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Wild ungulate use of underpasses: tunnel length and availability of crossing opportunity matters

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Underpasses have a fundamental potential in mitigating infrastructure barriers for wildlife, considering that they are a relatively common feature across traffic networks. Increasing our understanding of the functionality of the different designs and localities of underpasses is therefore crucial within infrastructure planning and management. We analyzed crossing probability, based on movement-triggered automatic cameras, in moose (*Alces alces*) and roe deer (*Capreolus capreolus*), common wild ungulates in Scandinavia, in relation to underpasses with different designs and localities. We analyzed the design through passage width, height, and length, including different combinations of these size dimensions. We also categorized underpasses into three size levels considering all dimensions. We included the nearest distance to the alternative crossing site while controlling for season, group size, and whether wildlife visits occurred during daytime or nighttime. We compared 797 visits by moose across nine underpasses and 1,433 visits by roe deer across 13 underpasses. Increasing tunnel length lowered the crossing probability in both moose and roe deer. Tunnel length not exceeding 16.5 m had a crossing probability above 50% in moose, whereas tunnel length not exceeding 12.0 m had a crossing probability above 50% in roe deer. However, we found no correlation between crossing probability and passage width and height. Tunnel length may describe a perceived narrowness more efficiently than other size dimensions. In roe deer, crossing probability increased when alternative crossing sites were situated further away, whereas moose showed a tendency toward the same pattern. Nearest distances to alternative crossing sites farther away than 1,150 m were related to more than 50% probability of roe deer visits resulting in crossing through underpasses. Thus, we conclude that tunnel length (ranging from 7.0 to 39.0 m) and nearness to alternative sites to cross seem to be more important factors than other size dimensions among underpasses (with passage width ranging from 2.8 to 42.0 m and passage height ranging from 2.0 to 10.2 m) to explain crossing probability in wild ungulates. The impact on crossing probability from the availability of other crossing sites stresses the importance of securing crossing opportunities along infrastructure barriers at the home range scale of focal species.

KEYWORDS

crossing probability, design, fauna passage, openness index, permeability, road and railway barriers, size dimension, under crossings

1 Introduction

Barrier effects of linear transportation features such as roads and railways, hereafter referred to as infrastructures, result in fragmentation and habitat loss (Jaeger, 2000; Trombulak and Frissell, 2000). Barriers from infrastructure arise mainly from road mortality, road avoidance, and physical obstacles such as wildlife fencing (Torres et al., 2016). Crossing opportunities for wildlife may mitigate these barrier effects for those individuals that can encompass suitable crossing sites within their home ranges (Clevenger and Waltho, 2005; Sawyer et al., 2012a). Crossing opportunities can be openings in wildlife fences in combination with overpasses or underpasses, or other types of designed wildlife passages (Glista et al., 2009; Smith et al., 2015; Elfström and Olsson, 2025). The type of crossing opportunities available along roads or railways with high traffic volumes is usually underpasses, whereas overpasses are more infrequent. Non-wildlife underpasses (e.g., conventional bridges, and water-conveying and non-water-conveying culverts) are abundant throughout global transportation networks and have the potential to function as mitigation for the barrier effects of linear infrastructure on wildlife movement. Thus, underpasses have a high potential to function as barrier mitigation for wildlife. However, the knowledge is still incomplete about the functionality of wildlife crossing among different-sized dimensions of underpasses.

The frequency of wildlife visits is influenced by numerous factors that are not related to locality or design of passages. The availability of suitable habitat around a crossing structure affects functionality in terms of the proportion of wildlife that can occupy the surroundings to cross infrastructure barriers (Ng et al., 2004). Thus, the frequency of wildlife visits at a crossing structure will be influenced by the density of wildlife occupying that specific area (Sawyer et al., 2012b). The abundance or density of wildlife fluctuates over time and space. Habitat use changes between seasons and years due to factors like land use, drought, rain, and human disturbance. Thus, the frequency of wildlife visits at a passage depends on a variety of factors that are difficult to control for and unrelated to passage design (van der Grift et al., 2013; Denneboom et al., 2021). However, the decision to cross once an animal encounters a passage (i.e., crossing probability) may be less influenced by the factors that determine how often animals visit a site. Each visit results in either a successful crossing or the animal remaining on the same side of the transportation barrier (Elfström and Olsson, 2025).

Species respond differently; typically, small- and medium-sized carnivores favor narrow or small underpasses and culverts, whereas ungulates seem to more often use wide and large underpasses to cross infrastructure barriers (Denneboom et al., 2021). We focus on common and large wild ungulates in Scandinavia, namely, moose (*Alces alces*) and roe deer (*Capreolus capreolus*), because roe deer are the species most involved in wildlife vehicle accidents, while moose are more likely to cause severe driver injuries (Jägerbrand et al., 2018). In addition, moose represents a high economic and social impact in society due to concerns within forestry and recreational purposes, such as hunting (Jägerbrand et al., 2018). Roe deer and moose also represent focal species with significantly different body sizes, which may impact their prerequisites when using underpasses to cross infrastructure barriers.

The abundance of non-wildlife underpasses along roads and railways stresses the importance of understanding how the design may impact its functionality in mitigating infrastructure barriers for wildlife. Passage width and height have been reported to be important in affecting wild ungulate usage of underpasses (Bhardwaj et al., 2020), as well as tunnel length (Clevenger and Waltho, 2005; Mata et al., 2005). Underpasses designed for wildlife to cross infrastructure barriers are typically located in areas with less human presence, and human usage may also be restricted around these crossing structures (Clevenger and Waltho, 2000). Wide and tall passages with not too long tunnel length are usually the objective when designing underpasses for wild ungulates to mitigate infrastructure barriers, but larger underpasses require higher construction and maintenance costs (Glista et al., 2009). This raises the need for providing the traffic and road administrators with accurate knowledge when planning mitigation efforts against infrastructure barriers, specifically, how to consider non-wildlife underpasses of different sizes.

We tested *a priori* hypotheses to determine how underpass design and landscape context influence crossing probability in moose and roe deer. We expected the crossing probability to vary with underpass design and the availability of alternative crossing routes. In addition, we assessed whether infrastructure type, river presence, and temporal and behavioral covariates (season, diel period, and group size) explain variation in crossing probability beyond structural dimensions. We formulated the following hypotheses regarding factors influencing the probability that a wild ungulate visit results in a successful crossing through an underpass:

H1: *Alternative crossing availability*. Crossing probability increases with increasing distance to the nearest alternative crossing site, reflecting stronger barrier effects and fewer available alternative routes (Model #8).

