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MARIS KRUUSE

Factors influencing the occurrence and reporting of wildlife-vehicle collisions and the performance of wildlife crossing structures as primary mitigation measures

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UNIVERSITY OF TARTU
Press

Department of Geography, Institute of Ecology and Earth Sciences, Faculty of Science and Technology, University of Tartu, Estonia

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following original papers which are referred to in the thesis by their Roman numerals:

I. **Kruuse, M**., Enno, S.-E., Oja, T. (2016). Temporal patterns of wild boar-vehicle collisions in Estonia, at the northern limit of its range. *European Journal of Wildlife Research* 62: 787–791. https://doi.org/10.1007/s10344-016-1042-9.

II. Bíl, M., Andrášik, R., Cícha, V., Arnon, A., **Kruuse, M**., Langbein, J., Náhlik, A., Niemi, M., Pokorny, B., Colino-Rabanal, V. J., Rolandsen, C.M., Seiler, A. (2021). COVID-19 related travel restrictions prevented numerous wildlife deaths on roads: A comparative analysis of results from 11 countries. *Biological Conservation*, 256, 109076. https://doi.org/10.1016/j.biocon.2021.109076.

III. Bíl, M., Balčiauskas, L., Bílová, M., Cellina, S., Favilli, F., Gačić, D., Guinard, E., Heurich, M., Ivanova, N., Junghardt, J., Keuling, O., **Kruuse, M**., Kukalaj, Q., Langbein, J., Laube, P., Licoppe, A., Masaryk, P., Maślanko, W., Mayer, M., Moroney, A., Moţ, R., Mrđenović, D., Náhlik, A., Nebunu, A., Nezval, V., Niemi, M., Pokorny, B., Psaralexi, M., Ralevic, S., Ricci, S., Rolandsen, C.M., Rosell, C., Santos, S.M., Seiler, A., Steiner, W., Swinnen, K.R.R., Šprem, N., Trajçe, A., Trpeski, V., van der Grift, E.A., Vogiatzakis, I., Zihmanis, I. (2025). Wildlife-vehicle collision liability in Europe: A review of existing approaches and their implications. *Journal of Environmental Management*, 380, 124986. https://doi.org/10.1016/j.jenvman.2025.124986.

IV. **Kruuse, M**., Tull, A., Valdmann, H. (2025). Changes in mammal crossings in less than 10 years after the construction of Estonia’s first wildlife overpass. *European Journal of Wildlife Research* 71: 109. https://doi.org/10.1007/s10344-025-01996-3.

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The articles are the result of collective work and contain an important contribution of all co-authors. The author’s contribution to the publications referred to by their Roman numerals is indicated in the Table.

Table. Author’s contribution to the publications (* – *minor contribution*, ** – *moderate contribution*, *** – *major contribution*).

	I	**II**	**III**	**IV**
Original idea	***	*	*	***
Study design	***	*	*	***
Data collection	***	**	**	***
Analysis and interpretation	**	*	*	***
Manuscript writing	***	*	*	***

LIST OF ABBREVIATIONS

AADT – annual average daily traffic
ASF – African swine fever
CRTR – COVID-19-related traffic reduction
LT – local time
UTC – coordinated universal time
UVC – ungulate-vehicle collision
VPD – number of vehicles per day
WBVC – wild boar-vehicle collision
WVC – wildlife-vehicle collision

¾ of my thesis is based on suffering and death of way too many living beings.
But the last ¼ consists of survival and hope.

1. INTRODUCTION

1.1. From earliest roadkill studies to road ecology – evolution of the discipline

While transport infrastructure is a cornerstone of economic growth and social mobility, its environmental footprint is vast and enduring (Abra et al., 2025). Very few regions remain untouched by the direct or indirect consequences of traffic and construction. Furthermore, these networks often act as a catalyst for urban sprawl and future land use change, creating a cumulative pressure that serves as one of the primary drivers of global biodiversity loss (van der Ree et al., 2015; Seiler et al., 2023).

The scientific study of roadkill traces origins back one hundred years to a seminal 1925 *Science* publication by Dayton and Lillian Stoner. Their documentation of 225 animal carcasses involving 29 reptile, bird, and mammal species over a 1017-km journey through Iowa (Stoner, 1925) shifted the perspective on road impacts from purely human safety to ecological health, establishing the foundation for modern road ecology. Initial observations of wildlife mortality have since matured into the systematic discipline of road ecology. Early milestones include structured studies in Sweden during the 1960s, which provided quantitative data on seasonal mortality trends and species-specific risks (Göransson et al., 1978). Parallel research in the Netherlands highlighted the critical correlation between traffic volume and roadkill frequency, while noting how results are shaped by sampling efforts and local population fluctuations (Bruinderink and Hazebroek, 1996). In the US, early roadkill insights were linked to habitat connectivity, ecological barriers, and biodiversity conservation (Forman and Alexander, 1998). Historical research in this field remained largely concentrated in North America and Europe; it was not until the 1990s or later that the first documented records from other global regions began to surface (Balčiauskas et al., 2025).

The publication of *Road Ecology*: *Science and Solutions* (Forman et al., 2003) marked the formal maturation of the field, offering a cohesive conceptual framework that integrates a diverse range of scientific inquiries. While road ecology only emerged as a formal discipline in the early 2000s, the field has since experienced significant academic and empirical growth, examining the multifaceted effects of roads on the ecological environment (Coffin, 2007; Abra et al., 2025).

In Estonia, systematic mammal related collision data collection and analysis started in the 1980s at the Estonian Forest Institute, led by Jüri Tõnisson and Malle Mardiste. Based on police and insurance records from various counties, 3377 collisions were registered between 1985 and 1990. The majority involved roe deer (50%), moose (30%), and wild boar (14%) (Mardiste, 1992). During the same period, the Estonian Ornithological Society intensified its research into avian road mortality. This initiative integrated systematic monitoring by professional staff with supplemental data contributed by hobby ornithologists (Lõhmus, 1994). These works refer to several rather small-scale vertebrate collision studies and notes (Sügav, 1969; Naaber, 1974; Poots, 1974; Sügav, 1974; Masing, 1983) from even an earlier period. In 2001, Lauri Klein defended master's thesis "Conflict situations between roads and animals in Estonia" at the University of Tartu (Klein, 2001). Since then, this topic has been explored across various universities, resulting in several master's and numerous bachelor's theses.

By the early 2000s, the Estonian Road Administration began addressing wildlife-road conflicts by integrating mitigation measures into infrastructure projects. These early efforts included the construction of tunnels for amphibians and small mammals, as well as the intentional preservation of riparian corridors under bridges for large game. This initiative continued in 2006 with the commencement of planning for Estonia's first ecoduct. Also, the performance of these crossings was monitored to validate their success as mitigation measures. While these early initiatives at first faced scepticism by society, the start of planning of the Rail Baltic high-speed railway approximately five years later served as a turning point. As this massive project highlighted the threat of habitat fragmentation and the disruption of local communities, public awareness shifted. Consequently, support for wildlife mitigation measures grew significantly as the ecological and social risks of large-scale infrastructure became more apparent.

In 2010, national guidelines were developed to identify conflicts between infrastructure and wildlife, proposing technical strategies for effective mitigation (Klein, 2010). Wildlife studies and the design of crossing structures and other mitigation measures have now become integrated, standard procedures within both major road construction and reconstruction projects.

1.2. Wildlife-vehicle collisions and consequences

Wildlife-vehicle collisions (WVCs) are widely recognized as one of the primary negative effects of roads on numerous wildlife species, while simultaneously imposing significant socioeconomic burdens when collisions result in human injury or property damage. In recent decades, collecting and collating data of WVCs has experienced a global surge, characterized by an exponential increase in the volume of scholarly publications (Schwartz et al., 2020). With the global road network now exceeding 21.6 million km (Meijer et al., 2018), the resulting traffic volume is responsible for millions of wildlife fatalities each year (Schwartz et al., 2020). In 2025, an open-access global dataset (Grilo et al., 2025) documented 208 570 roadkill records from 54 countries across six continents, covering 2283 terrestrial vertebrate species and subspecies. This database is instrumental in identifying high-mortality species and analysing the spatial and temporal dynamics of collisions, as well as their broader consequences for population viability and extinction risk (Abra et al., 2025).

Collisions with small to medium-sized wildlife typically prove fatal for the animal but pose minimal risk to human safety, however, motorcyclists face a much greater risk of serious injuries in WVCs compared to car occupants (Bíl et al., 2024). In contrast, accidents involving large ungulates represent a growing threat to traffic safety (Bruinderink and Hazebroek, 1996; Seiler 2004; Huijser et al., 2009). With annual incident rates over half a million in nineteen European countries (Linnell et al., 2020) and one million for whole Europe (Langbein et al., 2011); and even exceeding that figure in the United States (Huijser et al., 2007), these crashes result in tens of thousands of human injuries and substantial economic costs each year (Bissonette et al., 2008; Sullivan, 2011; Niemi et al., 2017). However, official statistics on animal-vehicle collisions likely underrepresent the true scale of the issue (Bíl and Andrášik, 2020). Research indicates that even for well-documented species like ungulates (Bruinderink and Hazebroek, 1996), actual accident rates are significantly higher than what is recorded in formal databases (reviewed by Bíl and Andrášik, 2020).

