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Research Paper

Effectiveness of pipe culverts in facilitating road crossings by clutter-adapted bats

Adina Sennblad, Isabella Honnér, Johnny de Jong *

Swedish Biodiversity Centre, Swedish University of Agricultural Sciences, Box 7012, 75007 Uppsala, Sweden

HIGHLIGHTS

- Pipe culverts could be useful as wildlife crossings for clutter-adapted bats.
- Small pipe culverts (80 cm in diameter) are occasionally used by bats.
- Bat activity increase with pipe culvert diameters.
- Pipe culverts with water have higher bat activity.
- Open-air foragers, such as the genus *Pipistrellus* did not use pipe culverts.

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ABSTRACT

Roads have several negative ecological effects on bats. Clutter-adapted bat species avoid roads as the open space increases the risk of predation. This results in the road acting as a barrier of movement, making otherwise suitable habitat inaccessible. Different approaches to mitigate the fragmentation and mortality caused by roads have been explored. Underpasses such as bridges or tunnels have proven to be used by clutter-adapted species to cross the road. A few studies have indicated that some species of bats could possibly use smaller structures such as pipe culverts. As pipe culverts are more cost-effective than bridges and tunnels, we set out to quantitively investigate what factors affect the usage of pipe culverts, aiming to produce recommendations for their implementation in the landscape. Clutter-adapted bats were surveyed with ultrasound detectors in 269 pipe culverts in Sweden. Each pipe culvert was surveyed for one night each and 73 pipe culverts with a high recorded activity were revisited and surveyed with mist nets. ***M. brandtii, M. daubentonii, M. mystacinus***, ***M. nattereri,*** and ***P. auritus*** were found to be flying in the pipe culverts. Factors affecting the activity and usage of the pipe culverts were the width of the pipe culverts, presence of water in the pipe culvert and the presence of forest at the openings of the pipe culvert. The results give insight into how pipe culverts could be designed and implemented in landscape planning to mitigate the fragmentation caused by roads and decrease their negative effects on clutter-adapted bats.

1. Introduction

About 1 % of Sweden is covered by roads which has several negative ecological impacts on wildlife populations (Fahrig & Rytwinski, 2009; Statistics Sweden, 2020). These impacts include habitat loss during road construction, degradation of habitats in the vicinity of roads and increased mortality from collisions (Trombulak & Frissell, 2000; Karlson & Mörtberg, 2015). Many species of animals exhibit changes in behaviour, such as home range shifts or changed movement patterns, as a direct result of avoiding the roads (Trombulak & Frissell, 2000). The increased mortality from collisions as well as avoidance behaviours causes fragmentation of wildlife populations, which increases the risk of local extinctions (Trombulak & Frissell, 2000; Coffin, 2007). Species with large movement ranges and low reproductive rates are especially vulnerable and almost always experience negative effects from roads (Fahrig & Rytwinski, 2009). One order of species that belong to this functional group is bats (Chiroptera), who, with their reproductive rate of only one offspring per year and large movement ranges, are threatened by the habitat loss and degradation caused by roads (Kerth & Altringham, 2016; Bhardwaj et al., 2021).

The extent to which bats experience negative effects from roads depends on their foraging behaviour (Abbott et al., 2012a). Three

* Corresponding author.

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functional guilds can be defined based on where the bats forage, which is reflected by adaptations in their wing morphology and sonar. Species with low wing aspect ratios and high frequency sonar, like the genera *Myotis* and *Plecotus,* are adapted to navigate and forage close to surfaces as in forests or over waterbodies and belong to the guild of clutter-adapted species (Aldridge & Rautenbach, 1987). These species have slower flying speed but better manoeuvrability than open-space adapted bats (Norberg & Rayner, 1987). Open-space-adapted bats, like *Nyctalus* and *Eptesicus*, have a lower frequency sonar and a higher wing aspect ratio making them faster but worse at manoeuvring, which is optimal for foraging high up in the free air (Norberg & Rayner, 1987). Species that forage in forest edges and open woodlands, like *Pipistrellus*, belong to the guild of edge-adapted species. These bats are slower but better at manoeuvring than open-space-adapted species, although not to the degree of clutter-adapted species (Denzinger & Schnitzler, 2013).

While species of all three guilds have shown lower activity on and in the vicinity of roads as a result of the road-induced degradation of habitat (Berthinussen & Altringham, 2012a; Bhardwaj et al., 2017; Claireau et al., 2019b), clutter-adapted bats are the most vulnerable to the fragmentation caused by roads (Abbott et al., 2012b; Frey-Ehrenbold et al., 2013). Clutter-adapted bats dislike flying in open areas and prefer to commute along linear features and in forests, as these provide protection from weather and predators (Krull et al., 1991; Frey-Ehrenbold et al., 2013; Kerth & Altringham, 2016). Some clutter-adapted species have been observed preferring to take a longer commuting route if this involves following a linear feature, rather than taking the shortest route if it involves crossing open grounds (Limpens & Kapteyn, 1991). Although, this open ground avoidance behaviour seems to be predominant mainly during the lightest summer months, as clutter-adapted species are known to migrate larger distances over open water during the darker autumn (Hutterer et al., 2005). As a result of the avoidance of open grounds throughout summer, clutter-adapted bats are negatively affected when a road interrupts their flightpath, as this creates an open space to cross (Kerth & Melber, 2009; Zurcher et al., 2010; Kerth & Altringham, 2016). When a flight-way is interrupted by a road, the majority of individuals choose not to cross the road and instead reverse (Zurcher et al., 2010; Bennett & Zurcher, 2013). This reluctancy to cross roads means that roads are barriers of movement for clutter-adapted bats (Bennett & Zurcher, 2013; Kerth & Altringham, 2016). The reason for avoiding the road might be complex, and sometimes not just dependent on the road itself (noise, light-pollution etc.), but a result of interruption in habitat connectivity (Pinaud et al. 2018). The avoidance of roads results in both habitat loss and habitat degradation, as both the habitat near roads is avoided and the barrier effect makes otherwise suitable habitat inaccessible for the population, which could result in population decline and fragmentation (Fahrig & Rytwinski, 2009; Kerth & Altringham, 2016).

