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Factors affecting usage of crossing structures by wildlife – A systematic review and meta-analysis

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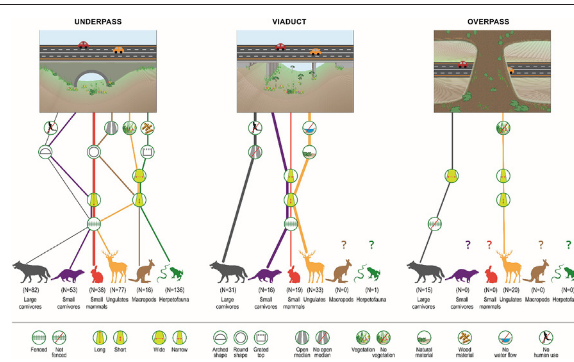
HIGHLIGHTS

- We reviewed 270 empirical papers on the effectiveness of wildlife crossing structures.
- Only 28% of global studies reported the proportion of successful crossings to overall approaches.
- Viaducts are the most effective type of crossing structure for large mammals.
- Natural materials and round shapes are preferable in the design of crossing structures.
- Structures designed for dual use are less effective than those designed exclusively for wildlife.

GRAPHICAL ABSTRACT



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ABSTRACT

Wildlife crossing structures (WCS) are widely used to allow for safe animal movement across roads, promoting both human safety and wildlife conservation. These structures are expensive to build and maintain, and therefore cost-effective design is essential. Although there has been much research to date on the factors affecting the usage of WCS by wildlife, no attempt has been made to synthesize these results and assess the current state of knowledge. We conducted a systematic review of the scientific and professional literature to assess the state of empirical evidence on WCS and a meta-analysis to explore the factors that influence their effectiveness. We identified a total of 270 studies that reported empirical results spanning four decades of research. Most studies (161) measured the number of crossing events without monitoring approaches to the structure, thus limiting the ability to assess WCS effectiveness. Only 77 studies measured the proportion of successful crossings to approaches, which was the type of data used for meta-analysis.

Our meta-analysis results show that viaducts are the most effective type of WCS for large mammals. For example, the odds of ungulates crossing through a viaduct are 2.9 times that of an overpass, and 3.6 times that of an underpass. WCS built specifically for wildlife are used significantly more than those built for dual use by humans and wildlife. For large carnivores, the odds of using a dedicated WCS are 15.9 times that of a structure used concurrently by humans. We additionally found that natural materials and round shapes are preferable in the design of effective WCS. Altogether, these results highlight the importance of adopting large-scale monitoring of wildlife crossing structures. More broadly, we conclude that further research focusing on under-studied species and structure characteristics is needed to facilitate cost-effective mitigation efforts that reduce wildlife-vehicle collisions and promote wildlife conservation.

Abbreviations: WCS, wildlife crossing structures; PSC, proportion of successful crossings.

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Contents

1. Introduction

The global transportation infrastructure network has been expanding rapidly in the past century, and is expected to expand much further in the coming decades (Laurance et al., 2014). Transportation infrastructures such as roads and railroads are recognized as a major threat to global biodiversity (Forman and Alexander, 1998; Torres et al., 2016). Roads act as a barrier to wildlife movement within and between habitats and increase mortality due to vehicle collisions (Fahrig and Rytwinski, 2009). Some wildlife species tend to avoid the unnatural surface of the road and the disturbances associated with roads such as moving vehicles, noise, and light (D'Amico et al., 2015a). Roads thus reduce connectivity, fragmenting animal populations into small subpopulations that are vulnerable to local extinction, threatening their long-term viability, and ultimately decreasing biodiversity (Rytwinski and Fahrig, 2015; Bennett, 2017). Much effort has been put forth to mitigate these effects (van der Ree et al., 2007). It is becoming increasingly common to install wildlife crossing structures (WCS) allowing for safe animal movement, improving human safety, and reducing property damage (Clevenger and Waltho, 2005; Forman et al., 2003; van der Grift et al., 2013). WCS are designed to facilitate movement of animals, connect populations, and reduce wildlife mortality (Corlatti et al., 2009). There are multiple types and designs of structures, from small culverts to open-span viaducts and large overpasses. Globally, hundreds of wildlife overpasses and underpasses have been constructed in the past 50 years, most commonly in Europe and North America, and the rate of construction has been steadily rising over time (Seidler et al., 2018). Although there has been much research to date on the factors affecting the usage of crossing structures in specific case studies, no attempt has been made to synthesize these results and assess the quality of research and the current state of knowledge. Here, we attempt to address these knowledge gaps using a systematic review and meta-analysis.

Wildlife crossing structures are expensive to build and maintain, costing up to millions of dollars for a single overpass, and global costs of these mitigation measures exceed hundreds of millions of dollars (Ascensão and Mira, 2007; Glista et al., 2009). Therefore, these structures should be cost-effective and designed to allow for maximal use by target species. Studies on the usage of WCS have explored the variation in species preferences for crossing structure characteristics. However, although preferences vary across species, some studies revealed that differences in use patterns are more pronounced between functional species groups, delineated by body size and ecological function (Clevenger and Waltho, 2000; Ascensão and Mira, 2007). Several studies have focused on the impact of structure dimensions (i.e., length, width, height, and openness), particularly for large mammals, demonstrating negative effects of structure length on use by ungulates (Ng et al., 2004; Clevenger and Waltho, 2005; Wang et al., 2018). For large and small carnivores, increasing WCS width was shown to have a positive effect (Craveiro et al., 2019; Serronha et al., 2013; Grilo et al., 2008; Mata et al., 2003), but these results were not consistent (Seiler and Olsson, 2009). Other structural attributes including shape, substrate and construction material have not been widely studied, although some studies have highlighted that these attributes can also influence use patterns (Smith, 2003). For example, it was shown that salamanders prefer a sandy substrate over bare concrete (Patrick et al., 2010). Studies of herpetofauna are scarce and show mostly insignificant results, although structure length has been shown to have negative effects for reptiles in some examples (Ascensão and Mira, 2007; Woltz et al., 2008). The large variation in responses to WCS characteristics poses considerable challenges to WCS planning and requires a better understanding of this interspecific variation.