H2: *Single-dimension effects of size*. Crossing probability is associated with individual underpass dimensions, such that probability increases with increasing passage width and/or height and decreases with increasing tunnel length (Models #1–3).

H3: *Relative importance of tunnel length*. Tunnel length is the strongest single size-related predictor of crossing probability, reflecting perceived openness and exit visibility within underpasses (Model #2, contrasted with Models #1 and #3).

H4: *Composite size metrics outperform single dimensions*. Crossing probability is better explained by composite measures of structural openness than by any single dimension, including a height × width metric, width/length ratio, height × width/length index, or categorical size class (Models #4–7).

H5: *Infrastructure type (road vs. railway)*. Crossing probability differs between road and railway underpasses, potentially due to differences in traffic intensity, disturbance, and structural design (Model #9).

H6: *River presence*. Crossing probability differs between underpasses with and without rivers, potentially due to habitat structure and movement corridors associated with watercourses (Model #10).

H7: *External covariates only (timing and group size)*. Crossing probability is primarily driven by temporal and behavioral conditions (season, diel period, and group size) and is independent of underpass design (Model #11).

H8: *Null model*. Only random variation in crossing probability among underpasses (Model #12).

2 Methods

2.1 Study areas

All underpasses were situated in forested surroundings and were distributed across Sweden (Figure 1). All underpasses were encircled by forest. The land cover around each passage site, i.e., within a 4-km radius, was provided from the Swedish Mapping, Cadastral and Land Registration Authority (downloaded during 2019; https://www.lantmateriet.se/en). The dataset represents an interpreted land-cover classification derived primarily from aerial photography, supplemented by satellite data and other geospatial information. The positional accuracy of the land-cover boundaries is approximately 10 m. The most common type of land cover was composed of primarily coniferous forest with mixed forest (coniferous and deciduous trees) (69% ± SD = 11%), and the second most common land cover was open pastures and crop fields (22% ± SD = 12%), whereas settlements made up a tiny proportion of the landscape (3% ± SD = 3%). We categorized available habitats into four main categories and estimated their proportions for each passage site (Supplementary Material; Table S1).

2.2 Underpasses

The underpasses analyzed were multifunctional, meaning that they were constructed to pass water streams in combination with connecting infrastructure across areas with lower terrain and offering vehicle crossing opportunities at different grades. All underpasses were selected to encompass different size dimensions

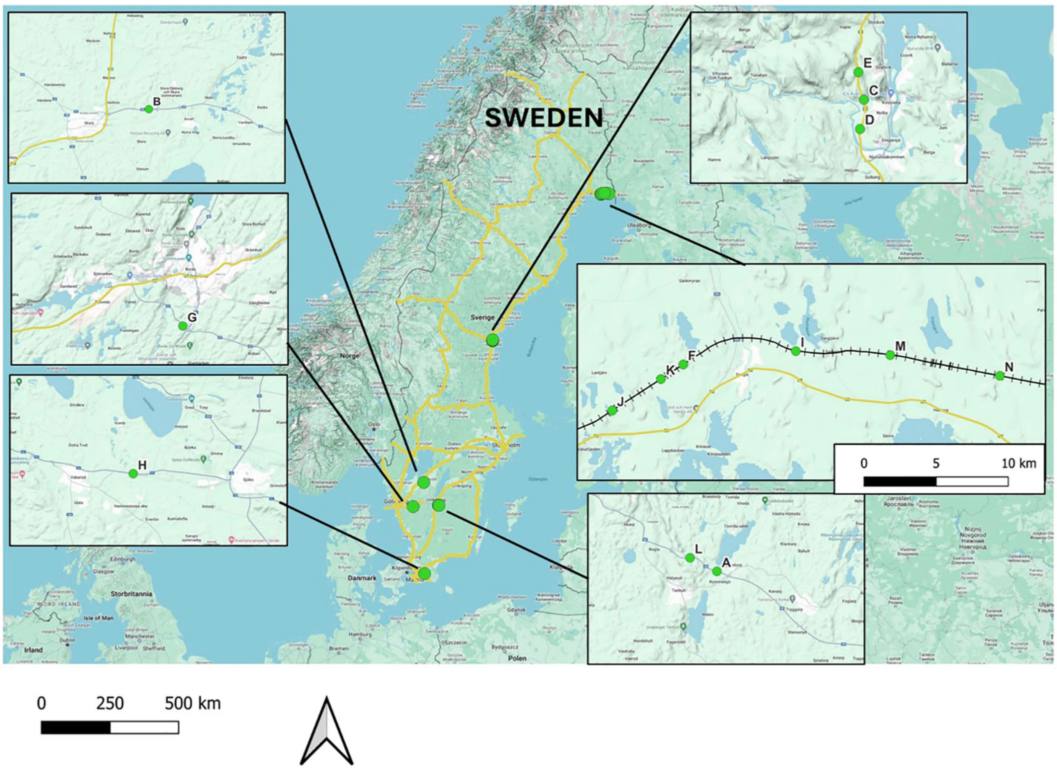

FIGURE 1
Study areas representing geographical positions for underpasses when analyzing crossing probability in wild ungulates in relation to design and locality during the years 2018–2021. The distribution of underpasses encompasses most ranges of both latitude and longitude in Sweden. Labels of each underpass passage refer to those in Table 1. All underpasses were situated in forested surroundings.

and required to have observed crossings made by the focal species, moose and/or roe deer, and a minimum of 15 visits per passage by the focal species. Thus, the size dimensions were all within ranges that allowed the focal species to use the selected underpasses.

The infrastructures above the underpasses were all considered to be significant barriers for wild ungulates, as all road and railway sections within a minimum length of 2.5 km from the underpass were equipped with fencing to prevent animals from crossing. All road and railway sections carried an average traffic volume above 9,000 vehicles per day or 7.4 trains per day. The size dimensions, sample effort in terms of monitoring days, and detection rates (i.e., the number of observed visits by moose and roe deer divided by the total number of monitoring days) at each underpass included in our study are presented in Table 1, and an example of the studied underpasses is depicted in Figure 2.