While the majority of individuals choose to not cross a road, the proportion that do cross exposes themselves to higher risk of mortality, risking predation and collision with vehicles (Kerth & Altringham, 2016). Bats have a slow reproduction rate, and cannot quickly enough compensate for the increased mortality causing a decline in population size (Fahrig & Rytwinski, 2009). Clutter-adapted species, with their slower flying mode and preference to fly closer to the ground, have a higher risk of collision, compared to open-space-adapted species, which fly higher, typically above the vehicles (Lesiński, 2008; Kerth & Altringham, 2016). It is clear that roads, through fragmentation and increased mortality, are a threat to clutter-adapted bats and it is important to mitigate the decreased connectivity between forest patches and linear elements (Frey-Ehrenbold et al., 2013). Different approaches to mitigate the fragmentation and mortality caused by roads have been explored. Overpasses such as green bridges (Ferraille et al. 2024), wires with polystyrene balls, or metal structures bridging the road, aim to give clutter-adapted bats a linear feature to fly along, and at the same time keeping them above traffic height, thereby minimizing the risk of collision (Claireau et al., 2021). The effectiveness of some of these overpasses is unclear. Some studies find no evidence of them being used, and others find them effective if placed in forested landscapes or along known commuting routes (Berthinussen & Altringham, 2012b; Claireau et al. 2019c; Claireau et al., 2019a). However, these studies are mainly relevant for open- and edge-adapted species, while studies for clutter-adapted species are fewer, and several studies indicate that these prefer underpasses (Abbot 2012b, Martínez-Medina et al 2022). Underpasses, such as flyways under bridges where the larger road bridges a waterbody, a smaller road or walkway, or flyways though tunnels built for a crossing smaller road or waterbody, are more effective as wildlife crossings for bats. Clutter-adapted species have been found to use underpasses more frequently than crossing over the road (Bhardwaj et al., 2017). Road sections with underpasses have been recorded to have a higher activity of *Myotis* spp. than road sections without (Laforge et al., 2019), and motorways without underpasses have been shown to act as a barrier for clutter-adapted bats (Kerth & Melber, 2009). Clutter-adapted species such as *M. bechsteinii*, *M. myotis, M. mystacinus*, *M. nattereri* and *Plecotus auritus* almost or completely exclusively use underpasses to cross roads instead of flying over (Kerth & Melber, 2009; Abbott et al., 2012b; Abbott et al., 2012a).

The surrounding landscape, as well as the design of the underpasses, have been found to influence the extent to which bats use them. Increasing forest cover in the surrounding landscape increases underpass use by *Myotis* spp. (Laforge et al., 2019), while the presence of a tree line leading up to the underpass does not seem to significantly affect its usage by any clutter-adapted bats (Boonman, 2011). The habitat within the underpass has been demonstrated to significantly increase underpass use by *Myotis* spp. Underpasses consisting of a bridge over a river having the highest activity, a river though a tunnel the second highest activity, while an agricultural track or a smaller road through a tunnel had lower activity levels (Laforge et al., 2019). The size of the underpass affects which species that use it. *Pipistrellus pipistrellus*, *M. bechsteinii*, *Barbastella barbastellus*, *Nyctalus noctula* and *M. brandtii/mystacinus* have previously been found to exclusively use large tunnels of 4-5x4-5 m while *M. nattereri* and *M. daubentonii* have been recorded also using smaller tunnels of 1,5x2 m containing a small creek (Bach et al., 2004). A study looking at tunnels leading rivers and larger water bodies under roads and railways found *M. daubentonii* to be the species using the smallest culverts, which should have a cross-sectional area of free space of at least 7 m^2 to be of significant use, while the minimal cross sectional area for *M. dasycneme* and *P. pipistrellus* should be 18 m^2 and 47 m^2, respectively (Boonman, 2011).

While large underpasses in the form of bridges and tunnels have been shown to be of great use for clutter-adapted species, they are expensive to build. Pipe culverts that mitigate drainage from one side of the road to the other or act as a passageway for pedestrians, cattle and wildlife, are much cheaper, but few studies have looked at bats' usage of these. Abbott et al. (2012b) compared the use of a larger road underpass and two pipe culverts intended for drainage and found that, while all species recorded in the area did use the underpass, only *M. nattereri* and *P. auritus* used the pipe culverts. Abbott et al. (2012b) suggested that the most strongly clutter-adapted species are the ones that can use the smallest passages.