Beyond WCS characteristics, the environment surrounding the structure can also play a role in the level of use by wildlife. Human activity near the structure was studied in several cases and results demonstrate conflicting responses to human presence, regarding both ungulates and large carnivores (Ng et al., 2004; Clevenger, 1998; Wang et al., 2018; Georgii et al., 2011; Grilo et al., 2008; Clevenger and Waltho, 2000). Fencing is considered as one of the key road mitigation measures that is used to prevent animals from accessing roads and direct movements towards WCS (van der Grift et al., 2013). Fencing appears to promote ungulate use of underpasses (Dodd et al., 2007; Huijser et al., 2016). Other attributes of the surroundings were studied, for instance vegetation cover at the entrance of the structure, with mostly conflicting results as in the case of small non-carnivores showing both negative and positive effects (Rodriguez et al., 1996; Grilo et al., 2008; Smith, 2003). Differences between the usage of various structure types has been explored by few studies, mostly for small mammals, for which a preference for overpasses over culverts has been found (Mata et al., 2003). These results regarding the effects of structural and environmental factors on usage reflect the risk-disturbance hypothesis. It has been suggested that risk-avoidance responses related to anthropogenic stimuli cause deviations in behavior relative to that expected without human influence (Frid and Dill, 2002). Thus, use of structures that allow for safe passage is diminished when the structure characteristics and surroundings are perceived as risky by wildlife.

Many studies on WCS have documented the use of crossing structures by recording the number of animals that cross through a structure. Researchers use motion cameras, track beds, radiotracking and human observations to identify successful crossing events (van der Ree and Tonjes, 2015). While this is an important measure for assessing functionality of each structure as a conduit for local wildlife movement, the number of crossing events alone provides little information on a structure's effectiveness in comparison with other possible structure designs (Chambers and Bencini, 2015). Wildlife population densities and the permeability of the surrounding landscape influence the number of approaches to individual structures. If the number of approaches to the structure is not measured, it is unknown whether the number of crossing events constitutes a large or small proportion of the individuals that could have potentially used the structure (Clevenger, 2011). Hence, conclusions from such studies might be biased regarding the effects of structure attributes on the expected usage by wildlife and are difficult to generalize. Studies that did report the number of approaches as well as successful crossings have used the same tracking methods as mentioned above, but at a larger area surrounding the crossing structure (Andis et al., 2017). This method allows for the identification of individuals that explore the area of the structure but avoid using it to cross through.

Planning of cost-effective WCS requires unbiased knowledge of the structural and environmental factors that affect usage by different taxa, so that funds can be effectively directed to build structures which will most likely be used by target species. In this study, we aimed to understand the current state of empirical literature regarding the effects of WCS use by wildlife. We ask how much of the current reported results in the literature are potentially biased due to lack of monitoring of approaches to the crossing structure. To answer this question, we carried out a systematic review of both the scientific and professional literature to map existing knowledge gained in the last four decades of empirical research. We also aimed at uncovering understudied and overarching effects of WCS characteristics on usage by six functional groups: ungulates, large carnivores, small carnivores, small non-carnivores, herpetofauna and macropods. Finally, we asked which WCS characteristics contribute to the effectiveness of crossing structures, and how do these effects vary among studies and WCS types. To this end, we studied the effects of multiple factors on the proportion of successful crossings out of overall approaches to the structure (PSC) by using a meta-analysis of the empirical data found in the literature. Based on the current literature, we expected to find that wider and shorter crossing structures would be more effective for most species groups, and that fencing will have a positive effect on usage. We also expected that viaducts and overpasses would be more effective than underpasses for large species, and that human use of WCS will have a detrimental effect on the levels of usage by wildlife species.

2. Methods

We carried out a systematic review (Hillebrand and Gurevitch, 2016) to identify all the existing literature in the field of wildlife crossing structures. First, we devised a protocol outlining the methods that will be used to conduct the systematic review. The protocol specifies the search terms, relevant databases, inclusion and exclusion criteria, data collection methods and data synthesis methods (Supporting information, Text S1). The protocol was sent to seven experts in the fields of road ecology and wildlife crossing structures (Supporting information, Table S1) to assure the quality of the systematic review and was revised according to their suggestions. We collected the relevant studies following the revised protocol and read each article to identify the types of usage data that were recorded, and which types were more prevalent in the current literature. Finally, we conducted a meta-analysis to explore the effect of crossing structure attributes on PSC by various species.

2.1. Literature search

Scientific and professional publication databases were chosen for the systematic review based on relevance of the database to the research question and the availability of access to the database. Additional databases covering grey literature were also included, specifically databases covering academic theses and specialist websites in the fields of transportation, conservation, and spatial ecology. The search included the following databases: Scopus, Web of science, Science direct, JSTOR, Greenfile, EBSCO, Proquest, Engineering village, Springer Link, TRID (Transportation Research Information Database) and Medline. Publication years were set to the earliest possible year in each database, up to the latest year, which was 2018 at the time the search was performed. We combined two sets of terms for the search of relevant papers: (1) terms that describe the taxa that commonly use WCS and (2) terms that describe the structures themselves. An asterisk was used with certain terms in the search string to expand the search by including the plural form. The final search string that was used in all databases is the following:

> (wildlife OR fauna OR mammal* OR reptile* OR amphibian* OR ungulate* OR *ivore*) AND ("crossing structure*" OR underpass* OR overpass* OR culvert*) OR "wildlife passage*" OR "wildlife bridge*" OR "fauna passage*" OR ecopassage* OR ecoduct* OR "green bridge*" OR "road mitigation"

The term *ivore* was used to include both the terms herbivore* and carnivore* in the search string. To assure the comprehensiveness of the search process, citations within articles and reports were also checked to identify additional relevant literature that was not found using database queries.