We compared the probability that wildlife visits resulted in a successful crossing versus no crossing across underpasses of different size dimensions distributed throughout Sweden. For each underpass, alternative opportunities to cross the same infrastructure barrier were available at different grades (i.e., overpasses or other underpasses) within a 4-km radius of the passage site. This distance corresponds to the approximate home-range scale of the focal wild ungulates and therefore represents the spatial extent within which individuals could reasonably access alternative crossing routes (Jarnemo et al., 2018). Alternative crossing sites consisted of either non-wildlife underpasses with comparable size dimensions or overpasses. For each underpass included in the study, we quantified the distance to the nearest alternative overpass or underpass that could potentially be used by the focal species.

2.3 Data collection

Animal movements were monitored by motion-triggered automatic cameras equipped with near-infrared during dark hours. Cameras were located within 10 m of the underpass openings and facing toward the opening. The study period for camera monitoring underpasses ranged from 86 to 387 days and occurred between May 2018 and July 2021.

An event or wildlife visit was defined as observations of the same species within 10 minutes (Elfström and Olsson, 2025). Individual identity was not possible to separate. Thus, we could not control for individual dependence, i.e., personality, among wildlife visits.

We analyzed passage width, passage height, and tunnel length in relation to the probability of passing through the underpass (Tables 1, 2). Group size, time of day, and season of the year varied among wildlife visits, and therefore, we controlled for these variables in all analyses of crossing probability. Daytime was defined as between 07:00 and 19:00, and other visits during other times as nighttime, i.e., reflecting when people are more active. Spring was defined as March 1–May 31, summer as June 1–August 31, fall as September 1–October 31, and winter as November 1–February 28.

2.4 Statistical analyses

All statistical analyses were carried out in R version 4.2.2 (R Core Team, 2023). Correlations among size measures of underpasses were controlled using Pearson's correlation tests (Pearson, 1895). The probability of animals passing through underpasses was analyzed using binomial generalized linear mixed-effects models (GLMMs) with a logit link function. The response variable was binary (1 = successful passage, 0 = no passage) and represented individual crossing events. Models were fitted by maximum likelihood using the Laplace approximation in the R package *lme4* (Bates et al., 2015).

Underpass identity was included as a random intercept to account for repeated observations within the same underpass. Predictor variables describing underpass size (e.g., width, length, height, and composite indices) were log-transformed prior to analysis to reduce skewness and improve model fit. Due to collinearity among size-related variables, only one size metric was included per candidate model. One model separated between railway and road underpasses, and another model separated between underpasses along rivers and underpasses without rivers. All models included the covariates for group size (number of individuals per visit), season, and diel period (day/night), which were treated as fixed effects, with categorical predictors entered as factors. Candidate models were specified *a priori* and compared using Akaike's information criterion corrected for small sample sizes (AICc) and AICc weights (AICcw) (Akaike, 1973; Burnham and Anderson, 2002). Candidate models represent different hypotheses and are presented in Table 3. Model-averaged parameter estimates (β) and 95% confidence intervals were calculated for models with ΔAICc < 4 and/or AICc weight > 5% in the R package *AICcmodavg* (Burnham and Anderson, 2002; Mazerolle, 2023). Model assumptions were assessed using simulated residuals in *DHARMa* (Hartig, 2022), and multicollinearity was evaluated using variance inflation factors (Zuur et al., 2009).

3 Results

We compared 797 visits by moose across nine underpasses and 1,433 visits by roe deer across 13 underpasses.

The proportions of land-cover types were similar among the three different size categories of underpasses (Table 1). The mean proportion (± SD) of settlements was 0.04 (± 0.02) around narrow underpasses, 0.05 (± 0.03) around medium-sized underpasses, and 0.01 (± 0.01) around spacious underpasses. The mean proportion (± SD) of open pastures and crop fields was 0.30 (± 0.17) around narrow underpasses, 0.17 (± 0.04) around medium-sized underpasses, and 0.21 (± 0.10) around spacious underpasses. The mean proportion (± SD) of forested areas was 0.59 (± 0.11) around narrow underpasses, 0.72 (± 0.04) around medium-sized underpasses, and 0.72 (± 0.11) around spacious underpasses. The mean proportion (± SD) of open water bodies was 0.06 (± 0.04) around narrow underpasses, 0.06 (± 0.03) around medium-sized underpasses, and 0.06 (± 0.02) around spacious underpasses.

TABLE 1 Underpasses across Sweden analyzed for crossing probability during 2018–2021 in relation to different passage size dimensions in meters.

Underpass ID	Days monitored (N)	Focal species [a]: visits (N)	Detection rate [a]: visits/day	Width (m)	Height (m)	Length (m)	Openness index [b]	Type of traffic	Size category	Nearest distance alt. crossing (m)
A	86	R: 82	R: 0.95	2.8	2	22	0.3	Road	Narrow	650
B	243	R: 73	R: 0.30	6	2.5	21.5	0.7	Road	Narrow	1,502
C	375	R: 48	R: 0.13	6	4	33.6	0.7	Road	Narrow	530
D	387	M: 15 + R: 94	M: 0.04 R: 0.24	7	4.7	23.9	1.4	Road	Medium	471
E	370	M: 18 + R: 31	M: 0.05 R: 0.08	9	4.7	21.5	2	Road	Medium	890
F	374	M: 33 + R: 21	M: 0.09 R: 0.06	5.5	3	7	2.4	Rail	Medium	1,405
G	285	R: 131	R: 0.46	14	7	39	2.5	Road	Medium	375
H	361	R: 380	R: 1.05	10	4.4	15.3	2.9	Road	Spacious	1,845
I	300	M: 29	M: 0.10	8	4.7	7	5.4	Rail	Spacious	675
J	370	M: 75 + R: 114	M: 0.20 R: 0.31	12.8	6	7	11	Rail	Spacious	1,045
K	368	M: 91 + R: 55	M: 0.25 R: 0.15	22	6	7	18.9	Rail	Spacious	1,405
L	116	M: 27 + R: 318	M: 0.23 R: 2.74	35	10.2	16	22.3	Road	Spacious	630
M	358	M: 242 + R: 61	M: 0.68 R: 0.17	42	4.7	7	28.2	Rail	Spacious	1,408
N	356	M: 267 + R: 25	M: 0.75 R: 0.07	40	7	7	40	Rail	Spacious	2,070

[a]M denotes moose, R denotes roe deer, and values represent observed visit frequency.
[b]Width * Height/Length.