This study quantitatively investigated the use of pipe culverts by clutter-adapted species, with the aim to gain insight in how the design (diameter, length, presence of water) and placement (surrounding habitats) of the pipe culvert affect its usage. We hypothesized that the activity in the pipe culverts is a function of the diameter and length of the pipe culvert as well as of the surrounding habitats. An important potential outcome of the study was to provide recommendations about how underpasses, such as pipe culverts, can be designed and implemented to mitigate the negative implications of fragmentation for bats caused by road construction.

2. Material and methods

Fieldwork was carried out during July in 2022 and 2023. The selection of pipe culverts for the first year of fieldwork was made using data from the Swedish Transport Administration, searching for larger roads with a high density of pipe culverts (Swedish Transport Administration, 2022). Two larger roads, one in the county of Västmanland and one in the county of Skåne, and their smaller connecting roads were chosen for the first year of the study. Motorways, control access highways, and other large roads with more than one file in any of the direction (e.g. 2 + 1 roads) were excluded. Since the first year was a pilot study, pipe culvert length was not considered when selecting suitable pipe culverts for the fieldwork.

For the second year of fieldwork, the method of selecting the pipe culverts was modified to include more pipe culverts located under larger roads such as motorways. Suitable pipe culverts (both dry culverts and road-stream culverts) were selected using data from the Swedish Transport Administration over pipe culverts, road type and road width in the counties of Jönköping, Kalmar, Kronoberg, Halland, Västra Götaland, Södermanland, Östergötland and Örebro (Swedish Transport Administration, 2023a; Swedish Transport Administration, 2023b; Swedish Transport Administration 2023c). Pipe culverts were defined as suitable for the study if they had an outer diameter over 100 cm, a minimum length of 15 m, were located under a road of at least 7.9 m in width, and within 50 m of the nearest deciduous or coniferous forest patch (Lantmäteriet, 2021). For pipe culverts located under motorways, 2 + 1 roads or other controlled-access highways, another smaller road had to be within 150 m of the pipe culvert to allow for execution of the fieldwork. Four geographical areas with a high density of suitable pipes were selected for the project. One of the geographical areas had only 37 suitable pipe culverts so all 37 were selected for the sample. The remaining three areas had more suitable pipe culverts than what would be possible to survey. For each of these areas, stratified random sampling was used to select 120 pipe culverts. Strata were based on pipe culvert diameter and length. This way of sampling ensures an even spread among size and diameter in the random sample.

The selected pipe culverts for the first and second year of fieldwork were evaluated in the field and those that were deemed unsuitable were excluded from the study. To be selected for the study the pipe culverts had to be in either a forest landscape or in a mosaic landscape with patches of forest, thereby ensuring the presence of clutter-adapted bats in the area. Additionally, the pipe culverts used in the study were required to have a forest, a linear feature such as a hedgerow or creek, or other similar features directly at either opening, as otherwise the pipe culvert would not be useful in aiding clutter-adapted bats to avoid open areas. Similarly, pipe culverts that were overgrown, cluttered or were less than 80 cm in inner diameter were excluded from the study. In total, 83 and 186 suitable pipe culverts were selected for the first and second year of fieldwork, respectively.

Out of the selected suitable pipe culverts, 77 % had water in them at the time of the survey. Similarly, 40 pipe culverts (15 %) had no forest at either opening, 59 pipe culverts (22 %) had forest at one opening, and 170 pipe culverts (63 %) had forest at both openings. For most pipe culverts the openings that lacked forest had a linear feature instead. Only two pipe culverts (1 %) had neither forest or a linear feature on either side and 28 pipe culverts (10 %) had a forest or a linear feature on only one side. When there was no forest or linear feature at the openings of the pipe culverts, the surrounding habitat was dominated by agricultural fields, wooded pastures, and meadows. The width (measured as the horizontal inner diameter) of the pipe culvert varied between 60 and 370 cm. The length of the pipe culverts varied between 6 and 141 m, with the most pipes shorter than 50 m (Table 1).

Acoustic monitoring with Pettersson D500X bat detector (Pettersson Electronics, Uppsala, Sweden) was used to survey the activity of bats in the pipe culverts. At all localities and during both years the same settings were used: Sampl. Freq. = 500, Pretrig = OFF, Rec. length = 5 sek., HP-filter = Yes, Autorec = Yes, T.sense = High, Input gain = 60, Trig lev = 30, Interval = 0.

Table 1
Summary of pipe culvert characteristics. Pipe culvert design includes diameter, length and presence of water. Pipe culvert placement includes open/forest landscape.

Pipe culvert variables	Number of pipe culverts	Size (m)		
		Min.	Max.	Median
Without water	61			
With water	208			
In open landscape	40			
Forest at one opening	59			
In forest landscape	170			
Diameter		0.6	3.7	1.4
Length		6	141	24

In total, over the two years of fieldwork, 269 pipe culverts were surveyed for one night each from sunset to sunrise (Fig. 1). The ultrasound detector was placed as far into the pipe culvert as possible with the microphone directed into the pipe. For pipes with water in them, a small raft of polystyrene was used to place the ultrasound detector into the pipe (Fig. 2).

Both dry pipe culverts (e.g. for cattle) and road-stream culverts were used. The abundance of bats in the surrounding landscape was not measured. However, with the quantitative approach of this study, any anomalies in bat abundance in the landscape was assumed to have a negligible effect on the statistical results in this study. This assumption is supported by statistical theory, which indicates that random variation in unmeasured predictors tends to average out across large sample sizes, thereby reducing their potential influence on regression estimates (Ibe 2013).