2.2. Inclusion criteria for the review

Several conditions had to be met by each paper to be included in the review. The research reported in the paper must be focused on some form of linear infrastructure that has at least one WCS installed across it. There was no restriction on the type of structures (i.e., overpass, underpass, or viaduct), or the intended use of the WCS, meaning that it did not have to be built specifically for wildlife use. We only included studies that collected data regarding structural attributes or the surroundings of the structure and reported at least one measure of WCS usage of some type (i.e., counts of crossing events, presence data or PSC). Only empirical field studies were taken into consideration. Only texts in English were included in the review, and duplicated studies were identified and excluded. Studies that contained anecdotal mentions of results from previous studies were excluded from the database but were used to locate the original papers reporting the data.

2.3. Inclusion criteria for the meta-analysis

The most common data type reported in the literature is count of successful crossings. However, this measure is not an adequate proxy for the effectiveness of crossing structures, which should be comparable across studies of different taxa at different sites, because it does not account for the number of individuals approaching the structure (Chambers and Bencini, 2015). For example, measurements at two structures in different sites can show the same number of crossing events of a given species; yet if the number of approaches to one site is twice that of the other site, then its crossing effectiveness is halved in comparison. Therefore, only studies that reported proportions of successful crossing events out of overall approaches by the subject species were included in the meta-analysis. Researchers used a wide variety of statistical analysis methods to analyze the effects of WCS attributes on

PSC, so it was not possible to conduct a traditional meta-analysis based on pooling of effect sizes. Instead, raw data was used for the meta-analysis, excluding articles that only reported statistical results. This analysis type is based on the one-stage individual participant data method (Debray et al., 2013). This method pools raw data from multiple studies for a shared analysis and is used to identify effects that could not be identified using the data within each research. Articles that did not report the values of structural attributes for each crossing structure, but only a mean value or range of values for multiple structures were also excluded, as they could not be used for the meta-analysis. In cases where authors reported measuring PSC but did not publish raw data for each species or for each WCS, we contacted the main author and requested the data.

2.4. Data collection and variable selection

Each paper reported a unique set of WCS attributes, so the set of attributes for analysis was built incrementally, adding attributes with each additional paper. Independent variables were structural (e.g., length), environmental (e.g., human presence) methodological (e.g., surveying method) or random grouping variables (e.g., habitat type). The complete set of independent variables identified in all papers is shown in Table 1. Since each article reported data for a subset of the full set of attributes, there were missing data points for most variables (Supporting information, Fig. S1). We used Pearson's R, Cramer's V and the correlation ratio η to check for collinearity between variables pairs. For each statistical model, we removed all variables that had a collinearity of above 0.8, choosing to remove variables that were collinear with multiple other variables when possible. When collinearity was present between two variables solely, we excluded the variable with more missing data points, or variables that were of less interest to the analysis (e.g., methodological variables). To minimize missing data, we checked how many complete cases (i.e., records with no missing data points in any variable) remained in the data set after removing various combinations of variables. We used the largest set of variables that left at least 90% of observations as complete cases. If statistical models were unstable and did not converge numerically after the process of variable selection, we checked which variables can be removed to stabilize the model with maximal gain in number of complete observations and removed those variables.

2.5. Statistical analysis

After the collection of raw data, we clustered species into the following functional groups: ungulates, large carnivores, small carnivores, small non-carnivores, macropods, and amphibians and reptiles (herpetofauna). A body mass of 3 kg, similar to that of the Kit Fox, was used as a cutoff value separating small and large species. Amphibians and reptiles are both small-sized ectotherms, therefore they were designated as one group separated from mammals (Jochimsen et al., 2004). We separated large non-carnivores into ungulates and large marsupials (i.e., macropods) based on the difference in movement type and behavior (Chachelle et al., 2016). Data for several bird species was recorded as well in some studies but were too scarce to be included in the analysis. Statistical analysis was conducted separately for each of the six functional groups. For each group, analysis was further separated by the type of crossing structure (i.e., underpass, overpass, or viaduct). This was done because some variables and certain variable levels were exclusively related to specific WCS types. Viaducts and underpasses were considered as separate types of WCS, since these types of structures differ in characteristics such as the shape and building materials (Smith et al., 2015).

We used generalized linear mixed models with binomial error structure (logit as link function) for exploring the relationships between PSC and each set of independent variables. Variation in the number of individual observations (i.e., approaches) used to calculate PSC is accounted for in the model by using weights that are proportional to the number of approaches to the structure (Bates et al., 2015). Habitat type was chosen as a random variable to account for possible differences in the response of species of the same functional groups to WCS characteristics within various habitat types. Intra-species variance within each functional group was controlled by including species identity as a random variable in the model. We recorded the source of data (i.e., the study from which data was collected) and designated it as a random variable as well, to control for the effect of unique conditions under which each study was conducted. The variables ‘study’ and ‘country’ were found to be highly correlated (Cramer's V > 0.8) and therefore ‘country’ was not

Table 1
The full set of WCS variables gathered from all data sources. Variables marked with * were not used in any of the statistical models, due to exclusion by the variable selection process.