1.3. Spatio-temporal patterns of collisions

Understanding the spatial and temporal patterns of WVCs is essential for conducting accurate accident analyses and developing effective mitigation strategies. WVC frequency is likely shaped by a complex interplay of spatio-temporal variables, including traffic dynamics, vehicle speed, infrastructure design, weather, vegetation and other environmental conditions, and ecological factors such as animal behaviour and population density (Langbein et al., 2011). While numerous roadkill studies have examined the spatial distribution of WVCs and their contributing factors (reviewed by Oddone Aquino and Nkomo, 2021) to provide appropriate mitigation measures like wildlife passages, in contrast, temporal patterns have received somewhat less attention, and the results of available studies are often contradictory across various regions and species (Steiner et al., 2021). In general, the temporal trends of WVCs are known to reflect species-specific biological requirements and behavioural rhythms. These include seasonal peaks associated with reproductive and dispersal behaviours, as well as diurnal patterns driven by daily foraging and resting cycles (e.g., Bruinderink and Hazebroek, 1996; Diaz-Varela et al., 2011). Also road characteristics, traffic volume, drivers' visibility and alertness are important factors. For example, several studies have found that WVCs peak during the weekends and relate this phenomenon to increased traffic volume (Dussault et al., 2006) as no biological, ecological or behavioural factors depending on weekdays are known (Steiner et al., 2014; Hothorn et al., 2015), and other human factors (Lagos et al., 2012).

1.4. Traffic volume as one of the most important factors of WVCs

Traffic volume is a significant factor in wildlife-vehicle accidents (e.g., Charry and Jones, 2009; Pagany, 2020). Often quantified and compared through indicators such as annual average daily traffic (AADT) or vehicles per day (VPD), traffic intensity is considered a high wildlife death risk if VPD is 4 000–10 000 and very high death risk if VPD exceeds 10 000 (Seiler et al., 2023). However, the unique influence of traffic is difficult to measure. As interannual changes in traffic volumes are often slight and over time there may be parallel increasing trends in both animal and car numbers, researchers struggle to decouple the effects of traffic density from other variables (Hothorn et al., 2015).

The first half of 2020 presented an unprecedented scenario as travel restrictions and diminished traffic demand during the COVID-19 pandemic led to a sharp decline in road traffic. This period of significantly reduced human mobility, termed the ‘Anthropause’, offered a rare opportunity – despite its tragic origins – to examine how shifts in human activity influence wildlife behaviour and safety (Bates et al., 2020; Corlett et al., 2020; Rutz et al., 2020). Thus, this situation was called even *Global Human Confinement Experiment* (Bates et al., 2020). Initial data from the pandemic travel restrictions showed a major decline in WVCs, yet this trend was not universal. Because results were highly sensitive to local policy enforcement, different nations experienced divergent ecological outcomes.

Reductions in traffic volume varied significantly by country, reflecting the intensity of local lockdown measures. In April 2020, declines ranged from as high as 75–80% in Spain and Italy to a more modest 22% in Sweden or 10% in Estonia. While the initial shock caused a sharp dip, many countries experienced a relatively quick recovery in vehicle activity (ETSC, 2020). In Estonia the traffic density decreased by an average of 28% during the first weeks of COVID-19-related traffic reduction (CRTR), but as commercial and industrial companies continued to operate, the frequency of freight transport remained the same as before the emergency period. The number of passenger cars was reduced by 33% but started to recover soon. The primary change observed was the levelling of peak traffic loads near the cities. Although midday traffic remained consistent with historical data, morning and evening volumes saw a marked decline (Jairus, 2020).

Not surprisingly, various countries reported an increase in speeding violations. In Finland, the proportion of major speeding violations rose by up to 30%, and in France, a 50% increase in serious speeding violations was observed by law enforcement and speed cameras. In general, Europe saw a situation where traffic volumes fell while the number of traffic violations increased or remained the same. The data also reflected an upward trend in alcohol-related traffic incidents. Only Italy reported a decrease in traffic violations, as a direct result of the strict movement restrictions (ETSC, 2020).

1.5. Factors influencing the reporting of wildlife-vehicle collisions

Available statistics on WVCs underrepresent the actual number of these incidents (please see also subchapter 1.2.), and accident rates even for large mammals like ungulates are remarkably higher than official databases suggest. For example in Estonia, if there are no human fatalities or injuries in the WVC, there is no need to report the accident to the police. WVCs are registered by the Environmental Board in cooperation with the Rescue Board and communicated to Transport Administration. According to Estonian Hunting Act § 34 (4, 5), any large game killed in a traffic collision must be reported immediately to the local hunting district user or the Environmental Board. The carcass and its parts remain the property of the hunting district user; if the animal has no consumption value, the hunters are responsible for its disposal or on-site burial, subject to the landowner's approval. Moose (*Alces alces*), red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), wild boar (*Sus scrofa*), brown bear (*Ursus arctos*), wolf (*Canis lupus*), European lynx (*Lynx lynx*), or even grey seal (*Halichoerus grypus*) are listed as large game (Estonian Hunting Act § 4 (2)). However, many road users are still not aware of the reporting obligation but awareness is increasing year by year. In addition, the hunters are obliged to report the number of large game killed in traffic (or in other situations, for example drowned etc) in their hunting ground to the Environmental Board and this information is also used by Environment Agency. If a large carnivore (bear, wolf or lynx) is involved in WVC, Environmental Board must be notified immediately. Under Annex 1 of the Estonian regulation regarding environmental damage from illegal poaching or habitat destruction, fines for large game range from € 400 for a wild boar to € 2000 for a brown bear. These rates are not applicable to traffic collisions, however, as such incidents are not considered illegal kills. Consequently, in the case of a road accident involving a wild animal, no liability for compensation is assigned to any party. Conversely, hunters receive no compensation for collecting the carcass or for the effort of tracking wounded game.

Smaller animals pose less risk to vehicle integrity and passenger safety, leading to notably lower driver reporting rates (Borza et al., 2023). However, evasive manoeuvres taken to avoid even small wildlife can lead to secondary accidents with other vehicles or roadside obstacles (Balčiauskas et al., 2024; Bíl et al., 2024). These incidents are probably recorded as regular traffic accidents and not being attributed to wildlife. Conversely, motorists who crash due to negligence or other reasons may claim they were manoeuvring to avoid a wild animal. Nevertheless, these incidents are not registered as WVCs unless supported by evidence. Consequently, the probability of a WVC being officially registered depends on a range of factors, including regional reporting standards and the species involved.

1.6. Ecological impacts of roads and the performance of mitigation measures

Supporting increasing mobility demands for human society while maintaining ecological connectivity is a key factor to sustainable transport infrastructure (Forman et al., 2003). Therefore, comprehensive understanding of both the primary and secondary impacts – whether direct or indirect – exerted by infrastructure on the natural environment is essential to develop appropriate mitigation strategies (Seiler et al., 2023). Primary ecological effects are produced by the physical presence of infrastructure in the landscape, their structural design, maintenance, and use. Primary impacts include direct habitat loss, wildlife mortality (Grilo et al., 2020), barrier effects on wildlife mobility (Trombulak and Frissell, 2000), edge effects on adjacent habitats and corridor effects and transformation of habitat linked to infrastructure (Benítez-López et al., 2010). These effects are strongly interlinked with each other and must hence be addressed and mitigated in conjunction (Seiler et al., 2023). Roads with traffic intensity >10 000 vehicles per day are considered as strong barrier for many wildlife species; death risk on crossing attempt is very high. Moreover, such road sections are more likely to be fenced in order to improve traffic safety, thus forming total barriers for most animals (Olsson and Widen, 2008; Seiler et al., 2023). Wide ranging big mammals with lower reproductive rates, including apex predators and large ungulates and also slow-moving species, poor at evading oncoming vehicles, like reptiles and amphibians, are especially sensitive to the barrier effect (Rytwinski and Fahrig, 2015; for Estonian evidence regarding moose, see Adamoviča, 2025). Therefore, it is essential to enable safe road crossings for wild animals by identifying important wildlife movement corridors and use suitable mitigation measures in these locations (Iuell et al., 2003; van der Ree et al., 2015). These measures vary widely in both cost and effectiveness. Land and transport managers often tend to prefer less expensive measures that allow rather rapid implementation and cover long stretches of road. However, most of these measures tend to be ineffective – or do not have sufficient evidence concerning their effectiveness – for example static (standard) wildlife warning signs (Huijser et al., 2015), wildlife reflectors (D'Angelo and van der Ree, 2015), reduced speed limit (Riginos et al., 2022), etc. Electronic wildlife warning signs combined with animal detection systems can be effective in reducing the number and severity of collisions but fail to mitigate the barrier effect of roads and traffic (Huijser et al., 2015). Widely used wildlife-exclusion fencing is effective for reducing WVCs but cause even stronger barrier effect, as prevents animals from crossing the road. Therefore, the combination of fencing and suitable wildlife crossing structures (overpasses or underpasses) is the most effective known measure at reducing WVCs and simultaneously maintaining habitat connectivity for large mammals (reviewed in Rytwinski et al., 2016). However, the evidence base for assessment to what extent wildlife passages mitigate the barrier effect of roads is limited (Soanes et al., 2024). As known from the earlier experiences (e. g. Barrueto et al., 2014; Mysłajek et al., 2020), it may take years for big mammals like ungulates and large carnivores to habituate to new crossing structures in the landscape.