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FIGURE 2
Example of two medium-sized underpasses with quite different size dimensions. *Left*: width = 5.5 m, height = 3.0 m, and tunnel length = 7.0 m (Passage F). *Right*: width = 9.0 m, height = 4.7 m, and tunnel length = 21.5 m (Passage E). Underpass Passage E is 39% wider than Passage F, corresponding to 1.6 times wider, but the length is three times longer, compared to underpass Passage F.

The shortest underpasses were all crossing under railways; thus, shorter tunnel lengths were associated with railway underpasses. Size dimensions were correlated with each other. The heights of underpasses used by moose were positively correlated with width and length dimensions (Pearson's correlation: r = 0.27, 95% CI = 0.20 and 0.33, and r = 0.12, 95% CI = 0.05 and 0.18, respectively). The heights of underpasses used by roe deer were positively correlated with width but not correlated with length dimensions (Pearson's correlation: r = 0.81, 95% CI = 0.79 and 0.82, and r = −0.05, 95% CI = −0.10 and 0.01, respectively).

TABLE 2 Explanatory variables analyzed in relation to crossing probability from wild ungulate visits to underpasses in Sweden during 2018–2021.

Explanatory variables	Type of variable
Passage width	Ratio scale; in meters
Passage length	Ratio scale; in meters
Passage height	Ratio scale; in meters
Width * Height	Ratio scale; in meters
Width * Height/Length	Ratio scale; in meters
Width/Length	Ratio scale; in meters
Narrow, medium, or spacious	Categorical, 3 groups
Type of infrastructure	Categorical, 2 groups
Distance to alternative crossing site	Ratio scale; in meters
Group size	Ratio scale; number of individuals
Season of the year	Categorical, 4 groups
Daytime or nighttime	Categorical, 2 groups
Presence of rivers through passage	Categorical, 2 groups
Passage site ID (random factor)	Categorical, 14 levels in moose and 9 in roe deer

3.1 Moose

The most parsimonious model included separation between railway and road constructions to capture variation in crossing

TABLE 3 Candidate models created before model selection.

Candidate model ID	Variables
Width #1	Visit outcome ~ log(Width) + Group size + Season + Daylight [+Passage ID]
Length #2	Visit outcome ~ log(Length) + Group size + Season + Daylight [+Passage ID]
Height #3	Visit outcome ~ log(Height) + Group size + Season + Daylight [+Passage ID]
Height and Width #4	Visit outcome ~ log(Height * Width) + Group size + Season + Daylight [+Passage ID]
Width and Length #5	Visit outcome ~ log(Width/Length) + Group size + Season + Daylight [+Passage ID]
Height, Width, and Length #6	Visit outcome ~ log(Height * Width/Length) + Group size + Season + Daylight [+Passage ID]
Size category #7	Visit outcome ~ Narrow or Medium or Spacious + Group size + Season + Daylight [+Passage ID]
No dimensions; Distance to alternative crossing site #8	Visit outcome ~ log(Distance) + Group size + Season + Daylight [+Passage ID]
Roads *vs.* Railway #9	Visit outcome ~ Roads_*vs*_Rail + Group size + Season + Daylight [+Passage ID]
Rivers #10	Visit outcome ~ $Rivers_{Presence}$ + Group size + Season + Daylight [+Passage ID]
Only external covariates (timing and group size) #11	Visit outcome ~ Group size + Season + Daylight [+Passage ID]
Null model #12	Visit outcome ~ [+Passage ID]

H1: *Alternative crossing availability*; presented by Model #8. H2: *Single-dimension effects of size*; presented by Models #1–3. H3: *Relative importance of tunnel length*; presented by Model #2, contrasted with Models #1 and #3. H4: *Composite size metrics outperform single dimensions*; presented by Models #4–7. H5: *Infrastructure type (road vs. railway)*; presented by Model #9. H6: *River presence*; presented by Model #10. H7: *External covariates only (timing and group size)*; presented by Model #11. H8: *Null model*; presented by Model #12.

TABLE 4 The most parsimonious model to explain variation in crossing probability from 797 moose visits at nine underpasses in Sweden during 2018–2021.

Candidate models	K	AICc	ΔAICc	$AICc_{Wt}$	Cum.Wt
Roads *vs.* Railway #9	8	871.01	0	0.44	0.44
Length #2	8	872.28	1.27	0.23	0.68
Height #3	8	872.96	1.95	0.17	0.84
Nearness alternative crossing site #8	8	875.39	4.38	0.05	0.89
Only external covariates #11	7	876.54	5.53	0.03	0.92
Height and Width #4	8	877.21	6.19	0.02	0.94
Rivers #10	8	878.04	7.03	0.01	0.96
Width #1	8	878.15	7.14	0.01	0.97
Width and Length #5	8	878.24	7.23	0.01	0.98
Size category #7	8	878.56	7.55	0.01	0.99
Height, Width, and Length #6	8	878.58	7.57	0.01	1
Null model #12	2	900.5	29.48	0	1

AICc, Akaike's information criterion corrected for small sample sizes.

probability in moose while considering group size, season, and daylight (Table 4). The second most parsimonious model included the dimension tunnel length to capture variation in crossing probability (Table 4). However, an alternative model with the factor passage heights was also supported, capturing variation in crossing probability in moose successfully. There was no support for only passage width or any combinations of size dimension variables (Table 4). The fourth most parsimonious model (#8) had no dimension factors included except for the nearest distance to alternative crossing site, although weak support (ΔAICc = 4.38 and $AICc_{Wt}$ = 5%).

Coefficient estimates based on model average among the four highest ranked models revealed that constructions along roads had lower crossing probability than constructions along railways (β = −1.90; 95% CI = −3.04 and −0.76; Figure 3) and that increased tunnel length was correlated with lower crossing probability in moose (β = −1.67; 95% CI = −2.79 and −0.55; Figure 3 and separate candidate model in Figure 4). Model average for taller passage height was correlated with lower crossing probability (β = −2.59; 95% CI = −4.43 and −0.75; Figure 3). Model average for longer nearest distance to alternative crossing site showed a tendency but did not significantly increase the crossing probability (β = 1.42; 95% CI = −0.06 and 2.89; Figure 3 and separate candidate model in Figure 5).