Variable name	Category	Type	Variable meaning
Structure type	Structural	Categorical	An underpass, overpass or viaduct
Shape	Structural	Categorical	Shape of the structure
Material	Structural	Categorical	Building material of the structure
Substrate	Structural	Categorical	Covering material of the structure floor
Grated	Structural	Binary	Is there a grate on the structure top?
Creek	Structural	Binary	Is there water flow through the structure?
Open median	Structural	Binary	Is there an open mid-section in the structure?
Length	Structural	Continuous	Overall length of the structure
Height	Structural	Continuous	Structure height at entrance
Width	Structural	Continuous	Structure width at entrance
Structure age*	Structural	Continuous	Years since structure construction
Number of lanes*	Environmental	Categorical	Number of highway lanes
Purpose	Environmental	Categorical	The purpose for which the structure was built
Fencing	Environmental	Binary	Is there a fence leading to the structure?
Human presence	Environmental	Binary	Are humans using the structure?
Vegetation at entrance	Environmental	Binary	Is there vegetation near the entrance?
Fencing length*	Environmental	Continuous	Fencing length from both sides
Fencing height*	Environmental	Continuous	Fencing height
Traffic per day*	Environmental	Continuous	Number of vehicles per day
Human activity rate*	Environmental	Continuous	Number of humans present per year
Surveying method	Methodical	Categorical	Method used for wildlife counts
Number of cameras	Methodical	Continuous	Number of cameras used for monitoring
Monitoring distance*	Methodical	Continuous	Distance of monitoring from the structure
Days monitored	Methodical	Continuous	Days the structure was monitored
Habitat type	Grouping	Categorical	Habitat type surrounding the structure
Study	Grouping	Categorical	Study from which the data were recorded
Species	Grouping	Categorical	Species identity
Country*	Grouping	Categorical	Country where the research was conducted

used in the models. We used an analysis of variance to test if each variable had an overall significant effect on PSC for each group. For each statistical model, the proportion of variability in the data explained by the model was calculated using pseudo R-squared (Nakagawa and Schielzeth, 2012). Both marginal r-squared (fixed effects only) and conditional r-squared (both fixed and random effects) were calculated.

To increase numerical stability, all continuous variables were standardized to zero mean and unit variance by subtracting the mean and dividing by the standard deviation of the variable. Because statistical models were separated by type, we used a univariate mixed model to compare the effect of WCS type on PSC. Not all possible combinations of functional groups and structure types had enough data to be included in the analysis. For each functional group at each WCS type, a unique set of variables was chosen out of the overall variable set, following the variable selection procedure (Supporting information, Table S2). For categorical variables, effect sizes in the statistical analysis represent the natural logarithm of the odds ratio for two levels of the variable. For continuous variables, effect sizes represent the natural logarithm of the odds ratio for a unit change in the variable value. Since all continuous variables are rescaled by the standard deviation of each variable, the actual effect size is the value in the rescaled analysis, divided by the standard deviation of the variable (see Supporting information, Table S3 for means and standard deviations of continuous variables).

For each categorical variable that was used in the statistical analysis, a specific set of levels was recorded, depending on WCS type. Underpass shape was either arched, box shaped, round or elliptical. Viaduct shape was either sloped or walled, meaning either a slope on each side of the crossing, or conversely, a vertical wall on each side. Underpass construction material was either concrete, steel, wood, or PVC. Wood and PVC underpasses were only recorded in herpetofauna passages. Viaducts were either made of concrete or natural materials (i.e., exposed rock or soil). Overpass and viaduct floors were either covered in soil, or by a vegetation layer. Height was measured from the structure floor to the top at underpasses and viaducts, while for overpasses height was measured from the road surface to the structure. The purpose for which underpasses were constructed was either for water drainage, for human use (e.g., for agricultural vehicles), or specifically for wildlife use. Some viaducts were constructed for human use, while others were intended for wildlife use, or were retrofitted to be used by wildlife. Methods used to identify crossing attempts at underpasses were either mounted cameras, track beds (usually sand beds) or by direct observation of wildlife by the researchers. At viaducts, cameras and track beds were used. The presence of a creek was exclusively related to viaducts, while a grated top was exclusively related to underpasses. The existence of an open median was exclusively related to viaducts and underpasses.

3. Results

3.1. Systematic review

The number of papers found in all databases was 10176, out of which 1127 were left after removing papers with a title that was obviously irrelevant for the research topic and removing duplicates that appeared in multiple searches. Out of these 1127 papers, the full text of 41 was non-accessible and they were discarded. For the remaining 1086 papers the abstracts were read. Based on the abstracts, 270 papers that met the inclusion criteria were identified (see Supporting information, Table S7 for the full list of papers), ranging in publication years from 1982 to 2018. All other 816 papers discussed topics related to crossing structures and road ecology but did not report empirical data on crossing structure use or structure attributes. The full text of the remaining 270 papers was read, and 77 papers that reported the proportion of successful crossings to overall crossing attempts were identified. Most other studies reported only counts of successful crossings, while some reported presence data, or no data at all (Table 2). Out of the 270 papers, 41.1% were peer-reviewed articles, 22.2% conference papers, 21.5% reports and 15.2% were theses.

Table 2
Overall number of papers, by types of usage data reported in each type of publication.