1.7. The objectives of the thesis

Generally, this study aims to synthesize the evolution of road ecology in Estonia while presenting localized data on wildlife-vehicle collision patterns. Beyond mapping these incidents, the research evaluates the factors influencing reporting accuracy, the allocation of institutional responsibility, and the efficacy of current mitigation strategies. Ultimately, it argues that as road infrastructure and traffic density expand, we must prioritize the ecological integrity of natural systems.

The objectives of this study were as follows:

1. To identify the temporal patterns of WVCs in Estonian conditions, specifically examining seasonal, weekday and diurnal patterns (**I**).
2. To identify the relationship between WVC frequency and traffic volume by using the reduced traffic volume conditions resulting from the COVID-19 movement restrictions during spring 2020, which the available data allowed for both at the Estonian and European levels (**II**).
3. To describe the WVC liability among different stakeholders (drivers, police/ emergency services, hunters, transport authorities, etc.) both in Estonia and in other European countries, and to discuss how the responsibility falling on different parties might influence the reporting of WVCs (**III**).
4. To demonstrate, based on Estonian data, that wildlife crossing structures built to mitigate the barrier effect and reduce WVCs are adopted by even the more conservative large game species when the structures achieve a more natural appearance (the so-called adoption curve) (**IV**).

2. MATERIALS AND METHODS

2.1. Study area

The papers comprising this thesis featured varying study areas and spatial scales. In study **I**, we evaluated the temporal patterns of WVCs at the country level, covering entire Estonian road network consisting of national (28%), local (41%) and private and forest roads (31%) with total length of 58 787 km and an average road density of 1.3 km/km² at that time (Estonian Road Administration, 2014).

In paper **II**, we focused on WVC data from Czechia, Estonia, Finland, Hungary, Israel, Norway, Slovenia, Spain, Sweden, and for Scotland and England within the United Kingdom in order to evaluate to what extent the decline of road traffic volumes due to COVID-19 related travel restrictions prevented wildlife deaths on roads during spring 2020.

In study **III** we presented an overview of WVC liability covering 36 European countries – Albania, Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Cyprus, Czechia, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Kosovo, Latvia, Lithuania, Luxembourg, Moldova, Montenegro, North Macedonia, Netherlands, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland and UK.

Study **IV** was carried out at a local scale, using monitoring data of Kolu ecoduct, Estonia's first wildlife overpass located in Kose Parish, Northern Estonia (N 59.18785, E 25.06043).

2.2. Data and methods

2.2.1. Wildlife-vehicle collision data

The main dataset used in this thesis (papers **I** and **II**) for Estonia is a nationwide list of environmental emergency hotline calls – the information of WVCs received mostly from road users but also from hunters and police officers was collected earlier by the Environmental Inspectorate, since 2021 by Emergency Response Centre. If there are no human fatalities or injuries in the WVC, there is no need to report the accident to the police. However, according to Estonian Hunting Act § 34 (4), the user of a hunting district or the Environmental Board must be promptly notified of any large game that was killed in a traffic accident or that had to be killed as a result of a traffic accident, or of parts of such large game. Although public awareness on WVC reporting obligation is increasing year by year, some drivers are still unaware of this regulation or prefer to ignore it, as such behaviour will not be identified or fined.

Therefore, for **identifying temporal patterns of wild boar-vehicle collisions** (WBVCs; study **I)** we used additional datasets: data on WBVCs resulting in human injuries collected by the Police and Border Guard Board and data on WVCs resulting in property damage collected by the police and insurance companies. In this instance, only the cases when the vehicle had comprehensive insurance were notified, as the regular obligatory car insurance does not cover damage caused by wild animals.

Remaining entries were thoroughly reviewed. Duplications (the same WBVC was registered by both, the EI and the police) were removed. On the basis of the description of the case, reports were divided into three groups: (i) A – accurate (the accident had happened immediately prior to the notification), (ii) N – not sure (the accident could have happened immediately prior to the notification or slightly earlier), and (iii) I – inaccurate (the accident had happened earlier; for example, someone noticed an animal carcass in a road ditch). Only 'accurate' and 'not sure' entries were selected for further analysis, resulting in a data set of 918 WBVC reports for the period 2004–2013.

Initially, seasonal and weekly distributions of WBVCs were evaluated. It was hypothesized that collision frequencies would significantly deviate from a uniform distribution across these temporal scales. To test this hypothesis, a chi-square goodness-of-fit test was employed (van Emden, 2008), with all statistical procedures performed using R version 3.1.2 (R Core Team, 2014).

Subsequently, the diurnal patterns of WBVCs were analysed. Prior to analysis, all recorded incident times were standardized to Eastern European Time (UTC + 2 h), hereafter designated as local time (LT). This standardization was critical to account for discrepancies introduced by daylight saving time during summer months. For each recorded collision, specific astronomical parameters were calculated, including the duration (in seconds) relative to sunrise and sunset, as well as the solar and lunar altitudes (measured in degrees). These calculations were performed using a custom script based on *Ephem*, an astronomical module for the *Python* programming language. The script processed the temporal and spatial data of each WBVC to derive its corresponding astronomical context. In the absence of exact GPS coordinates for each collision, the geometric centers of Estonian counties served as proxy locations. Given that Estonian counties typically span less than 100 km, variance in sunrise and sunset times remains within a few minutes, and solar/lunar altitudes fluctuate by no more than one degree. Consequently, the use of county centroids provided sufficient precision, especially considering inherent minor timing errors in the original accident reports. For the purpose of this study, twilight was defined as the period when the sun's altitude is between 0° and −18°. This phase was further categorized into three distinct intervals: civil twilight (0° to −6°), the brightest phase; nautical twilight (−6° to −12°) and astronomical twilight (−12° to −18°), the darkest phase.

For **studying whether COVID-19-related traffic reduction (CRTR) resulted in WVC reductions** in different countries (paper **II**), we used WVC data from Czechia, Estonia, Finland, Hungary, Israel, Norway, Slovenia, Spain, Sweden, and from Scotland and England within the United Kingdom. Altogether, 645 496 recorded carcass data from period 1.01.2015 – 30.06.2020 were included to the analyses. The origin of the WVC data used in this study was (i) police crash data (CZE, ESP, HUN and SWE), (ii) carcass removal data (SCO) and (iii) data provided by hunters, rangers or wildlife managers (ENG, EST, FIN, ISR, NOR and SVN).

For Estonia, list of environmental emergency hotline calls was used, consisting of 23 951 WVCs – 19 161 collisions with roe deer, 3114 with moose and 1676 with other large game species. The period of CRTR was set from the 11th week of 2020 for all countries except ENG, SCO and SWE (12th week) to the end of June of 2020. During this period, European countries and Israel implemented lockdown measures that also affected transportation and travel.

Only data on WVC records were used directly in these analyses. Traffic intensity data were of varying quality, in some cases not representing entire countries, and therefore served merely as a demonstration of the traffic flow reduction. For Estonia, we had detailed traffic flow data (daily sums of vehicles from 41 counting sites, 1.01.2019 – 31.08.2020) provided by Teede Tehnokeskus AS as a supportive dataset.

We worked with weekly sums of WVC. First, we used available WVC data for 2015–2019 in order to build a seasonal ARIMA model (i.e., autoregressive integrated moving average model; Hyndman and Athanasopoulos, 2018). We then used this model to predict expected weekly sums of WVC in 2020. Consequently, actual recorded 2020 data (influenced by CRTR) were compared on a weekly basis with the forecasted data. Computations were performed in R Software with the library “forecast” (Hyndman et al., 2020) and routines “auto.arima” for an automatic selection of the model and “Arima” for further adjustments of the model. Akaike information criterion with correction for small sample sizes (AICc) was chosen for model selection. Ljung-Box test was applied to assess the quality of the resulting fitted models. This baseline model forecasted “expected” 2020 WVC counts (E) – counterfactual scenario representing the absence of traffic restrictions. Recorded 2020 observations (O) were compared to these forecasts using a Rate Ratio (RR), where RR = O/E. Results were presented as a percentage reduction to directly quantify the impact of restrictions. We specifically highlighted the maximum reduction per country to identify the peak impact during the restriction period, while the remaining time-series data illustrated variation over time.

