturbance from traffic noise (Olsson, Widen et al. 2008). The level of disturbance from traffic may, however, depend on whether the structure has noise and visibility shields. Other studies have shown negative effects of noise on species diversity in crossing structures and crossing structure use by grizzly bears (Clevenger and Waltho 2005, Shilling, Collins et al. 2018). However, another study showed no effect of noise level on use of crossing structures in any species group (Iglesias, Mata et al. 2012).

Time since construction also seems to be of some importance, suggesting that animals need time to habituate to a new crossing structure. Use has been shown to increase over time for several large carnivore and ungulate species (Barrueto, Ford et al. 2014).

Evaluating the effectivity of a crossing structure may require long study periods, especially if animal densities are low. Some of the studies mentioned only included a handful of crossing structures, the type of structures varied between studies and all implemented different methods of controlling for variation in animal abundances. Therefore, relative importance of dimensions, human disturbance, and other factors on the effectivity of crossing structures is still uncertain. Recently, in Sweden, more wide overpasses, often called ecoducts, are being planned. However, the effectivity of overpasses and how they compare to underpasses is even less well known.

Mitigation measures always needs to be efficient, therefore the end goal is to optimize the effectivity of mitigation measures in relation to the cost when making decisions on type of structure, location, dimensions, materials etc. Therefore, knowledge of what makes a crossing structure effective for different species is vital for making the best decisions on how to design and adapt crossing structures in order to restore connectivity.

1.3 Aim and Scope

The aim of this thesis was to answer the following question: How effective are crossing structures for wild mammals and what factors influence that effectivity?

All crossing structures that were included in the study are located in Sweden and the result therefore reflect Scandinavian conditions. I investigated the effectivity of crossing structures for medium- and large-sized wild mammal species which regularly visit and use crossing structures in Sweden. However, focus was placed on the effectivity for large species, specifically ungulates, since 1) most of the included crossing structures are constructed primarily for these species and 2) barrier effects are likely stronger and of greater concern for these species.

2 Method

2.1 The Study Sites

This study included 18 crossing structures. I selected these from a larger set of structures for which camera trap data was available. From this set, several structures were excluded because of dissimilarities in the camera set up (number and positioning of cameras). One structure was excluded because the area surrounding one entrance was almost completely fenced off which could affect the movement and behaviour of wild animals. Monitoring of most crossing structures started before the start of this project. Some structures were monitored as part of separate evaluation programs funded by the Swedish Transport Administration. Others were selected based on structure type so that structures of varying sizes and designs were included. For most sites either the images or the raw data was provided by the research program TRIEKOL (Helldin, Lennartsson et al. 2020). The first half of this project included additional fieldwork for camera management and image collection.

Eleven of the included crossing structures were located in the south of Sweden (Stockholm county to Skåne county, Figure 1). The other seven sites were located in the north of Sweden (Norrbotten county: six sites between Kalix and Haparanda and one site south of Kiruna). The size and type (underpass or overpass) of structures varied within each of the two regions. Eight of the crossing structures were overpasses and ten were underpasses. Table 1 gives a summarized description of all sites.

The width of the structures ranged from 2.8 to 54.0 meters for underpasses and from 5.0 to 50.0 meters for overpasses. Width was measured as the smallest width, usually at the middle, of the crossing structure (Figure 2).

Overpasses were typically longer, ranging from 21.3 to 64.0 meters, while the underpasses were 7.0 to 38.9 meters long. Note that, by necessity, length was defined in different ways for overpasses and underpasses since the structure types are inherently different. Length of underpasses and overpasses are likely also perceived differently by animals. For underpasses length was measured from where the ceiling begins to where it ends. For overpasses it is often not evident where the crossing structure starts. For consistency, length was measured from the points where the fence or shield is sharply angled away from the bridge as illustrated by Figure 2B.

All roads and railways that these structures cross have wildlife exclusion fences on both sides. The fences have a mesh size of approximately 15x15 centimetres and are 2 meters high. Although all of the structure can be used by wild mammals, some were constructed primarily for other purposes and thus may not have been adapted for animal use in any way.

Data was collected for several species: roe deer, moose, fallow deer (*Dama dama*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), red fox (*Vulpes vulpes*), mountain or European hare (*Lepus timidus* or *L. europaeus*) and badger.

Fallow deer, red deer and wild boar occur in the south of Sweden and, although their distribution and abundance may be varied, could occur at all crossing structures in the southern area included in this study (11 crossing structures). However, none of these species occur in the northern region

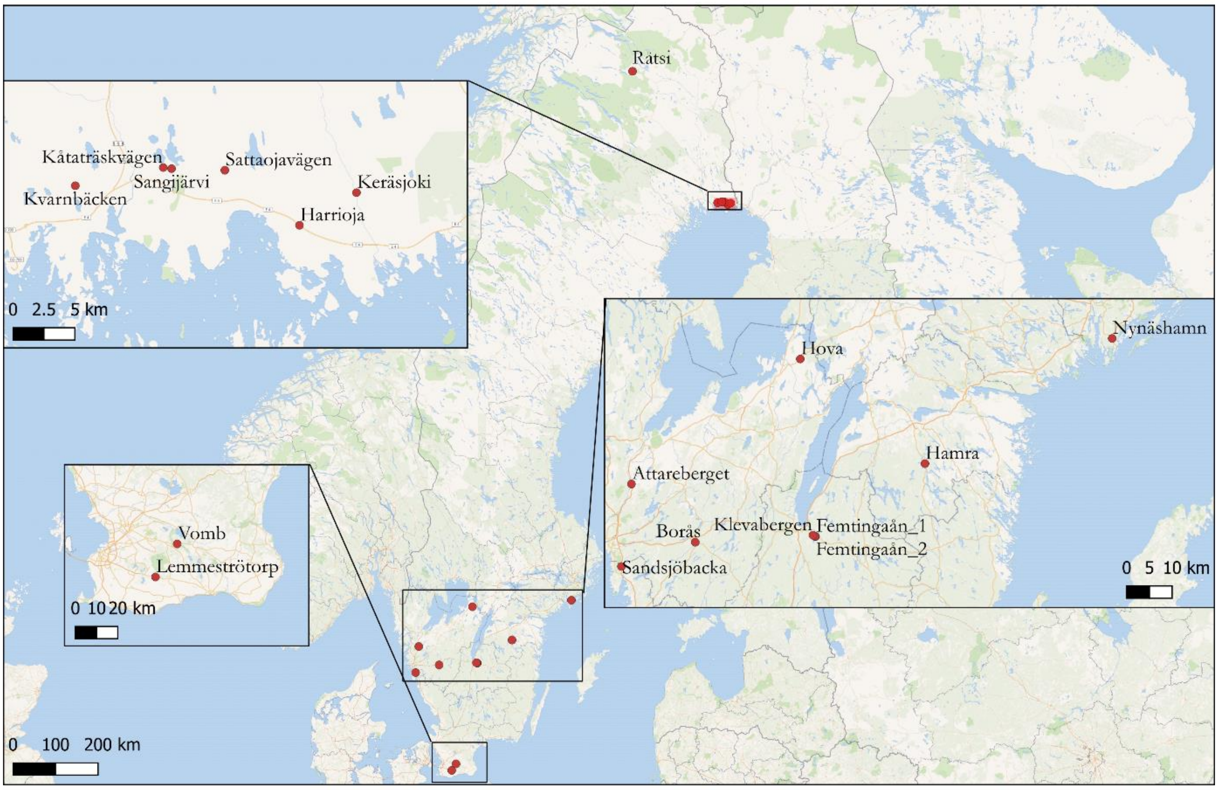

Figure 1 Map of Sweden showing the location of the 18 crossing structures included in this study. Eleven structures are located in the south and seven in the north**.**