	Article	Conference paper	Report	Thesis	Total
Number of crossings	79	31	27	24	161
Crossing proportion	22	18	22	15	77
Presence data	7	10	8	1	26
No reported data	3	1	1	1	6
Total	111	60	58	41	270

A thorough check of the 77 papers that reported proportions of successful crossing revealed that several studies were reported in multiple publications. This is due to peer-reviewed research being also published as a conference paper, in a professional report or in a thesis. Repeated reports were discarded, amounting to 13 out of the 77 papers. Another 33 out of 77 papers either did not provide adequate data on crossing structure attributes (15 papers) or reported summary statistics of PSC from multiples structures (18 papers). These types of data did not allow for inclusion in the meta-analysis, which requires per-structure measurements. An additional paper was excluded because its data were for a single species (bats) that did not belong to any of the functional groups. Another paper was excluded because data were only for usage of rope-bridges, which were not analyzed due to lack of data in other studies. Therefore, out of the overall relevant empirical WCS literature found in the review (i.e., 270 papers), only 29 papers could be used to explore the effects of attributes on the proportion of successful crossings in our meta-analysis (see Supporting information, Table S5 for papers included in the meta-analysis).

Out of 29 papers used for the meta-analysis, 10 were peer-reviewed articles, 4 conference papers, 2 theses, and 13 were professional reports. Conference papers, theses and professional reports were written in all cases by established authors that have also published in peer-reviewed journals. From each paper, data regarding successful crossing proportion and WCS attributes were recorded. In some cases, raw data was presented only in the appendix, and in other cases structural attributes such as shape and material were not mentioned in the text but were identified through photographs of the structures within the paper or the appendix. A total of 550 unique measurements of PSC were reported within the 29 papers, each measurement representing one species at one crossing structure. Most studies (23 out of 29) used cameras to identify approaches to crossing structures, while others used track beds, radiotracking or human observations. Cameras were mounted at varying distances from the structures, ranging from 1.2 m to record amphibian movements, and up to 804 m to detect ungulates approaching WCS. Data for a total of 72 species and 145 crossing structures were reported (see Supporting information, Table S6 for a list of species included in the analysis). The most common structure type was underpass with 75.1% of all recorded measurements. Viaducts and overpasses comprised 18.5% and 6.4% of all measurements, respectively (Table 3). The herpetofauna group was the most commonly measured

Table 3
Number of records of successful crossing proportion for each species group, at each type of crossing structure. The numbers in parenthesis to the right of the total number of records represents the total number of species studied in each group.

	Underpass	Overpass	Viaduct	Total
Herpetofauna	136	0	1	137 (17)
Ungulates	77	20	33	130 (5)
Large carnivores	82	15	31	128 (9)
Small carnivores	53	0	16	69 (8)
Small non-carnivores	38	0	19	57 (22)
Macropods	16	0	0	16 (5)
Birds	11	0	2	13 (6)
Total	413	35	102	550 (72)

within these studies, with 24.9% of the measurements, followed by ungulates with 23.6% and large carnivores with 23.3%. Small carnivores and small non-carnivores were represented by 12.5% and 10.4% of measurements, respectively. Macropods were represented by 2.9% of the data and Birds by 2.4% of the data.

3.2. Meta-analysis

Most variables included in the various models had significant effects on PSC (Supporting information, Table S3). WCS characteristics had complex and interactive effects on the PSC of different functional groups (Fig. 1). Crossing structure type analysis (Fig. 1a) revealed that ungulates, large carnivores, and small carnivores are more likely to use viaducts compared to both underpasses and overpasses. On the other hand, PSC of small non-carnivores in viaducts is reduced compared with underpasses. Ungulates showed a slight preference for overpasses over underpasses. At overpasses (Fig. 1b), length had a negative effect on ungulates, as so did vegetation cover at the overpass entrance. Surprisingly, overpass width was negatively correlated with PSC for ungulates but positive for large carnivores. Fencing had a strong negative effect on large carnivores but no effect on ungulates. At viaducts (Fig. 1c), small species (both carnivores and non-carnivores) showed a strong negative reaction to structure length and a weak negative reaction to width. Small species were also significantly more inclined to use structures that are fenced, and those that were built specifically for wildlife use, compared with retrofitted WCS. Ungulates crossing proportions were negatively affected by structure length and by the presence of a creek running through the viaduct. On the other hand, an open median and natural materials (as opposed to concrete) increased ungulate PSC significantly and ungulates also preferred vertical walls and not a sloped viaduct. In contrast to ungulates, large carnivores showed a strong negative reaction to an open median. Retrofitted viaducts were significantly preferred by large carnivores over structures that were built for human use.

At underpasses (Fig. 1d), fencing had a positive effect on PSC for both ungulates and carnivores (large and small). Small mammal species and macropod crossing proportions were positively affected by underpass length, whereas ungulate use was negatively affected. Width had a positive correlation with use by ungulates. An open median at an underpass had a positive correlation with PSC of macropods, but a negative effect for large carnivores and for ungulates, as opposed to the effect found in viaducts. Large carnivores showed a strong negative reaction to structures built for human use and preferred either drainage culverts or underpasses built specifically for wildlife use. In contrast with the effect found at overpasses, ungulates showed a preference for vegetation at the entrance of an underpass. Large carnivores showed a strong preference to use arched structures over elliptical and round underpasses. Ungulates showed a similar preference, but with reduced significance. In contrast, small non-carnivores preferred using box or round culverts and avoided arched underpasses. Macropods showed a significant preference for round underpasses over box shaped structures. Use of underpasses by herpetofauna had a strong negative correlation with length, and a strong positive correlation with width. Wooden underpasses were preferred by herpetofauna over those made of PVC, as were underpasses with a grated top.