2.2.2. Data on wildlife-vehicle collision liability in European countries

For study **III**, a web-based questionnaire, via Google Forms, was prepared in order to obtain structured answers on the **WVC liability approaches** across Europe. The questionnaire included questions about differences in WVC liability, followed by questions on WVC and roadkill data collection. It also explored the responsibility for WVC data collection (e.g., police, road administrators or hunters), whether there are any volunteer applications to collect data in the given country, or if any unique circumstances exist. The questionnaire further contained questions about recommended procedures when WVC occur, quantification of damages, and possible compensation. In general, the structure of the data requested was as follows: 1) animals involved and passenger fatalities from WVC; 2) WVC liability; 3) vehicle damage compensation; and 4) information on WVC and roadkill databases.

These questions were answered by a team of co-authors, consisting of experts who represented their respective countries or specific regions and states and were willing to confirm the validity and completeness of the information. Representatives of 36 European countries (Albania, Austria, Belgium, Bosnia and Herzegovina, Bulgaria, Croatia, Cyprus, Czechia, Denmark, Estonia, Finland, France, Germany, Greece, Hungary, Ireland, Italy, Kosovo, Latvia, Lithuania, Luxembourg, Moldova, Montenegro, North Macedonia, Netherlands, Norway, Poland, Portugal, Romania, Serbia, Slovakia, Slovenia, Spain, Sweden, Switzerland and UK) joined this research and responded to the questionnaire.

After completing the first phase of the questionnaire survey, the team carried out internal discussions in order to revise the responses and further clarify differences in approaches to this issue. Since some countries have certain regional specifics, they were represented by more than one contributor (Germany, Italy).

2.2.3. Wildlife crossings data

In paper **IV** we aimed to **evaluate changes in mammal species composition and crossing frequencies on Estonia`s first wildlife overpass**. We used data on animal crossing events on Kolu overpass from two monitoring periods – initial (2015–2016; 22 months) and follow-up (2020–2022; 25 months) monitoring. Crossing events were detected by camera traps located on a sand strip in the middle of the overpass. In addition, track observations were conducted as supplementary data but were not included in the analysis. Each recorded crossing event included date, time, species, number of individuals, crossing direction, and additional behavioural observations. Duplicate detections across multiple cameras were removed prior to analysis.

Differences in crossing frequencies among large game, small game, and domestic animals across the two study periods were assessed using parametric two-proportion z-tests. In this model, animal crossings were categorized as ‘successes’ and non-target species crossings as ‘failures’. Additionally, non-parametric Mann-Whitney U tests were employed to compare monthly roe deer crossings between the two monitoring periods. All statistical analyses were performed using R (version 4.1.3; R Development Core Team 2022).

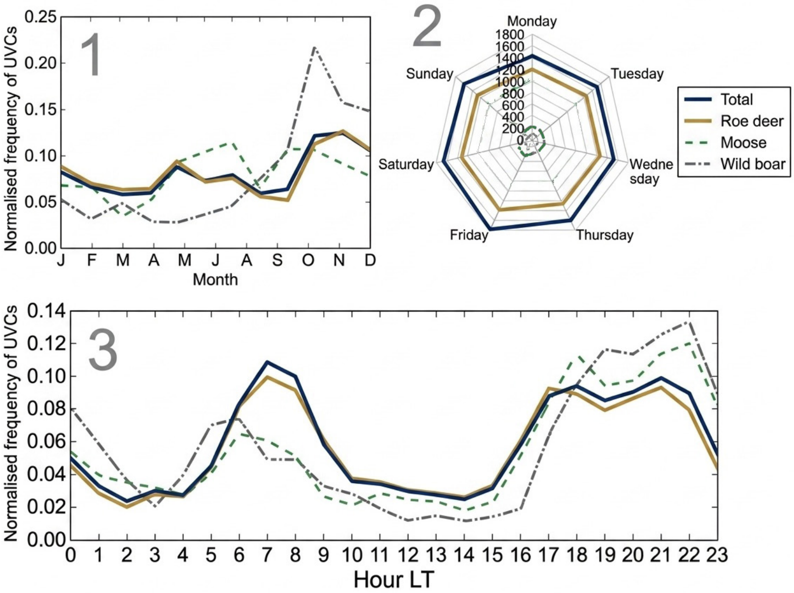
2.2.4. Supportive datasets

In addition to the data directly included in the analyses, different supportive datasets were used in the studies. Wild game populations monitoring data is collected, analysed and published by Estonian Environment Agency and was important background information in our research (papers **I** and **IV**). We also investigated hunting statistics provided by Environment Agency (game hunting by species and county) and Environmental Board (more precisely by species and hunting district). In addition, hunters estimation on large game abundancy by species and hunting district was inquired from Environmental Board. Data on Estonian road network (national, local, private and forest roads), average road density and speed limits on specific road sections is provided by Estonian Transport Administration (papers **I, IV**). Detailed traffic intensity data for national (main, basic and secondary) roads is provided by Teede Tehnokeskus AS (papers **I, II, IV**). The number of motor vehicles over time periods was found in Statistics Estonia database (paper **I**). Information provided by Estonian Health Board, national media and other public sources were used to describe restrictions related to the spread of COVID-19 in 2020 (paper **II**).

3. RESULTS

3.1. Temporal patterns of ungulate-vehicle collisions in Estonia

We analysed in total 11 195 ungulate-vehicle collisions (UVCs) in Estonia from period 2004–2013, out of which 78.4% were related to roe deer, 13.4% to moose and 8.2% to wild boar (for wild boar collision statistics please see paper **I**, for all analysed UVCs see Kruuse et al., 2017). The annual number of registered UVCs varied between 508 and 1696. The monthly, weekly and diurnal distribution of collisions regarding all three studied species followed certain patterns (Figures 1–3).



Figures 1–3. Monthly, weekday and diurnal distribution of ungulate-vehicle collisions in Estonia, 2004–2013. LT – local time. Source: Kruuse et al., 2017.

Focusing on wild boar, the number of registered WBVCs fluctuated considerably during 2004–2013, ranging from a low of 16 incidents in 2004 to a peak of 174 in 2013 (see Fig. 1 in article **I** for specifics). The data revealed several non-uniform patterns across different time scales. Monthly distributions deviated significantly from the expected average ($\chi 2 = 455.7$, df = 11, $p < 0.001$, n=918). Incidents peaked between September and December, with October seeing the highest frequency. Conversely, the fewest collisions occurred in February, April, and May.

Collisions were not evenly distributed throughout the week. There was a statistically significant increase in incidents during weekends, with a distinct peak on Fridays ($\chi 2 = 17.0$, df = 6, $p < 0.01$, n = 918).

Regarding diurnal patterns, the timing of collisions was closely linked to light levels. WBVC frequency increased sharply once the sun dipped 6–7° below the horizon and remained high throughout the night, including periods of total darkness when the sun was more than 18° below the horizon (see Figs. 2a and 2b in article **I**).

3.2. Impact of lower traffic volumes resulting from the COVID-19 movement restrictions on WVC frequency

During the COVID-19 related traffic restriction (CRTR) period in spring 2020, observed WVCs were significantly lower than predicted in seven of the eleven countries studied. Reductions ranged from 8.8% in Norway to 37.4% in Estonia (see Table 2 in article **II** for specifics). Across these seven countries, a total of 17 461 WVCs were recorded – an 18.9% decrease from the 21 530 incidents expected under normal conditions. In contrast, Sweden, Israel, Scotland and England showed no statistically significant deviation from predicted levels throughout the CRTR period.

However, when analysed weekly, every country except Scotland experienced a decline in WVCs for at least one week. The most substantial drops – exceeding 40% – occurred in Estonia, Spain, Israel, and the Czech Republic during the early phase of the restrictions, while other countries saw peak reductions between 17% and 33% (Figures 4–5, see also Table 2 in article **II**).

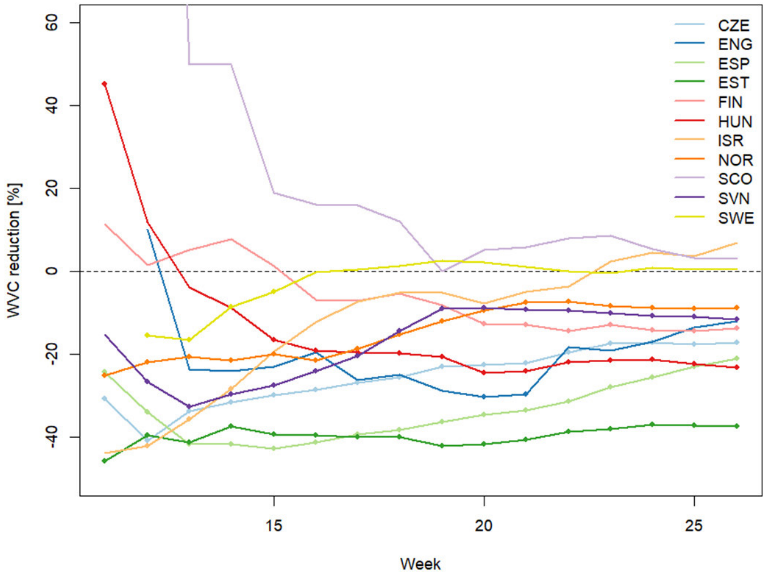


Figure 4. An estimate of wildlife-vehicle collisions reduction (%) during the COVID-19 related traffic restriction (11th–26th week in 2020) in relation to expected WVC. The dots represent statistically significant values. Source: Publication **II** Figure 4.