The recorded ultrasound files were manually analysed using the programs Omnibat (Ecocom AB, 2014), and Batsound (Pettersson Elektronik AB, 2016). The number of passages (one passage = one recording) by genus, or species in those cases where species were identifiable, for each pipe culvert was recorded. Species identification of bats flying in narrow structures such as a pipe culvert is however very difficult. There will be disturbing echoes, and the repetition rate, bandwidth, frequency and other sound characteristics are not typical. Therefore, a mist net survey was performed at selected sites to aid species identification. Pipe culverts with high recorded activity of bats were chosen for mist netting. The mist nets were placed in front of one of the openings to the pipe culvert, whichever side was more suitable, before sunset and kept until midnight. All captured bats were identified to species level. In total 73 pipe culverts were surveyed with mist nets (Fig. 2).

Weather conditions such as low temperatures have been shown to affect bat activity negatively (de Jong et al. 2021). To account for these environmental factors, temperature and precipitation data for each acoustic survey night and pipe culvert was obtained from the Swedish Meteorological and Hydrological Institute's (SMHI) weather stations around Sweden. Precipitation was calculated by adding up the hourly precipitation from 10 pm (approximate sunset) to 4 am (approximate sunrise) during the night of the survey. Data over the minimum temperature recorded between 6 pm the day of starting the acoustic monitoring and 6 pm the following day was used as an estimate of the nightly temperature at the time of the survey (The Swedish Meteorological and Hydrological Institute, 2023).

Statistical analyses were performed to answer two main questions: (1) whether and how the design and placement of pipe culverts influenced the number of passages by clutter-adapted bats, and (2) whether and how the design and placement of the pipe culverts affected the likelihood of pipe culvert use by clutter-adapted bats. In both analyses, temperature and precipitation data were included to account for potential effects of weather conditions on bat activity.

To investigate what factors affect the number of passages by clutter-

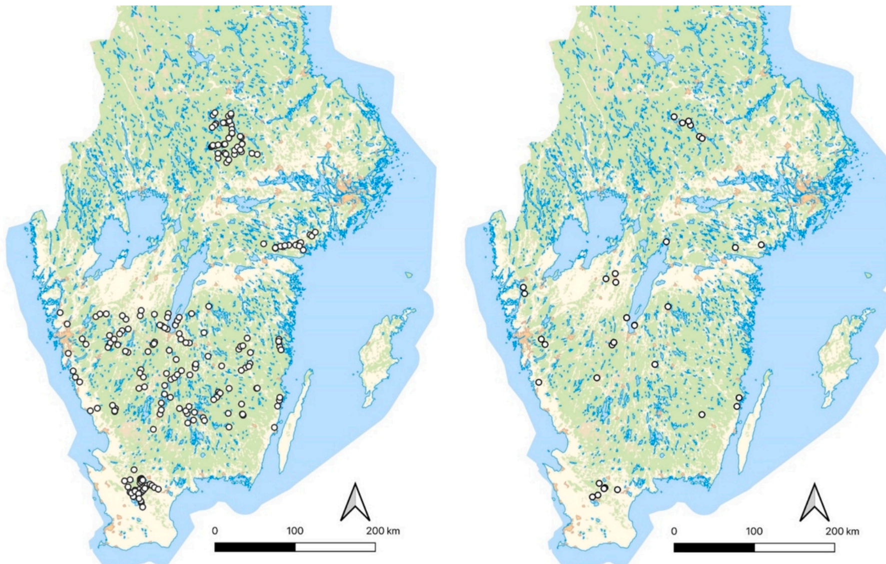

Fig. 1. a) Location of pipes surveyed with ultrasound recorders. b) Location of pipe culverts surveyed with mist nets.

Fig. 2. The ultrasound detector (Pettersson D500X) was placed on a small raft (left) and placed within the pipe culvert (right). There was no directional horn on the detector and consequently also bats foraging behind and above the detector was recorded. Photo: Johnny de Jong.

adapted species in a pipe culvert, the response variable *bat activity* (number of passages in one night in one pipe culvert) was analysed as a function of the predictor variables *width, length, presence of water in the pipe culvert* (factor with two levels), *presence of forest on either side of the pipe* (ordered categorical factor w. 3 levels), *temperature* and *precipitation*, using a generalized linear model (GLM) with a negative binomial dispersion distribution and a log link. As the width and height of the pipe were correlated, two separate models, each including only one of these predictors were tested; the model that produced the best fit was chosen as the final model.

To evaluate which factors affected the use of the pipe culverts, a binomial GLM (i.e., with a binomial dispersal function and an identity link function) were fitted. A binary response variable, *pipe culvert was used, or pipe culvert was not used*, was applied in the model. A used pipe culvert was defined as a pipe culvert with at least one recorded passing of a clutter-adapted species. The predictors in the model were *width, length, presence of water* (factor with two levels), *presence of forest* (ordered categorical factor w. 3 levels), *temperature,* and *precipitation*. To derive guidelines for optimal design and placement of pipe culverts for use by clutter-adapted bats, the fitted model was used to estimate threshold values for numerical predictor variables that in the model proved to significantly influence the pipe culvert usage. This was done by studying predictions from the model when the investigated predictor variable was varied, while the other, non-significant, predictors were kept constant at their means. Guideline values for 50 %, 80 % and 90 % probability of a pipe culvert being used was produced.

Statistical analysis of the data was performed using R (R Core Team, 2023), and the packages Mass (Venables & Ripley, 2002), DHARMa (Hartig, 2022), ggplot2 (Wickham, 2016), and ggeffects (Lüdecke, 2018).