An additional number of individuals (group size) per visit increased the crossing probability (β = 0.64; 95% CI = 0.37 and 0.92; Figure 3). Separation between daytime and nighttime did not impact crossing probability in moose (during nighttime: β = −0.01; 95% CI = −0.36 and 0.36; Figure 3). However, moose visits during winter had a lower crossing probability than during fall (β = −0.77; 95% CI = −1.28 and −0.26; Figure 3).

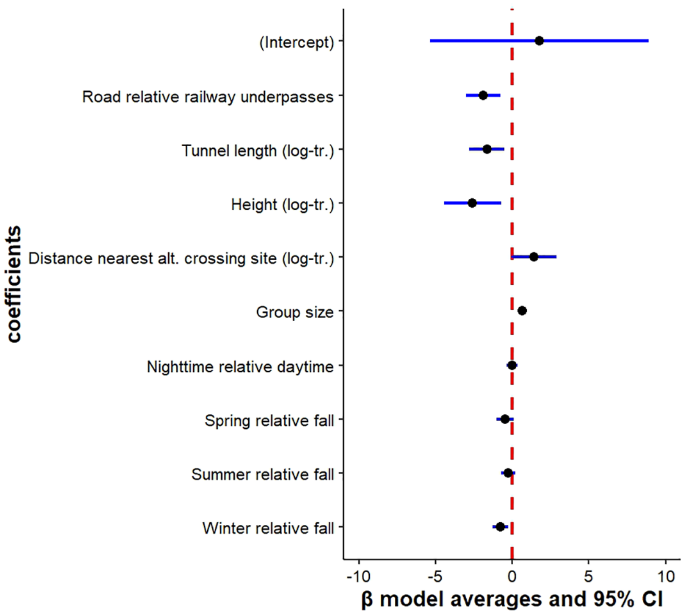

FIGURE 3
Effect plot for explaining variation in crossing probability in 797 moose visits across nine underpasses in Sweden during 2018–2021, based on model average for ΔAICc < 4.00 and/or $AICc_{weight}$ > 5%. Underpass identity was included as a random effect with variance = 0.64. Tunnel length model was ranked second-highest, passage-height model was third-highest, and alternative crossing availability model was ranked fourth as most parsimonious models (Table 4). AICc, Akaike's information criterion corrected for small sample sizes.

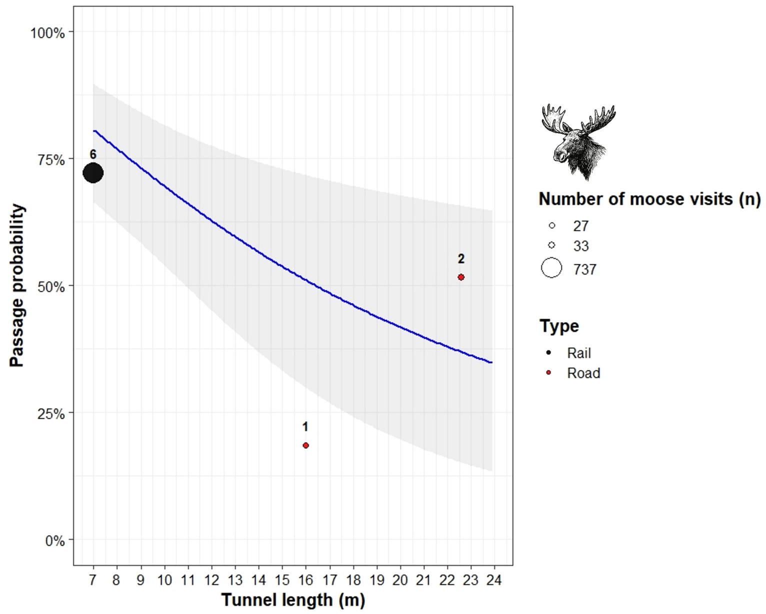

FIGURE 4
Crossing probability in 797 moose visits as function of tunnel length across nine underpasses in Sweden during 2018–2021, based on the partial effect from GLMM (ΔAICc = 1.27 and $AICc_{weight}$ = 23%). Tunnel length exceeding 16.5 m was related to less than 50% probability of moose visits resulting in crossing through underpasses. Label above each point refers to number of underpasses with the same x-axis value (tunnel length). GLMM, generalized linear mixed-effects model; AICc, Akaike's information criterion corrected for small sample sizes.

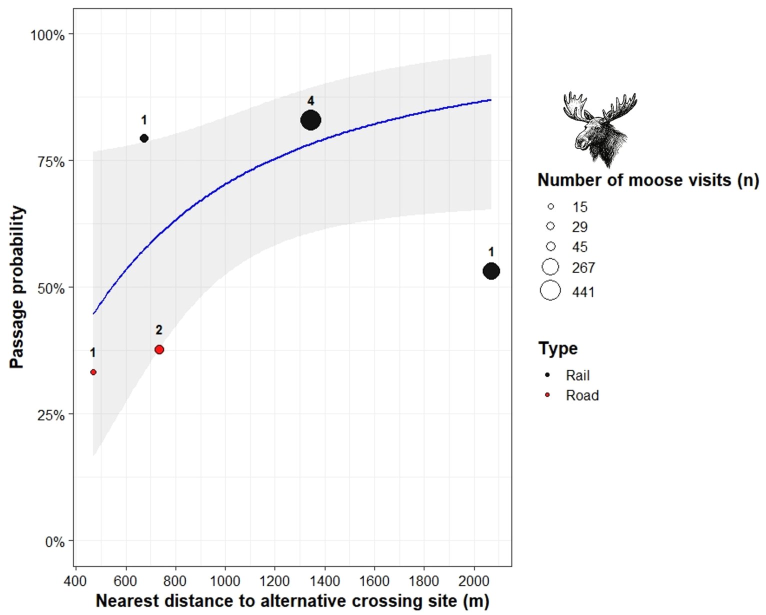

FIGURE 5
Crossing probability in 797 moose visits as function nearest distance to alternative crossing over- or underpasses across nine underpasses in Sweden during 2018–2021, based on the partial effect from GLMM (ΔAICc = 4.38 and $AICc_{weight}$ = 5%). Nearest distances to alternative crossing sites farther than 1,100 m were related to more than 75% probability of moose visits resulting in crossing through underpasses. Label above each point refers to number of underpasses with the same x-axis value (nearest distance to alternative crossing site). GLMM, generalized linear mixed-effects model; AICc, Akaike's information criterion corrected for small sample sizes.