Table 1 Overview and description of each crossing structure with dimensions, type and the period during which the structure was monitored

Site Name	Type	Area	Length (m)	Width (m)	Monitoring Period	# Weeks
Borås	Underpass	South	38.9	14.0	Jan - Jun 2019	26
Femtingaån_1	Underpass	South	22.0	2.8	Jun - Sep 2018	14
Femtingaån_2	Underpass	South	15.5	12.0	Jun - Sep 2018	14
Hamra	Underpass	South	17.1	3.0	Jun 2018 - May 2019	19
Keräsjoki	Underpass	North	7.0	54.0	Jul - Nov 2019	17
Klevabergen	Underpass	South	16.0	35.0	Jun - Aug 2018	12
Kvarnbäcken	Underpass	North	7.0	22.0	Jul - Nov 2019	17
Kåtaträskvägen	Underpass	North	7.0	8.0	Nov 2018 - May 2019	25
Sattaojavägen	Underpass	North	7.0	42.0	Nov 2018 - Jun 2019	25
Vomb	Underpass	South	15.3	10.0	Jan 2018 - Apr 2019	36
Attareberget	Overpass	South	44.0	14.0	Oct 2019 - Feb 2020	19
Harrioja	Overpass	North	59.0	5.0	Nov 2018 - Jul 2019	32
Hova	Overpass	South	41.0	40.0	Aug - Dec 2019	19
Lemmeströtorp	Overpass	South	44.0	40.0	Jul - Nov 2019	12
Nynäshamn	Overpass	South	58.8	8.0	Oct 2018 - Apr 2019	27
Råtsi	Overpass	North	21.3	50.0	Jul - Nov 2019	15
Sandsjöbacka	Overpass	South	64.0	32.0	Feb - Dec 2019	44
Sangisjärvi	Overpass	North	20.0	20.0	Nov 2018 - May 2019	25

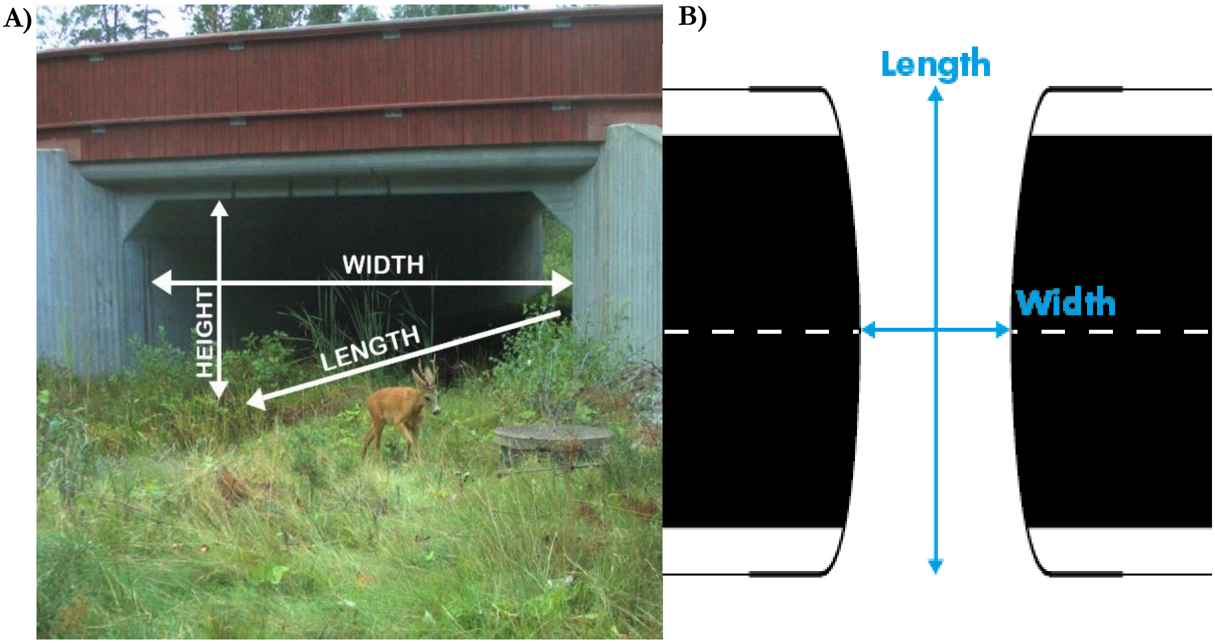

Figure 2 Images illustrate how dimensions are defined for each type of crossing structure in relation to the animal's path through the crossing structure, as demonstrated by the arrows. A: Underpass. B: Overpass.

The crossing structures in this study are primarily constructed for use by ungulates which are likely also more threatened by loss of connectivity than smaller mammals. Ungulates are therefore be the focal species group for this thesis. Since moose and roe deer are common throughout Sweden focus will be directed more specifically at these two species.

2.2 Monitoring with Camera Traps

Motion-triggered camera traps were used to monitor animal and human activity at each crossing structure. Three different camera models were used: Hyperfire 2 covert IR camera by Reconyx, both the regular and the professional model, and 2017 Spec Ops Advantage Trail Camera by Browning. All have internal infrared (IR) motion sensors and IR night vision (Browning 2018, Reconyx 2018a, Reconyx 2018b). All cameras were set to take 3-5 still images upon being triggered with the least possible delay between images (0.2s for Reconyx and 0.3s for Browning). All cameras were set to have the least possible delay until next trigger (no delay for Reconyx and 5 seconds for Browning). The range of the IR motion sensor and IR flash of the Reconyx cameras is 30 meters in optimal conditions, while the range of the Browning cameras is 24 meters. However, detection ranges are dependent upon weather conditions and the positioning of each individual camera. For all models, the motion sensor is activated by horizontal movement which means that they are more likely to be triggered by an animal moving past the camera rather than towards or away from it. Reconyx also specifies that movement should be in the bottom half of the frame.

For all but one location, only one brand was used. At one site (Hova) six Browning and two Reconyx cameras were used. The differences between the camera models in detection range and detection probability are assumed to be inconsequential for the purposes of this project.

At each location, 1-2 cameras were mounted to monitor activity inside or on the crossing structure, either in the middle of the crossing structure or by the entrance facing the structure. These are the passage cameras. In addition, 2-3 cameras were mounted at different locations within a radius of 20-40 meters from either entrance, a total of 4-6 cameras (Figure 3A). These cameras are referred to as reference cameras and the area that they monitor, the two half circles outside the entrances, is the reference area. In order to get an accurate estimate of animal activity in the reference area, reference cameras where spread out evenly and mounted so that their detection ranges overlapped as little as possible. If animal paths or tracks were visible, cameras were placed to monitor such paths whenever possible. This set-up was adapted from the method recommended by the Swedish Transport Administration for evaluating crossing structures using sand beds (Helldin and Olsson 2015).