3. Results

The total number of recordings of bats flying in the pipe culverts was 4431. Of these was 4365 *Myotis* spp and 66 was *Plecotus* spp. Some other species, foraging outside the culvert was also recorded (*Nyctalus* spp. 539, *Eptesicus* spp. 1442, *Pipistrellus* spp, 126, and unidentified Chiroptera 135). Out of the 269 pipe culverts surveyed, 131 (49 %) had at least one recorded passing by a clutter-adapted bat species. The acoustic survey identified 127 pipe culverts being used by *Myotis* spp. and 14 pipe culverts being used by *Plecotus* spp. Most calls were only identified to genus as the narrow conditions and echoes in the pipe culverts made it difficult to determine species with a reliable result. Although, in 27 pipe culverts one or more passing of *M. nattereri* could be identified with certainty due to this species having a more distinguishable sonar (Barataud, 2015). *M. brandtii, M. daubentonii, M. mystacinus*, and *P. auritus* were caught flying through the pipe culverts in the mist net survey (Table 2). The arrangement with detectors inside the pipe culvert did not totally exclude sound from outside. Sounds from species with strong sonar such as *Nyctalus, Eptesicus* and in some cases also *Pipistrellus* could sometimes be detected. However, based on the sound quality it was obvious that they did not used the pipe culvert. This was also confirmed with the trapping study. Furthermore, *Myotis*-species passing close to the entrance, but not using the pipe culvert could be detected, however, only with very weak sound of low quality, while individuals foraging or commuting inside the tunnel resulted in strong recordings. As the aim of this study was to investigate species flying inside of the pipe culverts only recordings when the bat was flying inside the pipe culvert was used in the statistical analysis. Hence, only clutter-adapted species from the genera *Myotis* and *Plecotus* were included in the analysis.

Most nights of survey there was no precipitation (min 0 mm, max 9.3 mm) and the temperature varied between 6.5 °C and 18 °C.

The activity of clutter-adapted species in the pipe culverts was significantly affected by the presence of water in the pipe culvert. When water was absent in the pipe culvert, the activity level was significantly lower (Fig. 3, Table 3). The width of the pipe culverts significantly affected the activity, so that pipe culverts with a larger inside diameter had higher recorded activity (Fig. 4). The precipitation, temperature, length of the pipe culvert, as well as the presence of forest at the openings of the pipe culverts were not significant in explaining the recorded activity level (Table 3).

When exploring what predictors could explain the usage of pipe culverts (at least one recording of a clutter-adapted species), only forest and width proved to be significant (Table 4). Pipe culverts with forest at both openings were used more often than those with forest at one or none of the openings (Fig. 5). Wider pipe culverts were more often used than pipe culverts with smaller widths (Fig. 6). Length, precipitation, temperature, and water did not significantly affect the usage of the pipe. Using the fitted binomial model threshold values for the pipe culvert width was estimated by varying the identified predictors forest and width (Table 5).

Table 2
Bats caught in the mist net survey.

Species	Total number of individuals caught	Males	Females	Sex not known	Number of individual pipe culverts where the species was caught
M. brantii	3	3	0	0	2
M. daubentonii	47	32	13	2	15
M.mystacinus	1	1	0	0	1
M.mystacinus/ M.branti	1	0	0	1	1
P.auritius	3	2	1	0	3

4. Discussion

M. daubentonii, M. mystacinus, M. brandtii. M. nattereri and *P. auritus* were the species found in the survey. These are the most common species of the genera *Myotis* and *Plecotus* in Sweden (de Jong et al., 2020). Hence, while most of the calls recorded in the acoustic survey could only be identified to genus, it can be assumed that they belong to one of the five species found in the survey. Another five species of *Myotis* and *Plecotus* have earlier been recorded in the study area but were not identified in this survey (*Myotis bechsteini, Myotis myotis, Myotis dasycneme, Myotis alcathoe, Plecotus austriacus,* de Jong, 2023). However, these are much rarer, and it is unlikely, although not completely impossible, that they are present among the recorded calls. While not shown here to be using the pipe culverts, these rarer species of *Myotis* and *Plecotus* most likely would benefit from wildlife crossings in the form of pipe culverts as they have similar behaviour, sonar and morphology as the species found in the pipe culverts (Barataud, 2015). In the mist net survey, the majority of captured bats were *M. daubentonii.* However, it is important to point out that the proportion of bat species caught in the mist net survey does not necessarily reflect the proportion of bat species using the pipe culverts. The mist net survey was designed to determine what species can be expected to use the pipe culverts. The locations for the mist net survey were therefore not chosen at random, and instead the pipe culverts with the highest recorded activity were chosen. Furthermore, the sample size in the mist net survey ($n = 73$) is relatively small compared to the sample size of the acoustic survey ($n = 269$). Consequently, the result of the mist net survey should not be used to infer anything about the proportion of species in the acoustic survey.