TABLE 5 The most parsimonious model to explain variation in crossing probability from 1,433 roe deer visits at 13 underpasses in Sweden during 2018–2021.

Candidate models	K	AICc	ΔAICc	$AICc_{Wt}$	Cum.Wt
Roads *vs.* Railway #9	8	1,494.82	0	0.39	0.39
Length #2	8	1,495.67	0.85	0.26	0.65
Nearness alternative crossing site #8	8	1,497.43	2.61	0.11	0.75
Width and Length #5	8	1,498.5	3.68	0.06	0.82
Only external covariates #11	7	1,498.98	4.15	0.05	0.86
Height, Width, and Length #6	8	1,499.38	4.56	0.04	0.9
Width #1	8	1,500.48	5.66	0.02	0.93
Height and Width #4	8	1,500.73	5.91	0.02	0.95
Rivers #10	8	1,500.95	6.13	0.02	0.97
Height #3	8	1,500.99	6.17	0.02	0.98
Size category #7	9	1,501.21	6.39	0.02	1
Null model #12	2	1,519.23	24.4	0	1

AICc, Akaike's information criterion corrected for small sample sizes.

3.2 Roe deer

The most parsimonious model (#9) included separation between railway and road constructions to capture variation in crossing probability in roe deer while considering group size, season, and daylight (Table 5). The second-highest ranked model (#2) included tunnel length (ΔAICc = 0.85 and $AICc_{Wt}$ = 26%). The third most parsimonious model (#8) had no dimension factors included except for nearest distance to the alternative crossing site (ΔAICc = 2.61 and $AICc_{Wt}$ = 11%). The fourth-highest ranked models were also parsimoniously supported and included width/length (#5) (ΔAICc = 3.68 and $AICc_{Wt}$ = 6%; Table 5).

Coefficient estimates based on model average among these four highest ranked and parsimoniously supported models revealed that constructions along roads had lower crossing probability than constructions along railways (β = −2.11; 95% CI = −3.58 and −0.64; Figure 6) and that increased tunnel length was correlated with lower crossing probability in roe deer (β = −1.53; 95% CI = −2.69 and −0.36; Figure 6 and separate candidate model in Figure 7). Model average for longer nearest distance to alternative crossing site was correlated with increasing crossing probability (β = 1.48; 95% CI = 0.02 and 2.95; Figure 6 and separate candidate model in Figure 8). However, the model average for the factor [passage width/length] was not significantly correlated with crossing probability (β = 0.56; 95% CI = −0.10 and 1.21; Figure 6). Thus, except for separating between railway and road underpasses, only the dimension factor, tunnel length, and nearest distance to alternative crossing site captured variations in crossing probability in roe deer while considering group size, season, and daylight (Table 5).

The number of individuals (group size) per visit and separation between daytime and nighttime did not impact crossing probability in roe deer (one more individual: β = 0.03; 95% CI = −0.33 and 0.38, and during nighttime: β = −0.16; 95% CI = −0.43 and 0.12,

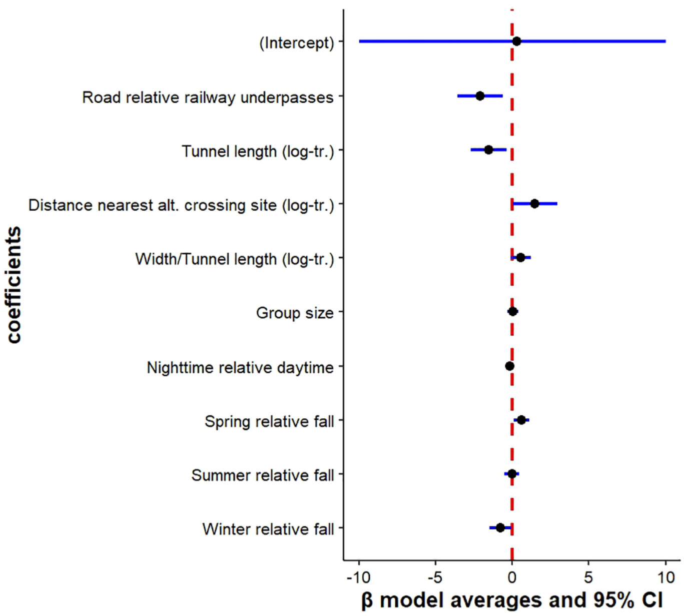

FIGURE 6
Effect plot for explaining variation in crossing probability in 1,433 roe deer visits across 13 underpasses in Sweden during 2018–2021, based on model average for ΔAICc < 4.00 and/or $AICc_{weight}$ > 5%. Underpass identity was included as a random effect with variance = 2.01. Tunnel length model was ranked second-highest, alternative crossing availability model was third-highest, and passage width/tunnel length model was ranked fourth as most parsimonious models (Table 5). AICc, Akaike's information criterion corrected for small sample sizes.