The number of cameras used, and the size of the reference area varied between the sites which could influence the results. The effects of variable sampling efforts are discussed in section 4.4.

Cameras were mounted on pre-existing fence poles, trees or new wooden poles, approximately 0.5 to 1.5 meters from the ground (Figure 3B). Camera monitoring of all sites took place during 2018 to 2020. Each crossing structure was monitored for a minimum of 12 and a maximum of 44 weeks.

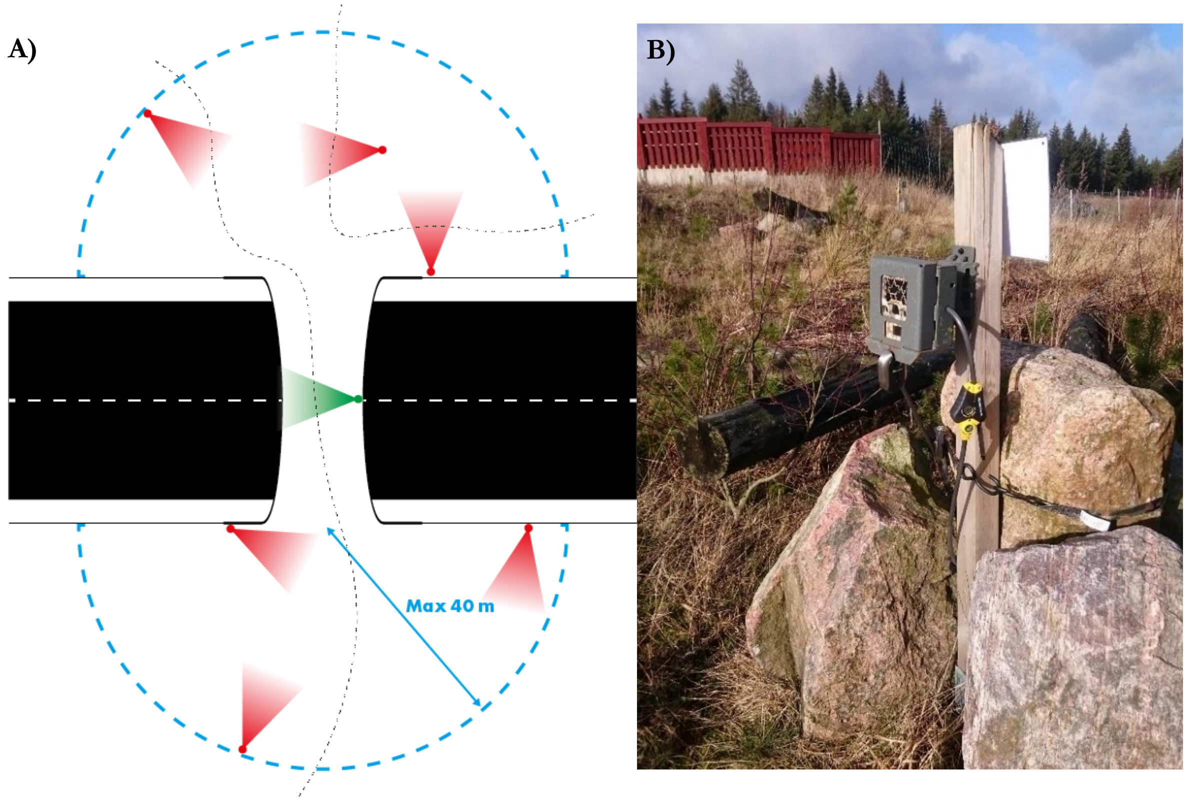

Figure 3 Images showing an example of how cameras were set up at a crossing structure. A) Example of placement of reference and passage cameras. Red dots with cones represent the reference cameras and their detection ranges. The green dot and cone represent the passage camera and its detection range. Blue, dashed lines mark the outer edge of the reference area. Black, dashed lines exemplify animal movement. B) Example of how cameras were mounted.

2.3 Analysing Images

I defined one animal activity as the observation of one individual of a certain species on one camera, separated by ten minutes or longer from earlier and later observations of the same species. All animal activities on all cameras were counted in this way. An animal was not counted again until it had been absent for more than 10 minutes in order to decrease the influence of a few highly active individuals (a method previously implemented by Keim, Lele et al. (2019)). Only if the images clearly showed different individuals was a species counted multiple times within 10 minutes, in which case all distinguishable individuals were counted. For example, five fallow deer walking past on one camera right after one another were counted as five animal activities for that camera.

When there was more than one passage camera (6 out of 18 structures), images from these cameras were analysed as one. This was done to avoid double counting of single activities in the same area since passage cameras always had partly overlapping detection ranges. However, since multiple passage cameras were used only for wide overpasses and underpasses the relative effectivity of these structures could potentially be overestimated.

Vehicles, pedestrians, cyclists etc. were also counted. Human use was counted using images from only the passage camera(s) for simplicity. Since humans typically entered the area in order to use the crossing structure, I judged that this would be enough to detect almost all human activity. At one site, Kåtaträskvägen, a large part of the human activity occurred on a connecting road within the reference area. Since most of this traffic was not captured by the passage camera it was included using additional cameras. The same human or vehicle was not counted again if it was recorded multiple times within 10 minutes since this was considered to be the same activity.

Empty images and images with animals where the species was indistinguishable did occur and were excluded from the analyses. This might have introduced a bias if detection probability and image quality differed between cameras and species (Hofmeester, Cromsigt et al. 2019).

2.4 Defining Effectivity and Calculating Activity Index

I defined effectivity as the difference in animal activity inside the crossing structure compared to the reference area. To calculate the effectivity of a crossing structure I firstly summed all activities per week for each reference camera and for the passage camera(s). To find the mean passage activity over the whole monitoring period, I calculated the mean weekly activity over all weeks for the passage camera(s). To get the average activity in any given part of the reference area (approximately the same size as was monitored inside the structure), I firstly calculated the mean activity over all reference cameras for each week. Using these values, I then calculated the mean weekly reference activity over the monitoring period. The effectivity response variable, hence called the activity index, was then calculated as the ratio of the total activity at the site which occurred inside the structure by dividing the passage activity by the reference activity added to the passage activity (Equation 1).

Equation 1 Calculation of activity index. The activity index is calculated by dividing the mean passage activity by the total animal activity, i.e. the sum of mean passage activity and mean reference activity.

$$Activity\ index = \frac{Mean\ passage\ activity}{Mean\ passage\ activity + Mean\ reference\ activity}$$

If the measured activity in the crossing structure is equal to the measured activity in the reference area the activity index will be 0.5. A low index value would indicate that a structure has a deterring effect while a high index value would indicate a funnelling effect. More importantly, the index can be used to compare the effectivity of different crossing structures.

The use of an activity index for controlling for animal abundance was first described by Yanes, Velasco et al. (1995) who used sand track data to analyse the effectivity of culverts for small vertebrates.

An activity index was calculated for a crossing structure only for species that were recorded, either in the reference area or in the crossing structure, at least five independent times. Since the raw data was the sum of activities over a week, at least one activity had to be recorded in at least five different weeks. This limit is used to avoid skewed indices due to random variation in data quality and behaviour of individual animals. A limit of tree independent observations has been used in a previous study (Seiler and Olsson 2009).