Increasing the width of the pipe culverts increased both the activity of clutter-adapted bats in the pipe culverts and the probability of the pipe culvert being used. In previous studies on other types of underpasses, larger variants such as bridges have had more species of different guilds using them compared to smaller variants such as tunnels (Boonman, 2011; Abbott et al., 2012b; Bhardwaj et al., 2017), which in turn could result in higher activity. For the studied pipe culverts this is probably not the case as only five species were detected to use the pipe culverts, all which were clutter-adapted and therefore had approximately the same preconditions to fly through narrow pipe culverts. Edge- and open-space-adapted species lack the adaptations in manoeuvrability and sonar to be able to fly through such narrow spaces as the pipe culverts surveyed in this study (Abbott et al., 2012b). Instead, the higher activity in the wider pipe culverts probably indicates presence of more individuals of the same species, not the presence of more species. This is supported by Boonman (2011) who found that, for all clutter-adapted species, the number of individuals recorded in the small tunnels increases with the height of the tunnel. Why more individuals use the larger pipe culverts is not clear and could be for several reasons. One could hypothesize that, because a narrower pipe culvert is more strenuous on the bat's echolocation and manoeuvrability (Abbot et. al., 2012b), fewer individuals view the pipe culvert suitable to fly though. Furthermore, larger pipe culverts could be easier for the bats to discover while narrower pipe culverts to a larger extent remain undiscovered as

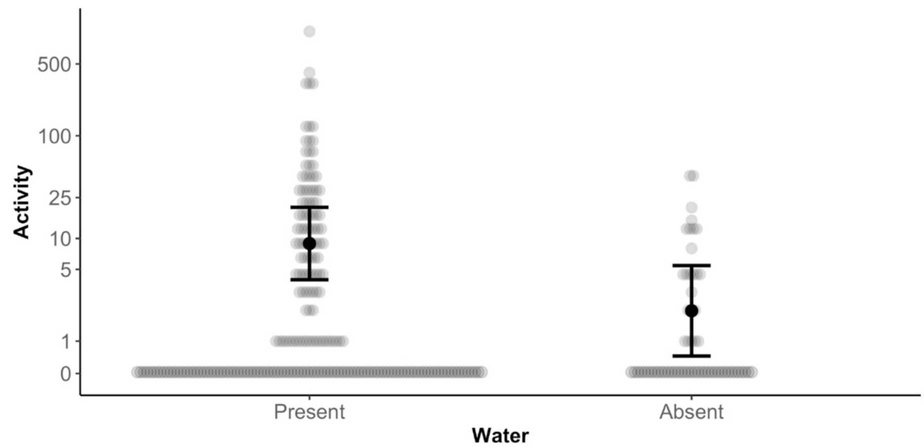

Fig. 3. Activity (number of recorded passages of clutter adapted species) in pipe culverts with water present and water absent. Error bars represent a 95 % confidence interval, and grey points shows the raw data (n = 269).

Table 3
Estimates (Est.), Standard errors (SE) and p-values for the predictors in the generalized linear model with a negative binomial distribution analysing activity in all surveyed pipe culverts.

	GLM: 'Activity' ~ 'Temperature' + 'Precipitation' + 'Water' + 'Length + 'Forest' + 'Width'.		
Predictor	Est.	SE	p-value
Temperature	0.0804	0.0720	0.264
Precipitation	−0.182	0.102	0.0728
Water (absent)	−1.51	0.377	**6.48e-5**
Length	−0.00424	0.00928	0.648
Forest (Linear)	0.227	0.318	0.476
Forest (Quadratic)	−0.0549	0.329	0.867
Width	0.0205	0.00356	**9.16e-9**

suitable passageways by bats.

For a 50 % probability of being used, a pipe culvert in forest habitat should be 126 cm wide. Further, for a 90 % probability of being used, a pipe culvert in a forest habitat should be 275 cm wide, which equals an opening area of approximately 6 m^2 (assuming a perfect circular opening). This is only slightly smaller than the threshold opening area of 6.5 m^2 for a 90 % probability of being used suggested for *M. daubentonii* by Boonman (2011). An important difference to the present study is that Boonman defines an underpass as used if it has a minimum of four recorded passings. Using the same definition in the present study, the estimated opening width thresholds would have been slightly wider. Defining a used pipe culvert as a minimum of one recorded passing allowed for more pipe culverts being defined as used, avoiding exclusion of potentially relevant cases. A higher required minimum amount of passings would, for example, define pipe culverts that are used regularly by solo male bats as unused. On the other hand, as pointed out by Boonman (2011), including pipe culverts with only one passing could result in the inclusion of random anomalies in the data, for example, instances of single isolated passings rather than regular ones. The quantitative approach to this study, surveying nearly five times as many underpasses than the study by Boonman, takes height for such outliers, as a single or few anomalies will have a negligible effect on the statistical

Table 4
Estimates (Est.), Standard errors (SE) and p-values for the predictors in the generalized linear model with a binomial distribution analysing the usage of the pipe culverts.

	GLM: 'Binary response variable' ~ ' Temperature' + 'Precipitation' + 'Water' + 'Forest' + 'Width' + 'Length'.		
Predictor	Est.	SE	p-value
Temperature	−0.0633	0.0608	0.297
Precipitation	−0.0172	0.0849	0.840
Water (absent)	−0.496	0.318	0.119
Forest (Linear)	0.620	0.273	**0.0234**
Forest (Quadratic)	0.0432	0.279	0.8771
Width	0.0145	0.00341	**2.00e-5**
Length	−0.00993	0.00813	0.222