Some methodological variables were also related to PSC recorded for certain species groups. At underpasses, using track-beds to identify small carnivores had a significant negative effect on recorded crossing proportion as compared with cameras. For herpetofauna, human observation of PSC was significantly higher than with the use of cameras. The overall monitoring time at underpasses had a positive effect for large and small carnivores, but a negative effect for ungulates. On the other

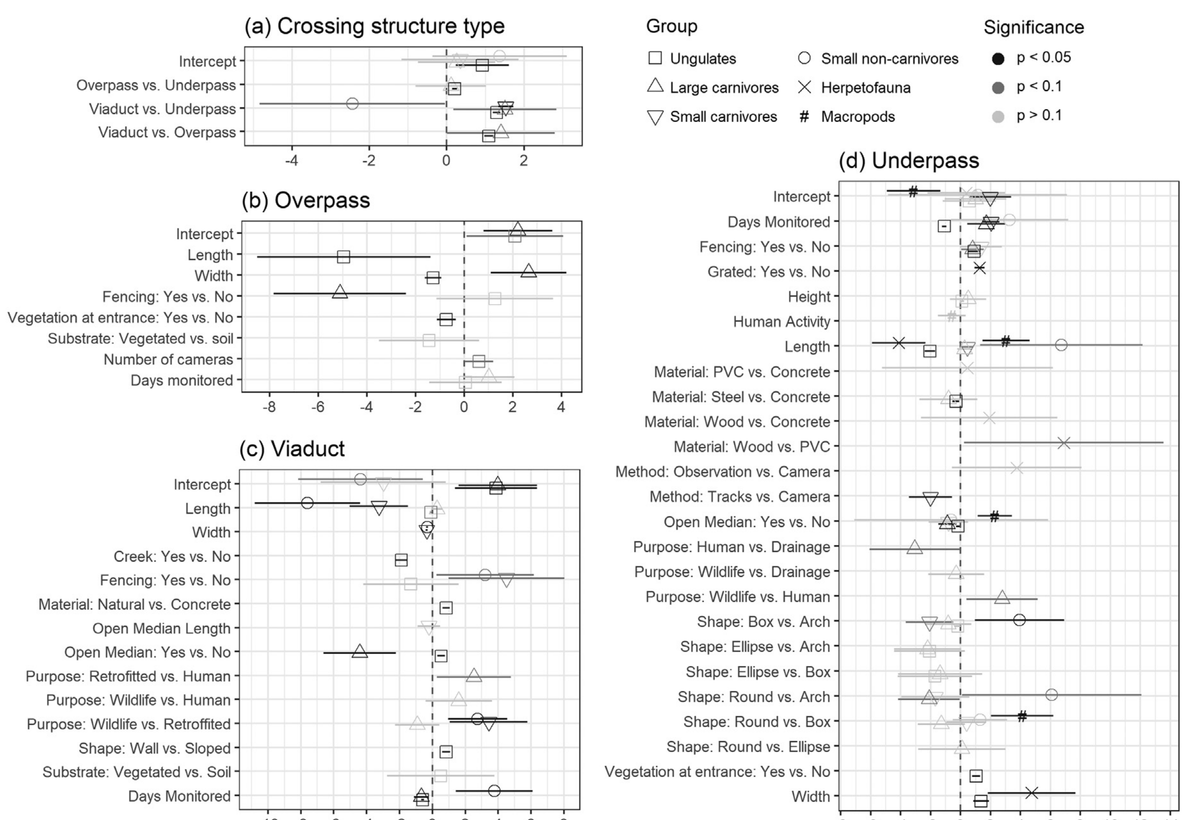

Fig. 1. The effects of wildlife crossing structure attributes on the proportion of successful crossings: (a) the effect of wildlife crossing structure type; (b) the effects of overpass attributes; (c) the effects of viaduct attributes; and (d) the effects of underpass attributes. Lines outside symbols represent standard errors. For representation of these effects as unstandardized odds ratios see Supporting information, Table S4.

hand, monitoring time at viaducts was negatively correlated with PSC of ungulates and large carnivores, and positively correlated with PSC of small non-carnivores.

4. Discussion

4.1. Current state of the literature

Transport infrastructures are increasingly recognized as one of the major drivers of biodiversity loss worldwide (Benitez-Lopez et al., 2010; Polak et al., 2019). Mitigation measures, such as WCS are gaining attention by transport agencies, because they can allow species movements across transport infrastructures and prevent wildlife-vehicle collisions (van der Grift et al., 2013). Yet, underpinning research is still needed to identify best practices and ensure funds are allocated in a cost-effective manner that optimizes ecological and societal benefits. Our systematic review showed that while much of the research effort in this field is important for understanding local trends in wildlife usage of WCS, the ability to draw broad conclusion from these studies is limited. This is because there is an inherent bias in analysing the effects of structure attributes based only on the number of individuals crossing a structure and not accounting for the number of overall approaches (Chambers and Bencini, 2015). Most studies in our systematic review did not measure approaches to crossing structures (71.5% of the studies we reviewed), and this can explain the inconsistencies found in the literature regarding the effects of structural and environmental attributes. We believe that the reason for this problem in research design is the difficulty of monitoring the surroundings of the structure, which requires larger scale monitoring and thus is more expensive and complicated to conduct (Andis et al., 2017). Another possible explanation is a false assumption of homogeneous exposure to structures within the same area, which may be erroneous in heterogenous environments (Barraquand and Benhamou, 2009). As the key challenge today is to accurately assess the effectiveness of WCS in order to use the most cost-effective solutions possible, future research should seek to alleviate this bias by monitoring the movement patterns of animals approaching the structures.