By defining effectivity in relation to the activity in the immediate surroundings, I control for differences in animal abundance between the sites. If one were to simply measured passage frequency this may describe landscape effects that differ between sites, rather than the effect of the crossing structure itself. However, since passage frequencies (number of passages per day) can be useful for comparison with similar studies this was also calculated. This was done by using the sum of activities per week for the passage camera(s) to find the average number of activities per day (dividing by 7) for each week and then taking the mean daily activity over the whole monitoring period.

2.5 Defining Covariates

The limited sample size in the data constrained the number of variables that could be included in a regression analysis. I therefore focused on the variables that were important for the effectivity of crossing structures according to the literature (Clevenger and Waltho 2000, Seiler and Olsson 2009) and that drive the cost of construction: Dimensions, human co-use and type of structure.

Crossing structure dimensions, width and length, were determined using construction plans that were retrieved from the Swedish Transport Administrations management system for bridges (Trafikverket 2019). Type of structure was included as a binary variable coded as overpass=1 and underpass=0.

To express human use as a single value, the mean number of human activities per day (pedestrians, cyclists, riders, or motorised vehicles) was calculated. This disregarded the fact that the magnitude of the disturbance could vary between different types of human use (e.g. the difference between a single passing pedestrian and five passing mopeds within 10 minutes) but it did indicate how frequently human activity occurred on average.

Crossing structures were monitored at different periods during 2018, 2019 and early 2020. To account for this difference, a variable representing the weight of the individual data collection period was defined for each crossing structure. Each week of the total data collection period was given a number where the first week was week 1 and the last monitoring week was week 111. For each crossing structure, the median data collection week was then determined. This variable was added as a covariate reflecting when the data was collected. However, this variable did not control for effects that may be caused by the season during which structures where monitored or the number of weeks and observations at a structure (see discussion on seasonal variation and sampling effort in section 4.4).

Table 2 describes all variables included in the global model which was then used for model selection. Values of these covariates are available in Appendix II.

Table 2 Descriptions of all variables included in the global regression

Variable	Description
Type	Overpass or underpass (coded 1, 0)
Width	The width of the crossing structure
Length	The length of the crossing structure
Human use	Mean number of human activities per day
Week	Median week of the data collection period

2.6 Statistical Analysis

Statistical analyses were only performed for moose, roe deer, fox and hare. For the other species (fallow deer, red deer, wild boar and badger) activity index values could only be calculated at fewer than ten crossing structures and I determined that this was too small of a sample size.

For the four species included in statistical analyses, firstly, a Mann-Whitney U test was performed in order to detect differences between data collected in 2018 and 2019. There was no significant difference between the groups for any species (Appendix III). Only one crossing structure was monitored in 2020 which is why this year was not included in the test.

Multiple linear regression analysis requires normally distributed residuals and uncorrelated covariates. For all but one out of the four species (roe deer, $W = 0.847$, $p=0.012$, $n = 16$; Shapiro-Wilks test), the activity index data was normally distributed ($W > 0.90$, $p \geq 0,05$, $n = 11, 17, 13$). Moreover, the distribution of the residuals from the multiple regressions did not show any strong tendency for deviation from normality (data not shown).

A Spearman's rank correlation matrix revealed significant correlation between width and median survey week ($r_s = 0.571$, $p = 0.013$, Appendix IV). This correlation did not cause any strong collinearity in the regression models (collinearity tolerance > 0.1) but may, however, make results more complicated to interpret.

The variables described above and summarized in Table 2 were included in a global regression model. To potentially reduce the number of variables further, while simultaneously identifying the most relevant variables, model selection was performed.

Firstly, the R function *regsubset* in package *leaps* (Lumley 2020) was used to find the best fitting model of each size, i.e. comparing R^2 of models with all possible combinations of one variable, two variables, three variables and so on.

Since goodness-of-fit increases with the number of predictor variables used (i.e. overfitting), another method was used to compare the models of different sizes returned by *regsubsets*. Akaike Information Criterion (AIC) estimates the log likelihood of a model and introduces a penalty for increased number of covariates. In this case, the function extract*AIC* in the R package *MuMIn* (Barton 2019) was used to calculate the AIC value of each of the models returned by *regsubsets* and the null model (including no covariates). In addition, the function *Weigths* from the same R package was used to calculate the relative likelihood of each model. The complete results of model selection are presented in Appendix V.

The model with the lowest AIC is the most parsimonious. However, this does not automatically mean that all other models can be rejected. The models that were selected for regression analysis were separated from the second most parsimonious model by at least 1 ΔAIC. Multiple linear regression analyses using the most parsimonious models were executed using the statistical software SPSS (IBM Corp. 2019).

3 Results

The activity index values for all species and for each site are presented in Appendix VI. Since passage frequencies can be useful for comparison with similar studies, these are presented in Appendix VII.

As shown by Figure 4, the median activity index was higher than 0.5 for all species. However, there was also great variation in the activity index at different structures for all species.

For several species there was not enough data to perform multiple linear regression analyses. The results for these species are instead presented descriptively. For roe deer, moose, fox and hare the results of model selection and multiple linear regression analyses are also presented in the following sections.