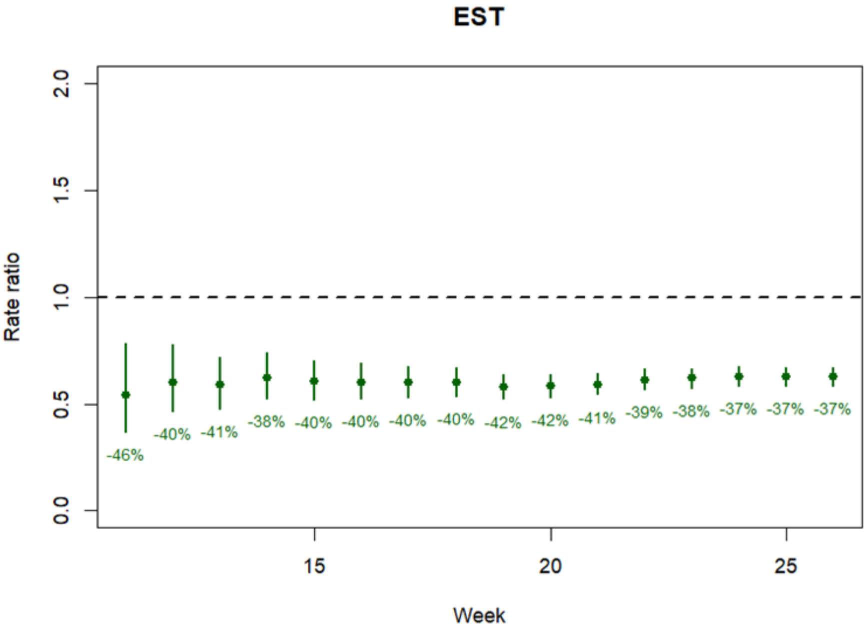


Figure 5. Weekly wildlife-vehicle collisions reduction (rate ratios) during the COVID-19 related traffic restriction (11th–26th week in 2020) in Estonia. The graphs contain rate ratios (RRs) and their corresponding 95% confidence intervals. The confidence intervals shrink over time as the data are cumulating. Green colour highlights statistically significant results and the corresponding figure stands for the relative difference between observations and predictions. Source: Publication **II** Appendix C.

Due to available data being incomplete or limited to specific road networks, changes in traffic volume were not included in the statistical analyses. Instead, traffic volume data were utilized as illustrative examples of mobility shifts during the CRTR period (please see Appendix A in article **II**). In all countries studied, weekly traffic indices followed a consistent trajectory – a sharp initial decline at the onset of lockdown, followed by a gradual recovery toward baseline levels (Figure 6).

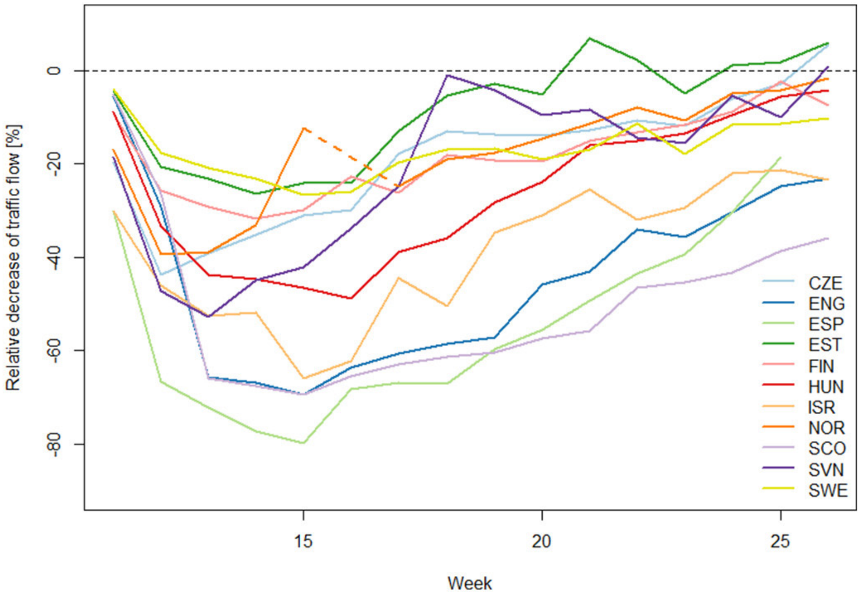


Figure 6. Relative decrease (%) in traffic flow during the COVID-19 related traffic restriction period for 11 countries in relation to the same week of 2019 (CZE, ESP, EST, FIN, HUN, NOR, SVN, SWE) or the 10th week of 2020 when records for 2019 were not available (ENG, SCO) or the 9th week (ISR; national holidays in the 10th). For a description of data see publication **II** Appendix A. Data for week 16 in NOR were not available (we used linear interpolation of the neighbouring values, see the dashed part of the respective curve). Source: Publication **II** Figure 2.

3.3. Wildlife-vehicle collision liability in European countries

3.3.1. WVC liability and compensation

Liability protocols for WVCs vary significantly across Europe. In 19 countries, including Estonia, no specific party is held liable for such incidents. Conversely, Switzerland mandates driver liability and compulsory reporting of all collisions, with vehicle damage typically covered by insurance. In Serbia, liability is restricted to hunters and hunting ground managers, though only for incidents involving game species. In Italy and Slovenia, road managers may be held liable.

Furthermore, representatives from 14 of the 36 surveyed countries (39%) reported that liability is conditional. In these regions – for example Croatia, France, and Spain – responsibility depends on factors like the presence of wildlife signs and fencing, road class, road owner, driver compliance, the animal species involved, hunting activity or whether the incident occurred within a protected area (see Table 2 in article **III** for specifics).

Liability variations based on road class often stem from the distinct legal status of motorways, which typically feature wildlife fencing. In these contexts, 'road owners' may include private entities managing toll motorways under concession.

Furthermore, ‘driver law compliance’ pertains to legal infractions such as speeding or driving under the influence of alcohol or drugs. Species-specific liability often arises because hunters are frequently held responsible only for game species, sometimes restricted to active hunting seasons. Notably, in Lithuania, drivers face heightened responsibility if the collision involves a protected species.

Financial compensation regarding game animals killed in WVCs varies considerably by jurisdiction. In countries such as Bosnia and Herzegovina, Serbia, and Switzerland, hunters may receive compensation for lost game. Conversely, in Hungary and Slovenia, legislation requires drivers to compensate hunters if the accident resulted from driver negligence, such as speeding; however, such claims are rarely pursued in practice. In other countries, hunters receive no compensation. Some countries, such as Spain, even hold hunters liable for vehicle damages if the collision occurs on the same day as an organized hunt or within a 12-hour window following its ending.

3.3.2. Reporting roadkill and WVCs

Official traffic and WVC databases rarely document incidents involving small animals, as these collisions seldom result in significant property damage or human injury (Figure 7). However, citizen-science initiatives in several countries allow volunteers to record these incidents via mobile or web applications (see Table 3 in article **III**). These platforms predominantly capture smaller mammal species, which can skew cross-country comparisons of “most exposed” species. For instance, while the hedgehog (*Erinaceus europaeus*) is the most frequently reported road-killed species in Flanders, Belgium, it likely suffers similar mortality rates in other countries; however, its small size leads to significant underreporting in those national databases.

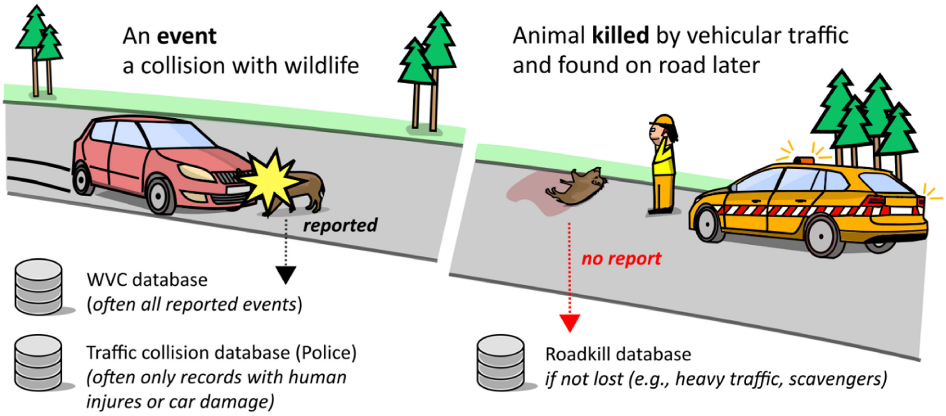


Figure 7. An explanation of the differences between wildlife-vehicle collision and roadkill and the three types of databases used: traffic collision, WVC and roadkill. Source: Publication **III** Figure 1.