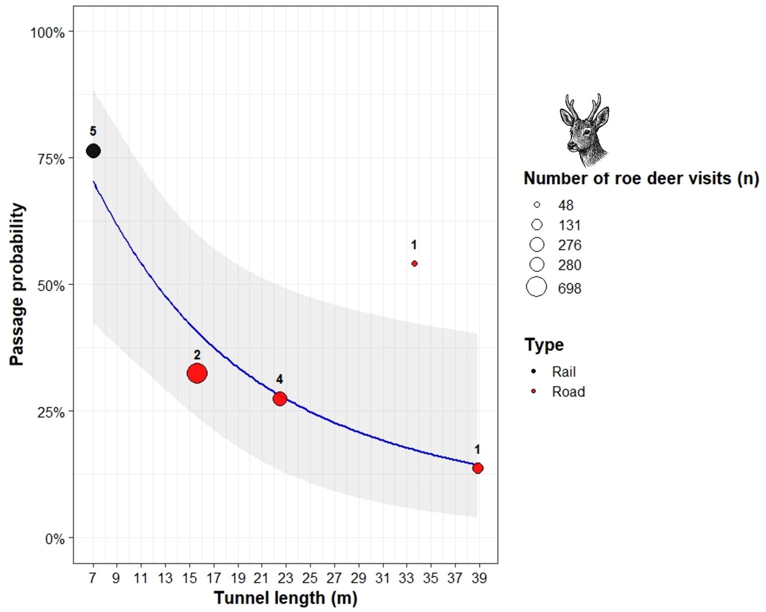

FIGURE 7
Crossing probability in 1,433 roe deer visits as function of tunnel length across 13 underpasses in Sweden during 2018–2021, based on the partial effect from GLMM (ΔAICc = 0.85 and $AICc_{weight}$ = 26%). Tunnel length exceeding 12 m was related to less than 50% probability of roe deer visits resulting in crossing through underpasses. Tunnel length exceeding 25 m was related to less than 25% probability of roe deer visits resulting in crossing through underpasses. Label above each point refers to number of underpasses with the same x-axis value (tunnel length). GLMM, generalized linear mixed-effects model; AICc, Akaike's information criterion corrected for small sample sizes.

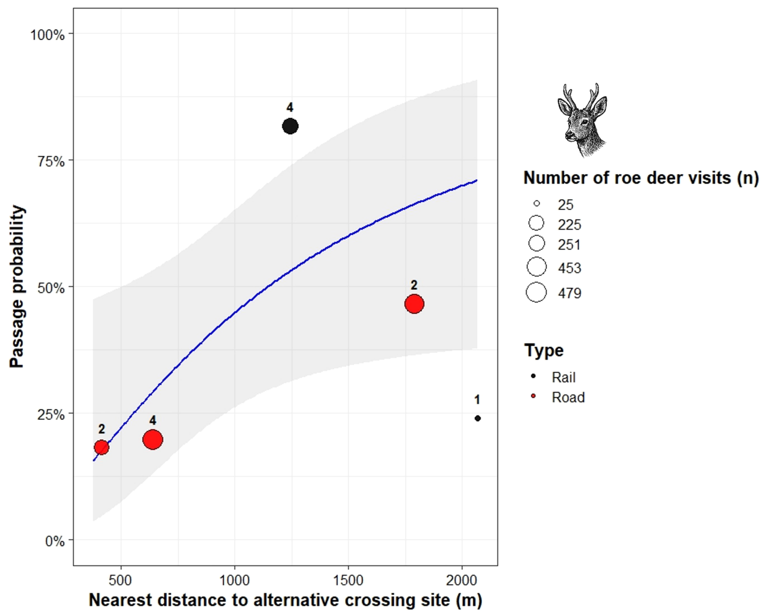

FIGURE 8
Crossing probability in 1,433 roe deer visits as function of nearest distance to alternative over- or underpass from 13 underpasses in Sweden during 2018–2021, based on the partial effect from GLMM (ΔAICc = 2.61 and $AICc_{weight}$ = 11%). Nearest distances to alternative crossing sites farther than 1,150 m were related to more than 50% probability of roe deer visits resulting in crossing through underpasses. Label above each point refers to number of underpasses with the same x-axis value (nearest distance to alternative crossing site). GLMM, generalized linear mixed-effects model; AICc, Akaike's information criterion corrected for small sample sizes.

respectively; Figure 6). However, roe deer visits during spring had a higher crossing probability (β = 0.59; 95% CI = 0.07 and 1.11), whereas visits during winter had a lower crossing probability than during fall (β = −0.79; 95% CI = −1.48 and −0.09; Figure 6). Roe deer visits during summer had no greater impact on crossing probability than during fall (β = −0.03; 95% CI = −0.52 and 0.46).

4 Discussion

Our study reveals that tunnel length was the most important measure to explain crossing probability in both moose and roe deer through underpasses. Clevenger and Waltho (2000) also identified tunnel length as the most important size dimension for use by red deer in Canada, although they also reported increased use by ungulates with shorter passage width. Our results suggest that when comparing crossing probability in wild ungulates among, for instance, underpasses of different size dimensions, it is important to account for different seasons of the year, group size, and nearness to alternative crossing sites.

Railway bridges were correlated with shorter tunnel length compared to road bridges, which may explain why we found a higher crossing probability below railway bridges than road bridges. However, other factors except for tunnel length, such as lower traffic frequency and also different traffic disturbances, may have impacted differently on the crossing probability between railway bridges and road bridges (Lucas et al., 2017).

Fencing has been proven to increase the crossing probability through underpasses (Dodd et al., 2007a; Huijser et al., 2016). Bissonette and Adair (2008) stressed to consider the home range scale of the focal species for placement of wildlife crossings. We found that distance to the nearest alternative crossing site explained more variation in crossing probability than passage width or height among the underpasses within our study when analyzing crossing probability in roe deer. In contrast, we found only a tendency but no significantly correlated increase in crossing probability with longer distance to the nearest alternative crossing site in moose. However, considering that moose have much larger home ranges compared to roe deer (Cederlund and Sand, 1994; Guillet et al., 1996), moose have, in general, more crossing sites available compared to those in roe deer. This may account for the absence of a significant correlation between moose crossing probability and the nearest alternative crossing site. Bhardwaj et al. (2020) also reported a correlation between nearness to alternative crossing sites and the use of underpasses by roe deer, whereas no correlation was found in use by moose. In contrast to our results, Bhardwaj et al. (2020) reported a lower use of underpasses with increasing distance to the nearest alternative crossing site.

We found an increased crossing probability with a farther distance to the nearest alternative crossing site. This suggests 1) that the infrastructure indeed has a barrier effect restricting wild ungulate habitat use; 2) that the barriers from infrastructure, such as fencing, will compel animals to use available underpasses; and 3) that fencing is a necessity to increase the use of crossing opportunities by wild ungulates. However, to mitigate the overall degree of fragmentation and other barrier effects, it is crucial not to allow too long distances in between crossing opportunities. Forcing or re-routing wildlife in their habitat use constitutes one example of barrier impact, risking increased stress and energy costs when infrastructure restricts animal movements. The impact on crossing probability from the availability of other crossing sites stresses the importance of securing crossing opportunities along infrastructure barriers within a home range scale of focal species.