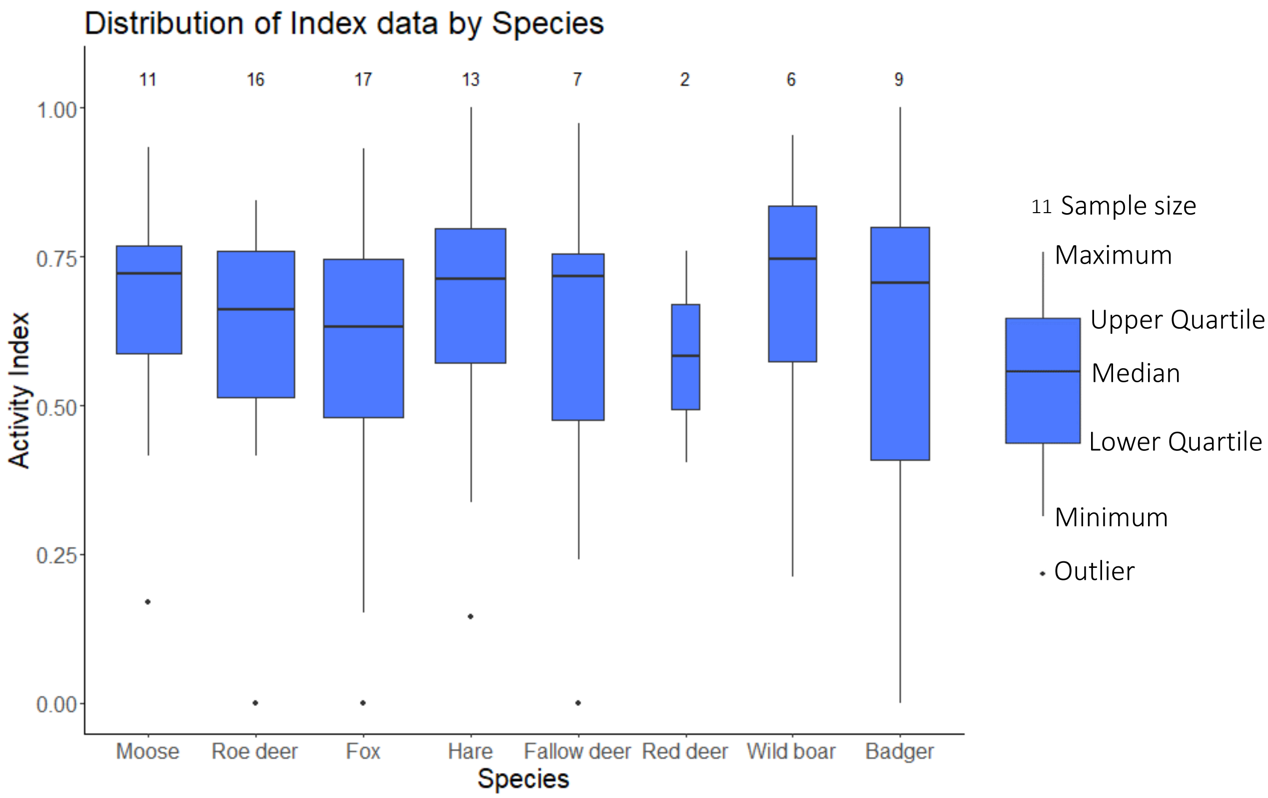

Figure 4 The boxplots describe the distribution of activity index values for each species. Sample sizes, number of structures where the species occurred five or more independent time, are given above each box.

3.1 Effectivity for Moose

For moose, activity index could be calculated for 11 out of 18 crossing structures. Five of these were underpasses and six overpasses. All the excluded structures were located in the southern region, this left four southern and seven northern sites. The activity index was highest at an eight-meter-wide and seven-meter-long underpass (0.93, Kåtaträskvägen) located in the northern region. The most parsimonious model according to R^2 and AIC included length, human use and type. The R^2 of this model was 0.70 and it had an AIC value 1.43 lower than the second best model (Appendix V). The result of the multiple linear regression is presented in Table 3. Human use and type were positively correlated with the activity index. A positive correlation with type means that the index was higher for overpasses. Length was negatively correlated with the activity index; this effect was small compared to the estimates of the other variables. Length and human use were significant at $p < 0.05$ while the effect of type was not.

Table 3 Result of multiple linear regression with activity index of moose.

Parameters	Estimate	SE	t value	p	Collinearity T
Intercept	0.7485	0.0723	10.359	1.69*10^-5	
Length	-0.0127	0.0035	-3.612	0.0086	0.339
Human use	0.1403	0.0559	2.510	0.0404	0.771
Type	0.2219	0.1387	1.600	0.1537	0.375

3.2 Effectivity for Roe deer

For roe deer, activity index could be calculated for 16 out of 18 crossing structures. The two excluded structures were both located in the northern region (one overpass and one underpass). The highest index was measured for the overpass Attareberget (0.86, 14m wide). For one of the narrowest underpasses (Hamra, 3.0m wide, 17.1m long), the activity index was zero.

The most parsimonious model of activity index according to R^2 and AIC included width, type and human use. The R^2 of this model was 0.58 and it had an AIC value 1.94 lower than the second best model (Appendix V). The result of the multiple linear regression of activity index for roe deer using this model is shown in Table 4. Human use was negatively correlated with the activity index, while the other covariates, type and width, were positively correlated (higher index for overpasses). The effects of width and human use were significant at $p < 0.05$ while the effect of type was not. The effect of type and human use were greater (larger estimates) than that of width.

Table 4 Result of multiple linear regression with activity index of roe deer.

Parameters	Estimate	SE	t value	p	Collinearity T
Intercept	0.4529	0.0742	6.107	5.28*10^-5	
Width	0.0069	0.0023	2.962	0.0119	0.976
Human use	-0.1306	0.0594	-2.197	0.0484	0.739
Type	0.1914	0.0922	2.077	0.0599	0.725

3.3 Effectivity for Fox

For fox, activity index was calculated for 17 out of 18 crossing structures. Only one underpass was excluded. The activity index was highest at a 20-meter-wide overpass (Sangijärvi, 0.93) and lowest at a 40-meter-wide overpass (Hova, 0.15). The most parsimonious model according to R^2 and AIC included only length (negative correlation). The R^2 of this model was 0.166 and it had an AIC value 1.09 lower than the second best model (Appendix V). The result of the multiple linear regression is presented in

Table 5. The effect of length on the activity index was small and not statistically significant.

Table 5 Result of multiple linear regression with activity index of fox.

Parameters	Estimate	SE	t value	p	Collinearity T
Intercept	0.0740	0.1002	7.390	2.25*10^-6	
Length	-0.0050	0.0029	-1.730	0.1040	1.000

3.4 Effectivity for Hare

For hare, activity index was calculated for 13 out of 18 crossing structures; seven underpasses and six overpasses. The activity index was highest at a 12-meter-wide underpass (Femtingaån_2, 1.00) and lowest at a 40-meter-wide overpass (Hova, 0.15). The most parsimonious model according to R^2 and AIC included human use and length, both negatively correlated with activity index. The R^2 of this model was 0.50 and it had an AIC value 1.31 lower than the second best model (Appendix V). Only the effect of human use on activity was significant at $p < 0.05$ (Table 6).

Table 6 Result of multiple linear regression with activity index of hare.

Parameters	Estimate	SE	t value	p	Collinearity T
Intercept	0.8965	0.0969	9.257	3.21*10^-6	
Human use	-0.1397	0.0626	-2.230	0.0498	0.955
Length	-0.0054	0.0032	-1.703	0.1193	0.955

3.5 Effectivity for Species with Limited Data

For fallow deer, activity index was calculated for seven crossing structures; two underpasses and five overpasses. The activity index was high (above 0.7) at all overpasses and low (0 and 0.27) at the two underpasses. However, all but one of the overpasses were also larger than the two underpasses. The activity index was highest at Nynäshamn (0.97, 8m wide overpass).

Red deer was only recorded at four out of 18 crossing structures, three overpasses and one underpass, and activity index could be calculated for only two (one overpass and one underpass). The activity index was highest at the overpass (Attareberget, 0.76, 14m wide) and lowest at the underpass (Vomb, 0.42, 10m wide).

For wild boar an activity index was calculated for 6 out of 18 crossing structures; five overpasses and one underpass. The activity index was highest at Nynäshamn (0.95, 8m wide overpass) and lowest for Sandsjöbacka (0.21, 32m wide overpass).

For badger activity index was calculated for 10 out of 18 crossing structures; three overpasses and seven underpasses. The activity index was low (<0.5) at three structures and high (>0.6) at the rest. At one underpass (Femtingaån_2, 12m wide, 15.5m long), the activity index was 1 (no activity recorded in the reference area).

4 Discussion

According to my results, there was a small positive correlation between effectivity for roe deer and width while effectivity for moose had a small negative correlation with the length of structures. For both species, there was a strong tendency for overpasses to be more effective than underpasses. In addition, human use was positively correlated with effectivity for moose but negatively correlated with effectivity for roe deer. In addition, length was negatively correlated with the effectivity for both fox and hare and human use was negatively correlated with the effectivity for hare.