The comprehensive systematic review carried out in our research also revealed that the empirical evidence regarding WCS usage is both sparse and inconsistent in many cases. Some species groups are over-represented in comparison to others in the empirical literature, specifically large mammals over small mammals, amphibians, reptiles, and birds. This trend is evident in the lack of results for these groups in the meta-analysis, since not enough data points were available. Most evidently data for overpasses was limited to only large carnivores and ungulates (see Fig. 2 and Table 3). Empirical evidence was also lacking regarding design attributes, such as shape and building material, which are under-represented in the literature compared with structural dimensions. Furthermore, in many cases, variability among structural attributes within a given research area was insufficient to conduct a formal statistical analysis of the effect on usage by local species, thereby limiting the scope of research results. In fact, in some papers a single structure was monitored, so no comparison of usage was possible (e.g., Kleist et al., 2005). This is an inherent problem in WCS research, based on the spatial sparsity of these structures which limits ability to conduct comparative research (van der Ree et al., 2007).

Finally, our results also revealed that important research is being conducted in the context of governmental agencies (22% of all papers found in our review), most prominently in transportation or nature and parks authorities (e.g., Smith, 2003). The results of these efforts are usually not formally published to the scientific community, and therefore valuable information regarding structure effectiveness may be lost. This highlights the importance of covering both peer reviewed and grey literature when conducting meta-analysis on topics with high relevance for applied ecology questions (Haddaway and Bayliss, 2015). Adopting a meta-analytical approach enables the rectification

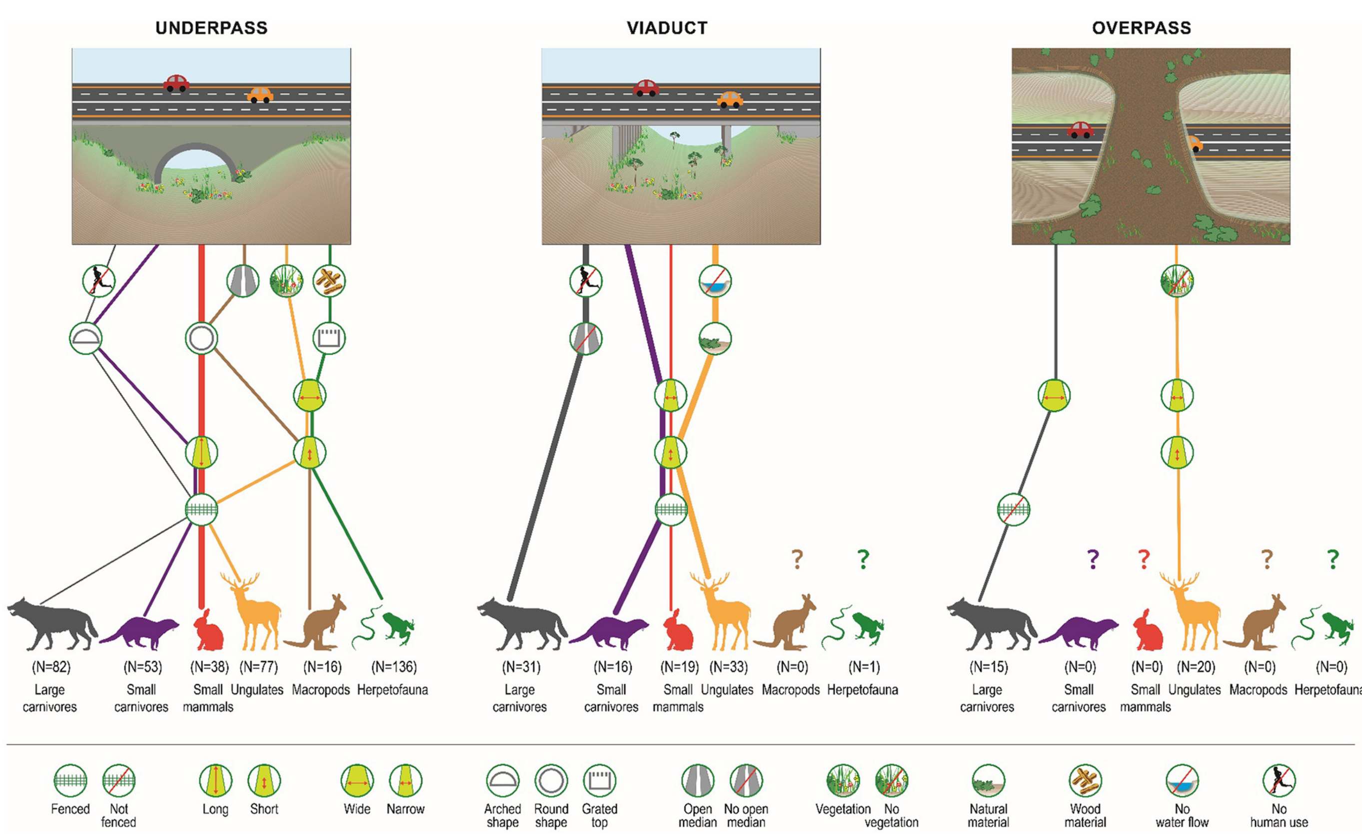

Fig. 2. Species groups' preferences for crossing structure characteristics. Line width indicates relative preference within species group for different types of crossing structure. Question marks indicate lack of sufficient data for analysis.

of several of these problems, by gathering data that would otherwise not be used for analysis.

The results of our meta-analysis should be considered with some caveats, due to several study limitations. Only a small percentage of the literature contained data compatible for analysis, so some species groups and ecosystems were under-represented in the analysis. Furthermore, data were not sufficient for an analysis at the species level, therefore differences in WCS attributes effects on usage by species within the same functional group were not explicitly identified in this study. Lack of data also prohibited the examination of the effects of some attributes on PSC, for example structure age and road traffic volume, and limited the comparison of WCS types for some species groups. Regarding data collection methods, a lack of standardization of monitoring methods and monitoring distances to crossing structures may negatively affect the reliability of PSC measurements (Andis et al., 2017; Ford et al., 2009). Furthermore, differences between studies in research duration and sampling effort are possible reasons for biases that are not accounted for in this study.