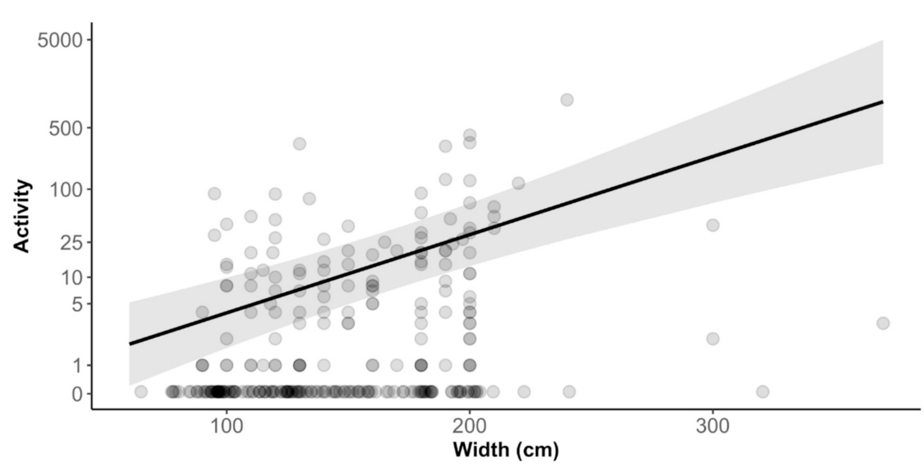

Fig. 4. Relationship between activity (number of recorded passages of clutter adapted species) in the pipe culvert and the width. Grey area represents the 95 % confidence interval, and points show the raw data (n = 269).

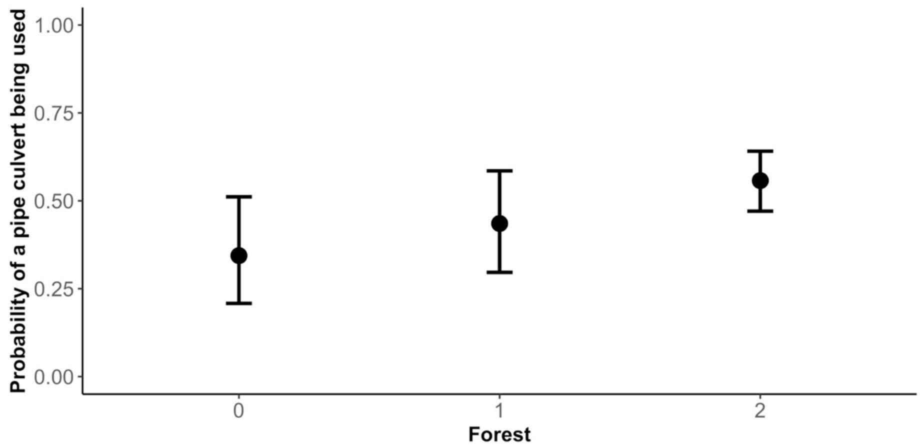

Fig. 5. Probability of a pipe being used depending on the presence of forest at the openings of the pipe culverts (n = 269). Pipe culverts had either forest at both openings (2), forest at one opening (1), or forest at neither opening (0). Error bars represent the 95 % confidence interval.

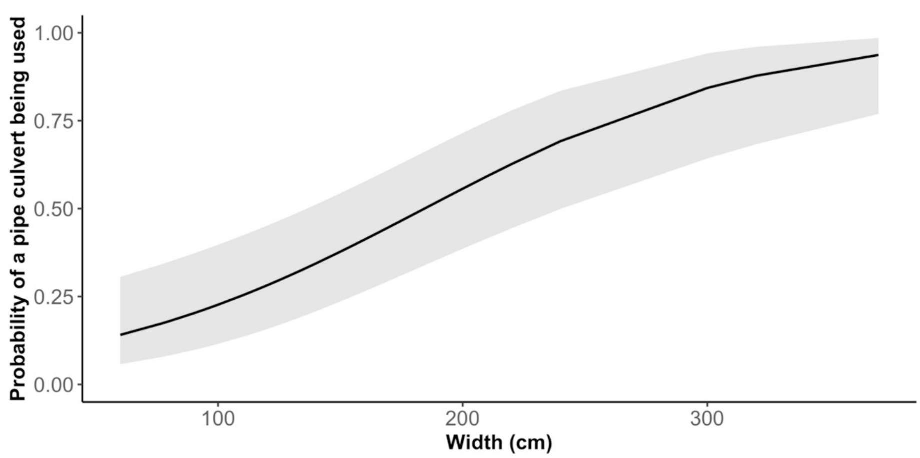

Fig. 6. Probability of a pipe culvert being used when varying the width of the pipe culvert (n = 269). Grey area represents the 95 % confidence interval.

Table 5
Width of pipe culvert (cm) corresponding to 50%, 80% and 90% probability of being used for pipes with no forest at either opening (forest 0), forest at one opening (forest 1), forest at both openings (forest 2).

	50 %	80 %	90 %
Forest 0	185	280	335
Forest 1	165	260	315
Forest 2	126	220	275

result.

While the width of the pipe culvert affected its usage, the length did not. Previous research on the topic has had mixed results. Boonman (2011) found no significant relationship between the use of tunnels by bats and the length of the tunnel. Laforge et al. (2019) found that the use of underpasses by *Plecotus* spp. increased with the number of lanes on the road and hypothesized that this was either due to the size of the road being a proxy for the amount of traffic, or larger roads simply imply a larger open space for the bats to cross. One could hypothesize that a longer pipe culvert could be less attractive for bats to fly through, but at the same time, longer pipe culverts are usually under wider roads, which implies a larger gap in the canopy to cross and therefore providing more incentive to fly under the road. A wider road, and therefore also a longer pipe culvert, could also correlate with more traffic deterring the bats from the area around the road. These possibly mixed effects from length of the pipe culvert, gap width, and traffic could be the reason that no clear trend can be found. Further studies, isolating factors such as length, gap width and traffic, would be needed to resolve this.