For the other species, fallow deer, red deer, wild boar and badger, there was not enough data to statistically evaluate the variation in effectiveness between crossing structures. However, for all species, it is possible to draw the conclusion that many crossing structures in this data set seemed to be effective in facilitating animal movement. For all species, a third or more of the structures had index values above 0.7. The average activity index values are high compared to those in a previous study which included narrower structures (Seiler and Olsson 2009). This study also used activity index values for estimating effectivity and should be comparable to a degree, although the methods differ in some ways.

The activity index values also reiterated the fact that not all crossing structures function equally well. Some structures did seem to have a strong deterring effect on one or more species, as their index values were well below 0.5. One structure that stood out in this respect was Hamra. This structure had an activity index of 0 for both roe deer and fallow deer, despite activity of these species being high in the reference area. This would suggest that this structure is not at all suited for use by large mammals.

4.1 What Factors Influence Effectivity?

Dimensions of the crossing structures were not as influential to the effectivity as expected compared to previous studies on effectivity for wild ungulates (Clevenger and Waltho 2005, Seiler and Olsson 2009).

The effectivity for moose seemed to be higher at shorter crossing structures. This effect was much smaller than that of human use and type and may be a by-product of a few highly used structures in the northern region during spring migration. Most structures in the north are railway crossings which are shorter than road crossing structures. The pressure on migrating moose to use less suitable crossing structures may be higher than under normal circumstances which might skew the activity index at these sites. With that said, it is possible that length can become a limiting factor for effectivity of structures that are otherwise wide enough, at least for underpasses. That is because increased length will reduce the overall openness (the ratio between length, width and height) which has previously been shown to reduce effectivity of underpasses (Clevenger and Waltho 2005, Seiler and Olsson 2009). Unfortunately, the length may be more difficult to adjust than the width when planning the construction of a new crossing structures.

The reason why there is no strong effect of width in this data set might be because it includes wider structures than previous studies (Seiler and Olsson 2009). For moose, only three of the included structures were less than 20 meters wide.

For both moose and roe deer the correlation coefficient of type was larger than that of the other variables. Although these correlations were not significant, they indicate that, with all other parameters held equal, overpasses are more effective than underpasses. To the best of my knowledge, no study has investigated the difference in effectivity between overpasses and underpasses previously.

The reason overpasses are more effective than underpasses might also relate to openness; since overpasses do not have a ceiling, they are inherently more open. However, it is possible to imagine other reasons such as vegetation or connection to the surrounding landscape.

A negative correlation between effectivity and human use is expected since increased human use can be predicted to increase disturbance and stress to animals which could make animals less likely to use a structure. This relationship between human use and effectivity has also been demonstrated previously (Clevenger and Waltho 2005). Therefore, the positive correlation between human use and activity index for moose is counterintuitive. It could be interpreted that moose are less sensitive to human use than roe deer or it might be the case that moose, for any other reason, use crossing structures that humans also prefer for recreational use.

In this study, human use was measured as the average number of human activities per day. This measure of activity disregards the time separation between animal activity and human activity. Most animal activity occurs during dusk and dawn (Bonnot, Couriot et al. 2020) while most human activity occurs during the day (Knufinke, Helldin et al. 2019). To better understand the true effect of human use may require studying the interactions on a finer scale, a subject that is currently being explored (Knufinke et al. in prep).

4.2 Effectivity for Medium-Sized Mammals

An important aspect to consider regarding the medium-sized mammals included in this study is that, while the road or railway at all crossing structures in the study are fenced, all are fenced with wide mesh fences for large mammals. Hare, fox and badger will easily pass through these fences. One study showed that, at least for elk, the probability that an animal will use a crossing structure is much lower when there is no fencing (Dodd, Gagnon et al. 2007). While there is some risk of mortality, small, mobile animals may be crossing over even major highways and railways with high traffic density just as frequently as they are passing through a crossing structure. Therefore, the barrier effects are likely to be minor and it is not possible to draw the same conclusions about the effectivity of a structure in restoring connectivity if it has not been lost to begin with.

In addition, monitoring medium-sized animals with camera traps in large areas is challenging. Detection probability decreases with body mass (Hofmeester, Cromsigt et al. 2019), meaning that there will be more uncertainty in the data for these smaller species. Badger was rarely ever detected in wide (>20 meters) over- or underpasses. It might be possible that this species prefers narrow crossing structures, but it is more probable that they are simply easier to detect in smaller structures.

For fox the most parsimonious model had a low R^2 value and clearly did not explain any large proportion of the variation in the activity index. These things combined imply that another approach may be necessary in order to properly understand the effects of crossing structures on medium-sized mammals. However, the model of effectivity for hare had better support and, despite the mentioned issues, it is interesting to note that there is a significant negative effect of human use on this species as well.

4.3 Implications for Management and Efficient Mitigation

When assuring the efficiency of mitigation, maximizing the effectivity of one single crossing structure is not necessarily the best plan of action (Karlson, Seiler et al. 2017). Economic and environmental costs must be taken into consideration as well.

Karlson, Seiler et al. (2017) demonstrated that many small crossing structures created more connectivity across a barrier than did fewer large structures, which is why it is important to find the minimum size requirements for different species in order to maximize the benefit, number of functional crossing structures, with a limited amount of resources.

In this study, the width of crossing structures was not as important as previously suggested, possibly because many of the included structures were generally wide enough. More detailed research is needed but, even though the width had a small effect on roe deer, it is possible that the widest structure types do not add much benefit to the effectivity for ungulates.

The results of this study also indicate that overpasses support a higher activity index for moose and roe deer compared to underpasses. This may be the case also for other ungulates, although further data collection is needed. The decision of whether to construct an overpass or an underpass is usually dependant on the topography of the area. However, if more evidence can be made that an overpass is more effective than the same size, or even a larger, underpass this would likely sway the decision in some cases.

In theory, limiting human use, for example by creating protected areas, is an easy and cheap adjustment and my results indicate that this could benefit some species. However, limiting human movement may be more difficult in practise.

In this study I only considered effectivity at the species level. It is also interesting to consider effectivity at the multi-species level. If different species have different requirements it may be necessary to make the decision on whether to optimize a new crossing structure for as many species in that area as possible or to focus on optimizing for one or a few focal species.

It should also be reiterated that crossing structures can only restore connectivity for animals (species and individuals) that come close to roads and railways. By defining effectivity in relation to the reference area that was defined in this study, I excluded avoidant animals and disregarded the abundance of animals in areas further from the infrastructure. Other study designs would be necessary to understand the effectivity of crossing structures beyond their basic function; how they impact landscape connectivity for populations.

4.4 Limitations and Considerations for Future Research

Sample selection and sampling effort

Unknown variation is likely introduced into the data due to variation in the camera set-ups, detection ranges of cameras, number of cameras used, time of year, size of the reference area etc. The crossing structure sites are inherently different, but some factors could be controlled for to a greater extent. In this study, monitoring roughly covered between 15% and 46% of reference areas due to variation in both number of cameras and size of reference areas. These percentages are only correct provided that all cameras had the same detection range (I selected

20 meters as a plausible average) while in practise, detection ranges varied due to vegetation, topography and how each camera was angled.