4.2. Effects of structural attributes

Wildlife species are predisposed to move through specific landscape types and habitat elements within them, so specific preferences for WCS designs are expected to vary among species (Clevenger et al., 2009). Our results support this hypothesis, as the differences between usage of various types of structures (Fig. 2) imply that species groups are inclined to prefer a passageway that most closely resembles their natural habitat. This is notable in the strong preference of large mammals to use open-span viaducts and overpasses compared with underpasses, which may be attributed to their preference for open spaces as opposed to confining structures (Ruediger and DiGiorgio, 2007). In contrast, we have also found that ungulates prefer to use narrow overpasses, which is counter intuitive. One possible explanation for this effect may be that wider overpasses are used more often by large carnivores and therefore ungulates could be avoiding these structures due to fear of predation. Ungulates have also shown a reluctance to cross viaducts with the presence of flowing water, compared to dry viaducts. It is possible that water flow deters crossing during the high-flow season, as was previously found for small mammals and carnivores (Mata et al., 2009). This result may indicate that during high flows at winter, viaducts over creeks or rivers may not function as effective crossing structures for ungulates.

Our analysis further showed that for different types of structures, the effects of structural attributes differ significantly, even for the same species group. This interaction between structural attributes and structure type has not been explicitly shown so far in the literature. For example, it is expected that ungulates would most likely prefer structures with no vegetation cover, as open areas near passages facilitate mechanisms for predator avoidance or escape (Clevenger and Waltho, 2005). This is indeed the case when encountering an overpass. However, at underpasses the presence of vegetation cover has a positive effect on the probability of successful crossing by ungulates. This effect may be attributed to vegetation providing a more natural environment than an exposed structure, thus encouraging use. Such differences in preferences may be indicative of complex interactions between structural attributes.

Considering the need to preserve large carnivores, which are often the focal species of fragmentation mitigation efforts (e.g., the Iberian Lynx), some important insights arise from the results. It has been formerly advised that crossing structures should always be fenced (Huijser et al., 2009, 2016). Our results confirm this notion for most species but show that fencing acts to lower the probability that a large carnivore will use an overpass. It is also clear that structures designed for human use are very unlikely to be used by large carnivores, even in comparison with drainage culverts. This effect may be explained by fear of human presence (Clevenger and Waltho, 2005; Glista et al., 2009). Structure length was shown to have an overall negative effect for almost all groups. An interesting exception is for small non-carnivores and macropods, which show a preference for longer underpasses. This preference may be related to the need of locating places to hide from predators (Grilo et al., 2008), or due to the behavioral adjustments of small mammals to confined spaces (McDonald and St. Clair, 2004). Underpass shape displayed an impact on usage, with most groups showing a clear preference for open shapes, especially arched underpasses. Small non-carnivores are distinct in their preference for box or round shaped passages over arched ones, perhaps due to avoidance of co-use with potential predators (D'Amico et al., 2015b). Large and small species alike exhibited a preference for natural materials over steel and concrete. These results are indicative of an overall trend, showing a preference for shapes and materials that resemble natural environments, and reduce the avoidance behavior caused by anthropogenic stimuli (Frid and Dill, 2002).

5. Conclusions

Our systematic review results highlight the importance of adopting large-scale monitoring of wildlife crossing structures, so that probabilities of use by approaching individuals may be measured. This metric of crossing structure effectiveness should become the standard for future research in the field. To this end, we recommend the development of standardized monitoring schemes and methods, adjusted for specific species groups, so that structure effectiveness could be measured and compared systematically. Specifically, guidelines for selection of methods to monitor the surroundings of WCS, and for adequate monitoring distances to identify approaches, should be developed based on species traits. Dissemination of standardized monitoring methods to professional organizations will promote better data collection and robust analysis. Our meta-analysis has revealed some overarching trends that should be adopted as best practices of wildlife crossing structure planning. Viaducts are the most effective type of structure with regards to large mammals, compared with overpasses and underpasses. Fencing is important and contributes to the probability that a structure will be used as a passageway for most wildlife species. We have also shown the advantage of using natural materials as opposed to metal or concrete in the design of crossing structures, which promotes use by decreasing avoidance of the structure.

While these general trends are important for planning effective solutions for fragmentation, we also acknowledge that the variability in the response of various species groups to structural factors prohibits a "one size fits all" planning approach to WCS construction. Therefore, planning of mitigation measures for multiple species should optimally include multiple structures designed to accommodate the preferences of different functional groups. We stress the importance of structure attributes beyond dimensions alone, which should be taken into consideration when planning a crossing structure. Shape, building materials, vegetation cover, water levels and human presence are important factors that must be accounted for when plans are drawn, and while managing the surroundings of an existing structure. It is also imperative to take these factors into consideration when planning to retrofit existing structures. As the costs of crossing structures are substantial, it is worthwhile to invest the resources needed for more robust research and planning methods that will facilitate cost-effective mitigation efforts and promote wildlife conservation.

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CRediT authorship contribution statement

Dror Denneboom: Conceptualization, Methodology, Software, Validation, Formal Analysis, Investigation, Data curation, Writing - Original draft preparation, Writing - Review & Editing, Visualization. **Avi Bar-Massada:** Conceptualization, Methodology, Writing - Review & Editing. **Assaf Shwartz:** Conceptualization, Methodology, Writing - Review & Editing, Supervision.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability statement

Data is available from Figshare at https://doi.org/10.6084/m9.figshare.12623756.

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