The results suggest that roads intersecting a forest should be prioritized for the implementation of pipe culverts as wildlife crossings for clutter-adapted bats. Pipe culverts with forest at both openings were used most frequently. Most of the surveyed pipe culverts with forest at neither opening had a linear feature leading up to the pipe culvert. While clutter-adapted bats can fly along linear features, these bats are far more common in forests (Ekman & de Jong, 1996; Zahn et al., 2006). Consequently, the probability of finding bats in pipe culverts with forest at both openings is higher.

Bach et al. (2004) suggested *M. daubentonii* to predominately use underpasses with a stream flowing through them. The present study found no significant effect of water being present in the pipe culverts on the probability of a pipe culvert being used by clutter-adapted bats but did find a positive trend between presence of water and the activity in the pipe culverts. It seems that while the size of the pipe culverts and the presence of forest are the only significant factors affecting whether a pipe culvert is used, water will influence the number of individuals using the pipe culvert. *M. daubentonii* forages above lakes and other larger water bodies and often follow smaller streams from the forest where it roosts to the hunting grounds (Downs & Racey, 2006). For an area with a population of *M. daubentonii* it is likely that several, if not the majority, of its individuals will forage over the same lake and follow the same stream to the lake. We suggest that if the stream goes through a pipe that is deemed suitable for flying through, it is likely that several or all foraging individuals would use it, which could explain the result observed in this study. It is important to consider that pipe culverts with water absent were still used, although with lower activity. Possibly, species other than *M. daubentonii* could be more common in pipe culverts with water absent as they don't show the same preference to navigate along water. Thus, to increase the possibility of accommodating for numerous different species of clutter-adapted bats pipe culverts of both types should be considered for implementation.

The weather was stable during the fieldwork, with only small variance in temperature and few nights with heavy rain. This is important since bat activity is lower at low temperatures and during heavy rain (Rydell, 1989), and large variations in temperature or precipitation could have skewed the results. Moreover, both temperature and precipitation were included as co-variates in the statistical models to account for any confounding effects. Neither temperature nor precipitation had any significant effect in the statistical models.

While the present study has proven clutter-adapted bats to be flying in the pipe culverts, it is not known how or for what purpose the bats use the pipe culverts. The pipe culverts could be part of a regularly used commuting route but could as well only be used at random during foraging. Previous studies have proven that clutter-adapted bats prefer to fly in an underpass instead of over the road while commuting (Kerth & Melber, 2009; Abbott et al., 2012a; Bhardwaj et al., 2017; Laforge et al., 2019), therefore it is likely that the pipe culverts are used in the same way, but more research would be needed to confirm this. Another interesting aspect for future studies is the influence of the larger landscape context on the usage of the pipe culverts. How does the placement of used pipe culverts correlate to the bat activity in the area and possible roosting spots and foraging grounds in the surrounding landscape? The present study has looked at the habitat closest to the openings of the pipe culverts, including a larger landscape parameter in future studies would give even more insight on how the pipe culverts should be placed in the landscape for maximum benefits.

This study has demonstrated that pipe culverts could be useful as wildlife crossings under roads for clutter-adapted bat species. During the planning phase of new infrastructure, pipe culverts should be considered for implementation, especially in forested areas. The pipe culverts implemented should be as large as possible, and both culverts with water and without water could potentially be of value when aiming to be useful to as many species of clutter-adapted bats as possible. As an addition to installing dedicated pipe culverts for bats, pipe culverts used for other purposes could also be adapted. Pipe culverts are already abundant in the Swedish landscape (Swedish Transport Administration, 2023b), most of them for drainage purposes, but far from the majority of these culverts are useful for clutter-adapted bat species, as many are too small, located in the wrong habitat or are blocked by vegetation or wildlife barrier fencing. In general, pipe culverts are not installed with wildlife in mind, and traditional pipe culverts may impede ecological connectivity. O'Shaughnessy et al. (2016) demonstrated, however, that ecological design culverts were more cost effective than maintaining hydraulic culverts. Pipe culverts could be made useful for bats by increasing the size of the pipe culverts used and keeping the openings free from clutter, essentially combining the two purposes, drainage and enhancing wildlife crossings, and of course negative impact on fish populations and water quality must be avoided (Januchowski-Hartley et al. 2013). Given that pipe culverts are a cheaper option than the previously proven useful larger types of underpasses, pipe culverts will hopefully not replace the implementation of these larger underpasses but instead act as a complement. So that the total number of underpasses can be increased giving more crossing options to mitigate the fragmentation caused by roads and increase the connectivity for clutter-adapted bat species in the landscape. Also, overpasses will continue be important mitigation structures, not only for clutter-adapted species, but also for edge-adapted species such as *Pipistrellus*. With this study we have proven that pipe culverts may be a good solution for clutter-adapted bats, however, other alternatives must always be considered for other bat species and for wildlife connectivity in general.

CRediT authorship contribution statement

Adina Sennblad: Writing – original draft, Investigation, Formal analysis, Data curation. **Isabella Honnér:** Writing – review & editing, Investigation. **Johnny de Jong:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition.

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

Data will be made available on request.

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