To get an accurate estimate of the mean activity it is not necessary to cover the whole reference area or detect every animal, but if the coverage is low the risk of missing the variation in activity is high and thus also the risk of either over- or underestimating the overall activity level.

Future studies could also try to better standardize the way activity is measured in the reference area and in the crossing structure by only having a single passage camera or, for large structures, having multiple non-overlapping passage cameras from which an average passage activity can be calculated in the same way as for the reference area. This will make sure that the activity is not overestimated in either area.

In addition, the sample (included crossing structures) in this study was not randomly selected. Several structures in the northern region and a few in southern region are located close to one another and some of these northern structures are also similar in the sense that they are short, railway underpasses. This might mean that some structures were not statistically independent and that there is a risk of pseudoreplication.

Minimum number of observations

In this study I chose to only calculate activity index if there were at least five independent observations of a species at a certain crossing structure. This was a trade-of between being able to use data from as many crossing structures as possible while still obtaining reliable index values. I believe it would be beneficial to investigate the effect of the number of observations on the index to determine an appropriate minimum number of observations. It is possible that this number will be higher than five.

Model selection

When preforming model selection using AIC, the rule of thumb is that models for which $\Delta AIC < 2$ have good support and should not be rejected (Burnham and Anderson 2004). Even though this is only a guideline, it should be mentioned that I selected a lower ΔAIC threshold. The most parsimonious models in my analyses had an AIC value between 1 and 2 less than the second most parsimonious models. I decided that this was good enough for the purpose of this study and opted to proceed to regression analyses with the most parsimonious models only instead of proceeding with multiple models for each species.

Seasonal variations

The length of sampling period for each crossing structure should not impact the activity index values. In addition, a longer sampling period does not equal more observations since animal densities differed between sites. However, what time of year a structure was monitored could impact the activity index because some species exhibit different behaviour during different seasons. For example, the results for moose effectivity may be skewed due to migrating behaviour of moose in the northern region. Migration occurs in fall and spring and is directional (Cederlund and Sand 1994). For roe deer there is a similar issue with territoriality. Male roe deer are territorial from July to August (Cederlund and Liberg 1995), which will affect their behaviour and movement patterns and possibly skew the activity index during that period. Because of this it would be better to monitor all structures during the same season. Even better still would be to monitor all structures for several years to include between year variation which might occur.

Alternative response variable

While I believe the activity index to be useful for estimating and comparing the effectivity of crossing structures, its values are not easily translated into ecological effects. A different approach would be to, instead of estimating the activities, count direct ratio of passages to nonpassages. While this approach requires full coverage of a reference area (i.e. using more cameras or a smaller reference area) and a more labour-intensive image analysis procedure, it could be a suitable alternative method for monitoring large mammals at small and medium-sized structures. This method of determining the repel-rate has been implemented by Kintsch, Cramer et al. (2020) and this camera set-up is also described in the Swedish transport administrations guidelines for monitoring crossing structures with camera traps (Helldin and Olsson 2015). This method would result in a similar, but possibly more intuitively understandable response variable.

Further research on structure types

To continue to investigate differences between overpasses and underpasses, I think it would be useful to extend the dataset to include twice as many crossing structures of each type. In this way, direct comparisons could be made between the types. This dataset should include more narrow structures if the aim is to find the minimum acceptable size of each type. Preferably the included structures should all be located within an area with similar species composition and species behaviour (e.g. either northern or southern Sweden) to ensure that enough data can be collected for each species and that the data is comparable.

5 Conclusions

Most crossing structures included in this study were, according to the activity index, effective for many species in the sense that they supported higher activity than the reference area. However, it was also clear that not all structures function equally well and one was not at all functional.

The results indicated that both moose and roe deer used overpasses more effectively than underpasses. Dimensions had some impact on the effectivity but to a lesser degree than expected. Width was positively correlated with the effectivity for roe deer only. Future studies should focus on directly comparing the two types of structures and finding minimum size requirements for each type. Such studies should include more and narrower structures.

This study could not shed much light on how human use impact effectivity overall, but the fact that this factor was negatively correlated with the effectivity of crossing structures for two different species means that it should warrant attention in future studies.

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Appendix I

Popular Science Summary

WHY DIDN'T THE MOOSE CROSS THE ROAD?

No one would want to cross a busy highway first thing in the morning just to get some breakfast, it's a very stressful and not at all safe way to start the day. However, many wild animals, such as roe deer and moose, may not have a choice.

Many roads and railways divide natural habitats into small patches. This means that crossing them can be necessary for wildlife to access vital habitats and resources or to find a mate. In addition, since these ungulates can cause dangerous traffic accidents, exclusion fencing is often used to keep them accessing major roads and railways. This creates strong barriers which makes ecologically necessary movement even more difficult. The long-term consequences of this decreased landscape connectivity include reduced abundance of animals and loss of species richness. It is possible to restore landscape connectivity by providing enough places where wildlife can cross safely. Animals can use tunnels and bridges designated for smaller roads, cyclist, and pedestrians, but there are also structures created specifically for animal use.

The structures that ungulates can potentially use come in many shapes and sizes, ranging from 3-meter-wide pedestrian tunnels to over 40-meter-wide green bridges. By building many small, or otherwise cheap, crossing structures connectivity can be improved over larger areas then by building few large structures. However, structures still need to be functional and all structures do not function equally well, some may not be used by a single animal!

In my study I evaluate the effectivity of 18 different crossing structures across roads and railways in Sweden which could be used by moose and roe deer. In addition, I investigated how width, length, type of structure (bridge or tunnel) and human activity influence the effectivity. All crossing structures were evaluated using motion triggered camera traps. By placing cameras in and outside each crossing structures it was possible to measure animal activity and determine how the activity inside the structure compared to that in the surrounding habitat. For each structure, this gave a value of how attracting or deterring it was. This method controls for differences in animal abundances at different sites.

This moose cow has just used a greed bridge to safely cross the railway that can be seen in the background.

While most crossing structures in this study seemed to work well for moose and roe deer all did not function equally well and some very poorly. Previous studies have shown that the width of a crossing structure likely influences its effectivity for ungulates. According to my study there was a small effect of width on the effectivity of roe deer but for moose, width was not important. For moose, effectivity was higher at shorter structures and for both species the effectivity was higher at bridges compared to tunnels.

Mitigation measures should not use more resources than necessary. My results indicate that very wide structures may not add as much benefit as previously through. The decision of whether to construct a tunnel or a bridge is often determined by the topography of an area. However, if a smaller bridge can be shown to function as well as a wider tunnel, this may sway the decision toward bridges in some cases. The construction of more narrow bridges may be the way forward toward effective and efficient mitigation, but we still don't fully understand why an animal does, or does not, cross the road.

Appendix II

Table showing the values of all covariates for each site.