Currently, 21 countries provide national-level WVC data, though accessibility and detail vary (see Table 4 in article **III**). Some databases lack species-specific information (e.g., Slovakia), while others, such as the UK's national database, do not distinguish between wild and domestic animals. In Wallonia (Belgium), the regional forest administration tracks red deer (*Cervus elaphus*) mortality specifically, whereas police records are limited only to accidents involving human injury. Administrative and historical factors have led some countries to maintain fragmented regional systems; this is particularly evident in Germany (e.g., Bavaria), Italy (e.g., South Tyrol), and Spain (e.g., Catalonia, Basque Country). Additionally, road operators in Spain and France often maintain independent datasets that are not integrated into a central national overview.

3.4. Changes in mammal species composition and crossing frequencies on Estonia`s first wildlife overpass

Wildlife passages aim to improve connectivity between habitats fragmented by major transport corridors, thus systematic monitoring is essential to evaluate their functional success. Kolu ecoduct, Estonia's first wildlife overpass, was built in 2013 during the reconstruction of the Aruvalla-Kose section of the T2 (E263) road.

Initial monitoring during 2015–2016 identified 12 wild mammal species using the passage, including large game such as roe deer, wild boar, grey wolf, and Eurasian lynx. Small game and other mammals recorded during this period included red fox (*Vulpes vulpes*), raccoon dog (*Nyctereutes procyonoides*), European hare (*Lepus europaeus*), mountain hare (*Lepus timidus*), pine marten (*Martes martes*), European badger (*Meles meles*), European hedgehog (*Erinaceus europaeus*), and red squirrel (*Sciurus vulgaris*). Also, domestic cats and dogs were present (Valdmann and Kruuse, 2016).

Photos 1–2. Left: wolf family crossing Kolu ecoduct in February 2016. Right: moose feeding on Kolu ecoduct in July 2021. Source: Valdmann and Kruuse, 2016; Valdmann et al., 2022.

By the follow-up period in 2020–2022, species richness increased to 14 wild mammals. This period was characterized by the presence of all Estonian ungulate species – moose, red deer, roe deer, and wild boar – alongside large carnivores like lynx and brown bear. Smaller mammals recorded included the red fox, badger, raccoon dog, both hare species, pine marten, hedgehog, and an unidentified bat (*Chiroptera*), with domestic animals remaining present to a lesser extent (Valdmann et al., 2022) (see Table 1 in article **IV** for specifics).

Analysis of the two monitoring periods revealed significant changes in species composition and crossing frequencies. The proportion of large game crossings increased from 19 to 58% ($p < 0.001$; $\chi^2 = 453$; 95% CI −0.42 to −0.36), while domestic animal crossings declined from 36 to 9.4% ($p < 0.001$; $\chi^2 = 299$; 95% CI 0.38 to 0.31). Small game crossings slightly decreased from 37 to 31% ($p < 0.01$; $\chi^2 = 17$; 95% CI 0.04 to 0.1; Figure 8). In both monitoring periods, roe deer crossings dominated among large game (49% and 95%, respectively).

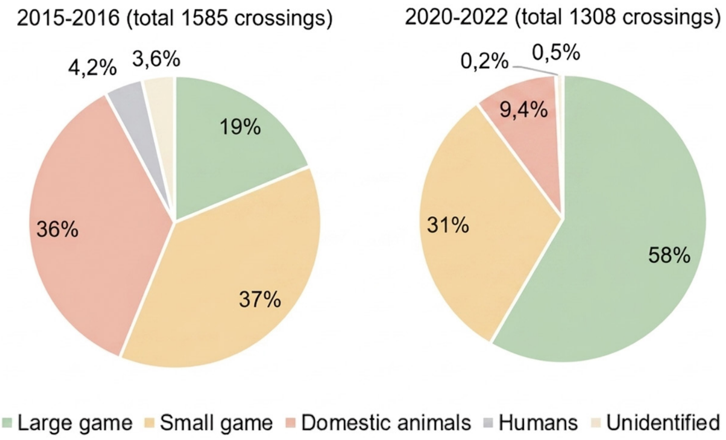


Figure 8. Proportions of different animal and human crossings on Kolu wildlife overpass during the initial and follow-up monitoring periods. Source: Publication **IV** Figure 1.

4. DISCUSSION

4.1. Wildlife-vehicle collisions in Estonia

The large majority of the registered WVCs in Estonia are related to ungulates. This is also typical for other countries in Northern Europe and North America (Bruinderink and Hazebroek, 1996; Romin and Bissonette, 1996; Conover et al., 1995). Collisions with moose – the largest mammal within boreal forest ecosystems – pose the most significant risk to motorists and typically cause extensive vehicular damage (Niemi, 2016; Gren and Jägerbrand, 2019; Conway et al., 2022; Estonian Police and Border Guard Board & Estonian Transport Administration, unpublished data). Due to the severity of these encounters, statistics regarding moose-related accidents are considered the most reliable. However, the scope of this research has expanded to include other large ungulates, most notably the roe deer, which accounts for the highest number of collisions, and the wild boar. Conversely, accidents involving large carnivores occur rather rarely.

Increase of reported WVCs in Estonia has been significant. 3377 WVCs were registered in 1985–1990. About 50% of these involved roe deer, 30% moose and 14% wild boar. 6% were related to other species or unidentified animals (Mardiste, 1992). Collision data was collected by police and insurance agencies of some counties at that time. Number of roe deer, moose and wild boar was 39 000–58 500, 11 000–12 000 and 9500–14 000, respectively, according to official data during that period (Estonian Environment Agency, 2014). In 2004–2013 19 533 WVCs were registered. 76% of these were related to roe deer, 9% to moose, 7% to wild boar and 8% to other species (Kruuse et al., 2017). In recent years approximately 3500–5500 collisions with large mammals have been registered annually, 90% of these with roe deer, 5% moose, 3% wild boar and 1% with other species (Estonian Hunters Society, 2025 https://www.ejs.ee/liiklusonnetused-metsloomadega/#statistika). However, rapid decrease in roe deer population (Estonian Environment Agency, 2025) has led to a decline of collisions since 2022, despite slight but continuous increase in traffic volumes on main and basic roads (Jairus and Metlitski, 2025).

Estonian road network consists of national (19%), local (27%), private (44%) and forest roads (11%) with total length of 89 716 km and average road density of 2 km/km² (Estonian Transport Administration, 2025). National roads are divided to main (9,4%, 1603 km), basic (14,2%, 2407 km) and secondary (73,6%, 12 513 km) roads. Over the past decade, the total length of road network has increased by 53% mostly due to the expansion of private and forest roads. The length of national roads has basically not changed (Estonian Road Administration, 2014, Estonian Transport Administration, 2025). Speed limit on the national roads is usually 90 km/h all year round and 110–120 km/h in summer on four-lane road sections.

Average traffic density was 812/1088 vehicles per day on all the national roads and 4388/5878 vehicles per day on the main roads in 2013 and 2024, respectively

(Kaal et al., 2014; Jairus and Metlitski, 2025). The number of registered motor vehicles has increased from 828 651 in 2015 to 1 095 613 in 2024 (Statistics Estonia, 2025), but the registration is active for only 757 500 in 2025 (Estonian Transport Administration, 2025).

Ungulate-vehicle collisions (UVCs) cause large economical cost. Estimated economic loss including vehicle repair costs and environmental damage due to collisions with big mammals (mostly ungulates) on Estonian roads was 4.7 million Euros in 2010 (Eilat, 2011). Additional costs regarding human injuries were not included in this calculation, so it can be assumed that the total costs far exceeded 5 million Euros.

Therefore, proper knowledge about spatio-temporal patterns of UVCs is key to developing better prevention measures, essential to effectively reduce collision rates and resulting socioeconomic and environmental damage.

4.2. Temporal patterns of ungulate-vehicle collisions in Estonia

Research focused on temporal patterns of UVCs is increasing rapidly. Typically these studies concentrate on seasonal, day of the week and diurnal patterns of UVCs (reviewed by Balčiauskas et al., 2025) but also effects of lunar phases have been studied (e.g., Colino-Rabanal et al., 2018). Wildlife collision trends vary greatly by location (Bruinderink and Hazebroek, 1996); therefore, it is important to identify the high-risk periods in specific area rather than to rely on broad regional data.

Our analysis focused on 11 195 UVCs documented over a ten-year span (2004–2013). While annual counts varied significantly – from a low of 508 to a peak of 1696 – the distribution of species remained relatively consistent: roe deer was the primary species involved (78.4%), followed by moose (13.4%) and wild boar (8.2%).