Tunnel length not exceeding 16.5 m had a crossing probability above 50% in moose, whereas tunnel length not exceeding 12.0 m had a crossing probability above 50% in roe deer. Bhardwaj et al. (2020) concluded that moose and roe deer preferred underpasses with a passage width of at least 11.5 m and a passage height of 5 m. We conclude that tunnel length (ranging from 7.0 to 39.0 m) and nearness to alternative sites to cross seem to be more important factors than other size dimensions to explain crossing probability in wild ungulates, among underpasses with passage width ranging from 2.8 to 42.0 m and passage height ranging from 2.0 to 10.2 m. Tunnel length may capture the perceived narrowness of an underpass more effectively than width or height, as longer passages reduce visible exit openings and increase the distance an animal must move through an enclosed space.

Surprisingly, we found that higher passage height was correlated with lower crossing probability in moose. However, our study does not suggest that crossing probability is increased due to shorter passage height, as we found a positive correlation between passage height and tunnel length among underpasses used by moose. Thus, the shorter tunnel length among the same passages with shorter passage height likely explains why a shorter passage height was related to higher crossing probability. In roe deer, we found no correlation between passage height and crossing probability, whereas there was also no correlation between tunnel length and passage height among passages used by roe deer.

In a previous study in Sweden, width and height were reported as the most important dimension factors (Bhardwaj et al., 2020), but our results did not confirm that conclusion. However, Bhardwaj et al. (2020) analyzed animal tracks deposited in sand beds and compared the use of underpasses with movements documented 50 m away. Wildlife observations in our study were made within 10 m of underpass entrances, and thus, there may be a higher proportion of wildlife observed with the intent to cross the infrastructure. Our openness index, including different combinations of width, height, and length, turned out to be a poor predictor of crossing probability. Openness index has been recommended in some varieties, combining several size factors such as width, height, and length (Iuell et al., 2022; Nevrelova et al., 2022). However, our results suggest that tunnel length can reliably describe narrowness for underpasses in relation to wild ungulate crossing probability, provided that passage width and height are above a critical minimum and that availability to alternative crossing sites is accounted for. Thus, we caution against only focusing on size index values when mapping permeability among potential passages for wildlife at different grades.

Passage width may be easier to adjust than passage height or tunnel length when modifying underpasses to improve wildlife permeability. In many cases, tunnel length is largely determined by road width and structural requirements and therefore cannot be easily reduced. However, because tunnel length was consistently associated with lower crossing probability in both moose and roe deer, our findings highlight the importance of minimizing tunnel length where feasible. Where shortening is not possible, future work should evaluate whether alternative design solutions that reduce the perceived enclosure of long underpasses—such as incorporating intermediate openings, segmented structures, or parallel shorter passages—can improve crossing rates.

No difference in crossing probability between visits during daytime and nighttime suggests that no potential human disturbance impacted the willingness of moose or roe deer to use underpasses. Ungulates have been reported to reduce their diurnal activity in response to human disturbance (Gaynor et al., 2018; Bonnot et al., 2019). Human activity seems to be correlated with temporal variation in wild ungulate use of crossing sites (Knufinke et al., 2024). Human disturbance was probably relatively low in our study, which may explain our result because human settlements were not common in the vicinity of the underpasses.

Aggregating in larger groups is a common animal behavior to reduce predation risks and other dangers (Creel et al., 2014). We found that a larger group size in visiting moose was related to increased crossing probability through underpasses. Perhaps individuals in a family group or other aggregation of conspecifics experience higher confidence compared to solitary individuals when approaching underpasses.

Moose visits during winter had a lower crossing probability compared to during fall. Moose visits during the winter season are perhaps more often related to the search for food at either side of the underpass rather than the intention to cross the infrastructure. During the fall, the crossing probability increases, which overlaps with the mating period and with migration between higher altitude summer pasture areas and lower altitude winter areas (Mysterud, 1999; Ball et al., 2001). Roe deer also showed lower crossing probability during winter compared to during the fall, confirming results from Ważna et al. (2020). In addition, roe deer visits during spring showed a higher crossing probability than during the fall. The different tendencies to cross through underpasses among seasons of the year may be a result of food availability impacting habitat use.

Large mammals may often approach near underpasses without using them to cross, e.g., within 50 m (Dodd et al., 2007b). This may reflect a reluctance by wild animals to use underpasses, but it may also reflect a lack of intention, need, or desire to cross the infrastructure. Thus, we do not know whether an observed crossing probability through one specific underpass accurately reflects the perceived barrier impact on wildlife. An increased crossing probability by wild ungulates can be the result of a suitable design in terms of not too narrow underpass, but also due to that animals lack other alternatives to cross and are therefore forced to utilize a specific underpass.

Wildlife observations close to underpass entrances do not necessarily reflect an intention to cross the infrastructure. Animals may approach underpasses while foraging or exploring without perceiving the infrastructure as a barrier. Consequently, crossing probability at a specific underpass may not directly reflect the perceived barrier effect of the infrastructure in our study.

Future studies should combine camera monitoring with independent data on animal movement routes (e.g., GPS telemetry) to distinguish between the availability of underpasses and actual crossing decisions. This would allow stronger inference about how underpass design influences barrier permeability at the home-range scale. Future studies combining size metrics of underpasses with direct traffic and disturbance measurements would improve inference.

Tunnel length emerged as a consistent predictor of crossing probability in both moose and roe deer, indicating that perceived narrowness may be better captured by passage length than by width or height alone, provided minimum dimensional thresholds are met. From a management perspective, this implies that shortening underpasses, where feasible, or subdividing long passages into multiple intersected crossings may be more effective in reducing barrier effects than increasing passage width alone. While fencing can increase the use of available crossings, it should be implemented in combination with sufficiently frequent crossing opportunities to avoid forcing animals into energetically costly detours or concentrated movement bottlenecks.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Ethics statement

Ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements. Data was collected by monitoring wild animal movements with motion-triggered automatic cameras; human access was restricted.

Author contributions

ME: Conceptualization, Formal analysis, Project administration, Validation, Visualization, Methodology, Data curation, Writing – original draft, Supervision, Funding acquisition, Writing – review & editing, Software, Investigation, Resources. EH: Writing – original draft, Writing – review & editing. JH: Writing – original draft, Writing – review & editing.

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Conflict of interest

Author ME was employed by company EnviroPlanning. Author EH was employed by company WSP Sverige.

The remaining author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fcosc.2026.1751415/full#supplementary-material

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