Site name	Type	Length (m)	Width (m)	Week	Human use
Borås	0	38.9	14.0	65.5	0.027
Femtingaån_1	0	22.0	2.8	30.0	0.051
Femtingaån_2	0	15.5	12.0	30.0	0.102
Hamra	0	17.1	3.0	54.0	1.694
Keräsjoki	0	7.0	54.0	89.0	0.314
Klevabergen	0	16.0	35.0	28.5	0.033
Kvarnbäcken	0	7.0	22.0	89.0	0.05
Kåtaträskvägen	0	7.0	8.0	58.5	2.096
Sattaojavägen	0	7.0	42.0	59.0	0.194
Vomb	0	15.3	10.0	19.0	0.115
Attareberget	1	44.0	14.0	102.0	1.213
Harrioja	1	59.0	5.0	64.5	0.694
Hova	1	41.0	40.0	94.0	2.580
Lemmeströtorp	1	44.0	40.0	88.5	0.333
Nynäshamn	1	58.8	8.0	54.0	0.373
Råtsi	1	21.3	50.0	90.0	0.419
Sandsjöbacka	1	64.0	32.0	82.0	1.889
Sangijärvi	1	20.0	20.0	59.0	0.415

Appendix III

Results of Mann-Whitney U tests for differences between passage frequency and activity index data collected in 2018 and 2019.

Species	Data type	Mann-Whitney U	p	N
Moose	Passage Frequency	94.0	0.311	18
	Activity index	88.5	0.334	11
Roe deer	Passage Frequency	94.0	0.311	18
	Activity index	51.5	0.444	16
Fox	Passage Frequency	91.0	0.387	18
	Activity index	61.0	0.726	17
Hare	Passage Frequency	89.5	0.428	18
	Activity index	35.0	0.115	13

Appendix IV

Spearman's rank correlation matrix showing Spearmans correlation coefficients (r_s) and significance levels for correlations between all pairs of covariates. Row one for each covariate shows the regression coefficients r_s and row two shows the p values.

Spearmans ranked corr.	Length	Width	Human use	Median week
Length	1.000	-0.182	0.350	0.246
	.	*0.469*	*0.155*	*0.324*
Width		1.000	-0.039	0.571
		.	*0.877*	*0.013*
Human use			1.000	0.386
			.	*0.114*
Median week				1.000
				.

Appendix V

The tables show results of the model selection for the activity index of each species. The model with the lowest AIC is given ΔAIC = 0. Weight is the relative probability that the model is the most parsimonious compared to the other models.

Moose index (N=11)

#	Covariates	R^2	AIC	ΔAIC	Weight
3	Length + Human use + Type	0.7036	-40.19	0.00	0.476
2	Length + Human use	0.5953	-38.76	1.43	0.233
4	Length + Human use + Type + Width	0.7040	-38.21	1.98	0.176
5	Length + Human use + Type + Width + Week	0.7042	-36.21	3.98	0.065
1	Length	0.3248	-35.13	5.06	0.038
0		-	-32.81	7.38	0.012

Roe deer index (N=16)

#	Covariates	R^2	AIC	ΔAIC	Weight
3	Width + Human use + Type	0.5759	-56.13	0.00	0.487
4	Width + Human use + Type + Length	0.5774	-54.19	1.94	0.185
1	Width	0.3611	-53.58	2.55	0.136
2	Width + Human use	0.4233	-53.21	2.92	0.113
5	Width + Human use + Type + Length + Week	0.5778	-52.20	3.93	0.068
0		-	-48.41	7.72	0.010

Fox index (N=17)

#	Covariates	R^2	AIC	ΔAIC	Weight
1	Length	0.1663	-47.56	0.00	0.397
0		-	-46.47	1.09	0.230
2	Length + Human use	0.1975	-46.21	1.35	0.202
3	Length + Human use + Width	0.2280	-44.89	2.67	0.103
4	Length + Human use + Width + Type	0.2499	-43.36	4.20	0.049
5	Length + Human use + Width + Type + Week	0.2504	-41.37	6.19	0.018

Hare index (N=13)

#	Covariates	R^2	AIC	ΔAIC	Weight
2	Human use + Length	0.4982	-41.81	0.00	0.419
1	Human use	0.3526	-40.50	1.31	0.218
3	Human use + Length + Week	0.5121	-40.18	1.63	0.185
4	Human use + Length + Week + Type	0.5419	-38.99	2.82	0.103
0		-	-36.85	4.96	0.035
5	Human use + Length + Week + Type + Width	0.5459	37.11	4.70	0.040

Appendix VI

Activity index values for each species and crossing structure.

Site name	Moose	Roe deer	Fallow deer	Red deer	Wild boar	Fox	Hare	Badger
Borås	-	0.485	-	-	-	0.667	-	0.381
Hamra	-	0.000	0.000	-	-	0.845	0.871	0.706
Harrioja	0.169	0.415	-	-	-	0.000	0.336	-
Hova	0.753	0.658	0.711	-	0.855	0.152	0.145	-
Klevabergen	0.645	0.795	-	-	-	0.4	-	-
Kvarnbäcken	0.530	0.646	-	-	-	0.746	0.571	0.667
Kåtaträskvägen	0.933	-	-	-	-	0.611	0.460	-
Lemmeströtorp	-	0.709	0.756	-	0.717	0.479	0.713	0.408
Nynäshamn	-	0.786	0.973	-	0.953	0.786	-	0.741
Vomb	-	0.546	0.269	0.423	0.525	0.695	0.662	0.730
Attareberget	0.850	0.844	0.717	0.759	0.774	0.499	0.620	-
Femtingaån_1	-	0.433	-	-	-	-	0.642	0.939
Femtingaån_2	-	0.615	-	-	-	0.632	1.000	1.000
Keräsjoki	0.671	0.747	-	-	-	0.474	-	0.000
Råtsi	0.721	0.750	-	-	-	0.725	0.770	-
Sandsjöbacka	0.416	0.663	0.753	-	0.213	0.630	-	-
Sangijärvi	0.755	-	-	-	-	0.931	0.824	-
Sattaojavägen	0.781	0.828	-	-	-	0.893	0.797	-

Appendix VII

Mean passage frequency per day for each species and crossing structure.

Site name	Moose	Roe deer	Fallow deer	Red deer	Wild boar	Fox	Hare	Badger
Borås	0.005	0.520	0	0	0	0.265	0.027	0.043
Hamra	0	0	0	0	0	0.839	0.756	0.089
Harrioja	0.004	0.018	0	0	0	0	0.281	0
Hova	0.391	1.622	0.812	0.022	0.098	0.029	0.179	0
Klevabergen	0.116	1.673	0	0	0	0.012	0	0.043
Kvarnbäcken	0.168	0.176	0	0	0	0.092	0.017	0.033
Kåtaträskvägen	0.168	0	0	0	0	0.066	0.061	0
Lemmeströtorp	0	2.889	17.480	0.062	1.472	0.090	0.562	0.069
Nynäshamn	0.010	0.815	0.047	0	8.355	0.283	0.005	0.026
Vomb	0.003	1.567	0.234	0.159	5.667	0.189	0.195	0.088
Attareberget	0.279	0.467	0.061	0.083	3.579	0.022	0.022	0.023
Femtingaån_1	0	0.336	0	0	0	0	0.132	0.276
Femtingaån_2	0	0.123	0	0	0	0.030	0.142	0.101
Keräsjoki	0.244	0.535	0	0	0	0.025	0	0
Råtsi	0.153	0.095	0	0	0	0.399	0.751	0
Sandsjöbacka	0.031	0.254	1.214	0	0.026	0.097	0.006	0
Sangijärvi	0.080	0.006	0	0	0	0.201	0.276	0
Sattaojavägen	0.692	0.200	0	0	0	0.132	0.286	0