The **monthly distribution** of collisions regarding all three studied species followed certain patterns (please see Fig. 1 in subchapter 3.1 for specifics). In contrary to most findings from earlier studies (e.g., Langbein and Putman, 2006; Balčiauskas and Balčiauskienė, 2008; Lagos et al., 2012; Rodríguez-Morales et al., 2013; Putzu et al., 2014), we noticed the main peak for roe deer collisions in November and a smaller peak in May. However, Madsen et al. (2002) had similar results in Denmark, demonstrating the highest number of traffic-killed roe deer in October. As spring peak may be explained by the fawning period and the dispersal of yearlings (e.g., Bruinderink and Hazebroek, 1996), in autumn the greater activity of juveniles (Pokorny, 2006) or collective hunting season (starts on the 1st of October for most ungulates in Estonia) could be the reason for the high occurrence of collisions. Furthermore, in Central (Hothorn et al., 2015) and South Europe (Rodríguez-Morales et al., 2013) the higher probability of roe deer collisions has been associated with rutting season from July to mid-August.

For moose, higher collision numbers were found in June-July and September-October. Similar results were provided for Lithuania (Balčiauskas and Balčiauskienė, 2008). In Finland the autumn peak is remarkably higher than the summer peak (Haikonen and Summala, 2001) as in Sweden most moose-vehicle collisions tend to happen from October to January (Neumann et al., 2012). Moose collisions tend to show very heterogeneous seasonal distribution (Steiner et al., 2014), thus such differences between study results in neighbour countries are not surprising. Similarly to roe deer, the higher occurrence of moose accidents in summer could be explained by the dispersal of yearlings who are abandoned by their mothers (e.g., Danks and Porter, 2010). The autumn peak coincides with the rutting period (see also Lavsund and Sandegren, 1991) and migration to the winter habitats. It is a common belief in Estonia that disturbance by hunting also increases the probability of WVCs in autumn but considering the results by Neumann et al. (2009), it is not necessarily true. However, as discussed by Lagos et al. (2012), hunting, especially collective hunts may have effect on game movement, resulting in higher probability of crossing roads. There are two documented cases from different moose mobility research projects in Estonia, as radio-collared moose cows, disturbed by hunting, moved 10 km from her usual home range but returned the next day (Lukk et al., 2007; Oja et al., unpublished data).

For wild boar, we witnessed the highest numbers of collisions in September-December (**I**). This pattern is similar to Lithuania (Balčiauskas and Balčiauskienė, 2008), Wallonia in southern Belgium (Morelle et al., 2013) and also Italy (Putzu et al., 2014), while in Galicia (Spain) and southern Sweden the peak occurs one month later, in October-January (Lagos et al., 2012; Rodríguez-Morales et al., 2013; Thurfjell et al., 2015). As suggested by Thurfjell et al. (2015), wild boar-vehicle collisions happen when traffic is at intermediate levels and when female wild boar are active. These two factors probably meet at long dark nights during late fall/winter. Poor light and road surface conditions (e.g., rain, snow, ice) may also increase the collision risk (Neumann et al., 2012).

During the week the number of UVCs was highest at weekends with a maximum on Fridays (**I**, see Fig. 2 in subchapter 3.1). This was true for all studied species. As no biological, ecological or behavioural factors depending on weekdays are known, this pattern is presumably related to traffic volume (Steiner et al., 2014; Hothorn et al., 2015). We did not manage to obtain detailed traffic data for all roads, but traffic count studies carried out in 2006 and 2007 on one of the main roads (E263 Tallinn-Tartu-Võru-Luhamaa) suggested that traffic volume increases sharply on Friday afternoon (Koonik, 2008; see also Järv et al., 2012). This is in compliance with other studies that relate the weekend UVC peaks to increased traffic (Dussault et al., 2006) and the drivers` habits (Lagos et al., 2012). In Estonia numerous city people drive to their country houses for the weekend, also people drive to the parties at night and return early in the morning like discussed by Lagos et al. (2012).

Two distinct peaks in the morning and at night were observed in the **diurnal distribution** of UVCs (**I**, see Fig. 3 in subchapter 3.1). This implies that the main activity of ungulates is related to sunrise and sunset. The finding that most of the roe deer and moose collisions happen around sunrise and sunset is supported by numerous earlier studies reviewed by Steiner et al. (2014) while wild boars are known as nocturnal animals (although according to Podgórski et al. (2013) they can be active throughout the day in areas where is no human distraction), thus the majority of collisions related to this species occurred in darkness. It is also interesting that a strong evening peak persisted throughout the year whereas the morning peak was obvious only from October to January. This is probably the effect of people behaviour and traffic density. From late autumn to early spring the sunrise and sunset times overlap with the morning and evening rush hours, respectively. As a result, an UVC peak appears around sunrise as well as after sunset. During spring the sunset time becomes later and the same is probably true for the related ungulates activity. Meanwhile people also tend to use longer daylight for outdoor activities which means that there is still enough traffic around and after sunset when ungulates become active. In contrast the sun rises as early as 3 to 5 hours AM from spring to autumn when most people sleep, thus the possible early morning ungulates activity peak does not overlap with high traffic density. This could explain why only the evening peak in UVC frequency is present from March to August. Probably the notable decrease in UVCs during the COVID-19 period (**II**) also occurred mainly due to significant decrease of evening and night traffic intensity.

4.3. Impact of the COVID-19-related traffic reduction (CRTR) on WVC frequency

Collisions with vehicles are a considerable cause of wildlife mortality. Early research has already indicated that WVC rates are highly influenced by traffic volumes (Bruinderink and Hazebroek, 1996) but this relationship is not always linear. For example, moose collisions are considered most frequent at traffic volumes between 4000 and 6000 AADT (Seiler, 2005). Once traffic exceeds this range, the risk of a collision decreases (Gagnon et al., 2013).

Standard circumstances rarely provide the controlled environment necessary to test to what extent decrease in traffic densities affects the number of WVCs. The spring of 2020 presented an unprecedented natural experiment as the COVID-19 pandemic triggered sharp declines in global traffic volume due to travel restrictions and reduced mobility demand. This period offered a rare window for researchers to analyse how sudden shifts in anthropogenic activity directly influence wildlife behaviour and mortality rates (**II**; Balčiauskas et al., 2025). The most substantial decline in WVC numbers was documented during the initial weeks of the CRTR, nevertheless, observed changes were highly sensitive to the severity of local lockdowns, resulting in divergent outcomes across different countries (**II**; Shilling et al., 2021). Regardless of these regional differences, in general the decline in WVCs resulted in the survival of many wild animals that would have otherwise perished under standard traffic conditions, even accounting for some potential under-reporting due to smaller number of road users.

Notable trend in Estonia was the flattening of peak traffic loads near urban areas. While midday traffic remained stable relative to historical averages, morning and evening volumes – which coincide with peak crepuscular wildlife activity, as also seen in study **I** – experienced a sharp decline (Jairus, 2020). This disproportionate reduction during high-risk hours may explain why WVCs decreased significantly, even though the total reduction in traffic volume was relatively modest. Consequently, implementing targeted and time-restricted traffic reductions – particularly in high-priority conservation zones – may serve as a viable strategy for decreasing WVCs (Manenti et al., 2020).

However, the data from Lithuania highlights a stark contrast in WVC trends during the lockdown period – while incidents on major transit routes dropped by 90%, urbanized areas paradoxically experienced an increase in WVC numbers. Presumably the increase in roadkill observed on urban roads was mainly driven by combination of modified human mobility patterns and changes in animal behaviour due to reduced stress (Balčiauskas et al., 2023). While the lockdown provided a brief reprieve, the post-restriction period saw a significant reversal. Collision numbers on roads increased again, eventually exceeding expected levels. This suggests that the ‘rebound’ in human activity may have created an even more hazardous environment for wildlife than existed prior to the pandemic.

Furthermore, as suggested by Pokorny et al. (2022), impact of CRTR on wildlife appears to be species-specific, also affected by season and spatial scale. Decrease in human mobility can initiate complex species-specific dynamics in wildlife communities, which may create long-term changes in wildlife populations that continue to evolve even after lockdowns end. Even if a one-year anomaly is unlikely to shift long-term population trends, the impact of recurring or sustained lockdowns remains uncertain (Pokorny et al., 2022). Therefore, accurate WVC data is needed to perform more profound research. The various factors that influence WVC and roadkill reporting quality are discussed in the next subchapter.

4.4. Factors affecting the reporting of wildlife-vehicle collisions

WVCs are distressing events that mostly result in the death or severe injury of animals involved, leaving even uninjured drivers in a state of shock (Bissonette et al., 2008; Conway et al., 2022). Establishing clear regulations on who is responsible for managing the aftermath is essential for supporting drivers and ensuring a prompt response. However, these regulations may be contradictory and vary from country to country (**III**).

In Estonia, if the WVC does not result in human casualties, there is no need to report the accident to the police. However, according to Estonian Hunting Act

§ 34 (4), the user of a hunting district or the Environmental Board must be promptly notified of any large game that was killed in a traffic accident or that had to be killed as a result of a traffic accident, or of parts of such large game (subchapter 1.5 and 2.2.1). 1247 (former 1313) is operated by Emergency Response Centre nationwide 24/7, and the number can be dialed from both mobile and landline phones. Road users call 1247 if they hit an animal or if they notice dead or injured wild animal on the road/roadside. Still, underreporting of WVCs remains a prevalent challenge for data accuracy. Although public awareness on WVC reporting obligation is increasing year by year, some drivers are still unaware of this regulation or prefer to ignore it, as such behaviour won`t be identified or fined. However, as no specific party is held liable for WVCs in Estonia, there should be no other common reason not to report except for state of shock and confusion, or ignorance. Alternatively, drivers might anticipate fines – particularly if they were speeding or ignored wildlife warning signs – without realizing that they are exempt from liability for the accident itself.

The informer and the reporting method also affect the quality of the collected WVC data (Balčiauskas et al., 2025). For example, confused driver may be not able to determine the species of animal and an exact collision location (Pagany, 2020), especially in darkness. The psychological impact of the WVC (Conway et al., 2022) may prevent individuals from exiting their vehicle to check the condition of the animal. In recent years, location has been determined using phone call positioning. However, in case if a random passerby reports a dead animal, they may make the phone call several kilometers after passing the animal. It may happen that the same incident is reported repeatedly (**I; III**), especially if it involves a large animal like moose or other ungulate whose carcass is highly visible on the road or roadside.

Therefore, it is highly beneficial that local hunters are involved in the process (in case of large game). The hunters verify the correct WVC location and their expertise allows for the accurate identification of the species, sex, and age group of the animal, providing vital data for wildlife management (e.g., Hansen et al., 2024; **III**). Furthermore, as hunters are responsible for disposal of the carcass, tracking down wounded animals and performing euthanasia, a compensation scheme should be considered to cover the costs associated with these specialized services.

Data on WVCs resulting in human injuries is, of course, registered by the police. Data on WVCs resulting in property damage may be registered by the police and insurance companies if the vehicle has special comprehensive insurance. Standard vehicle insurance does not cover damages from WVCs. Thus, there is no incentive to report it.

However, the reports on road accidents related to medium-sized and small mammals, birds or amphibians etc are rather incomplete (Pagany, 2020). In the event of a collision, they usually do not cause damage to the vehicle, and passersby may not notice small-sized carcasses on the roadside, or those may be quickly consumed by scavengers (e.g., Santos et al., 2016; Barrientos et al., 2018; Schwartz et al., 2018).

Under these circumstances it is clear that to create reliable datasets for mitigation planning, WVC information needs thorough inspection, data cleaning and adjustment by researchers as it often contains duplicates due to inconsistent reporting, multiple data sources (Emergency Response Centre, police, hunters, insurance agencies), and varied recording methods, leading to challenges in accurate analysis. Nevertheless, no data source should be excluded. According to Jørgensen et al. (2025) the ability to detect important factors that affect WVCs is negatively influenced by reduced sample size, in case if only incidents with human injuries or fatalities, or significant vehicle damage are recorded. To improve WVC data collection, it is essential to learn from international best practices and simplify the reporting process while maintaining information quality. Making WVC reporting user-friendly and removing the fear of punishment are critical steps toward ensuring more accurate records.

4.5. Importance of continuous monitoring in performance evaluation of wildlife passages

Roads with daily traffic volumes over 10 000 vehicles pose a lethal risk to crossing wildlife, acting as a strong barrier to movement. When combined with safety fencing, these road sections are transformed into impermeable barriers for the majority of species (Seiler et al., 2023). For example, recent study in North-Central Estonia utilizing GPS tracking data of eight individual moose from period 2018–2019 highlights how traffic volume impacts significantly animal movement and road-crossing behaviour (Adamoviča, 2025). It was found that moose actively avoid high-traffic areas, with the “avoidance zone” extending 1800 meters from national roads compared to only 400 meters for local roads. Consequently, the frequency of road crossings on national roads was, on average, 5.1 times lower per 100 meters than on local roads, demonstrating that high traffic intensity acts as a significant deterrent and barrier to movement.

Therefore, wildlife passages aim to maintain or even improve connectivity between habitats fragmented by road infrastructure and intense traffic (van der Ree et al., 2015; e.g., Denneboom et al., 2021). An additional significant yet often overlooked advantage is the facilitation of wildlife and ecosystems in adapting to climate change. Strategically located wildlife crossings ensure access to key resources amidst various challenges such as rising temperatures, droughts, or increasing human encroachment (Littlefield et al., 2024). These wildlife crossings – ranging from vegetated overpasses to diverse culverts and viaducts – vary in scale and material, yet they share a common design philosophy: they are specifically tailored to the biological needs of the target species (e.g., Glista et al., 2009; Clevenger and Ford, 2010; van der Ree et al., 2015).

As elsewhere, in Estonia more crossing structures, including wildlife overpasses suitable for large game, are being planned and built to mitigate the impact of roads and increasing traffic and to enhance traffic safety. Among other wildlife mitigation measures, Kolu overpass was built in 2013 during reconstruction of Aruvalla-Kose section of T2 (E263) Tallinn-Tartu-Võru-Luhamaa main road, aiming to maintain green network and connectivity between several important habitats of native wild mammals, including ungulates and large carnivores. Due to a well-known moose movement corridor in the area, moose was set as a target species.

The effectiveness of such passages depends on numerous aspects like appropriate location, dimensions, construction materials, vegetation (reviewed by Denneboom et al., 2021), ground substrate (Niemi and Helldin, 2025), etc. Also, human disturbance is an important factor (Warnock-Juteau et al., 2022). Crossings that serve both human activity and wildlife movement tend to be less successful than those designed exclusively for ecological connectivity (Denneboom et al., 2021). In open habitats and when human activity levels are high, the presence of vegetation cover near passage entrances may be particularly important to improve crossing chances (Rodriguez et al., 1997). Numerous international and national recommendations and guidelines are available to assist the successful engineering of fauna passages (e.g. Iuell et al., 2003; van der Ree et al., 2015; Rosell et al., 2023), including Estonian adaptation (Klein, 2010).

However, even if built based on requirements and best knowledge, it may take years for some wildlife species to habituate to new crossing structures in the landscape (Barrueto et al., 2014; Mysłajek et al., 2020; **IV**). Several species need time to get used to new movement routes, and as the vegetation is recovering and appearance of the wildlife crossing structure becomes more natural over time, even the most cautious species are more likely willing to use the facility (e.g. Ford et al., 2010). Conversely, open habitats may play a more critical role for ungulates than formerly recognized; consequently, it may be necessary to thin or clear encroaching woody vegetation (Niemi and Helldin, 2025). Therefore, long-term monitoring is necessary to investigate whether target species adopt the passage (Gagnon et al., 2011; Guinard et al., 2023; **IV**).

By now the 10-years-old Kolu wildlife overpass has overgrown by 3–4 meters high young forest consisting of willow (*Salix*), Norway spruce (*Picea abies*), rowan (*Sorbus aucuparia*) and common hazel (*Corylus avellana*) as well as non-native mountain pine (*Pinus mugo*). Piles of uprooted shrubs, large woody debris and stones were used to provide hideouts for small fauna. The overpass is spontaneously overgrown by local herbaceous vegetation and acquired more natural appearance (like suggested by Rosell et al., 2023) and by now is quite difficult to distinguish the bridge section from the forest on either side. Compared to other overpasses in Estonia (Valdmann et al., 2022; Erimäe et al., 2022), a positive aspect of the Kolu ecoduct is the very rare human presence, which encourages movement even by more cautious wildlife species. Data from initial (2015–2016) and follow-up (2020–2022) monitoring periods highlights significant changes in proportions of wildlife crossings (**IV**). Percentage of large game crossings nearly tripled (reaching 58% of all crossing events), while domestic animal activity saw a sharp decline and small game activity a minor decrease. Whereas roe deer remained the most prevalent species among large game across both monitoring phases, notably, the follow-up study documented the crossings of moose, red deer, and brown bear – none of which were present during the initial survey period.

However, as correlation has been found between crossing patterns and local wildlife population abundance (van der Ree et al., 2007), it is necessary to evaluate whether the changes in overpass uses are due to population evolution (population growth, displacement or relocation), seasonal activity patterns or to real crossing habits (habituation to the overpass, feeding and/or resting habitats). Schmidt et al., 2021 suggest that crossing rates studies are most meaningful when interpreted within the context of active population dynamics. Relying strictly on crossing frequency as a performance indicator risks overlooking broader factors that define true structure success. Furthermore, according to Barrientos et al., 2025, population abundance should be an essential biodiversity variable when evaluating the overall linear infrastructure effects on wildlife. Wild game population monitoring and hunting data was not included in our analyses but was used as supportive information in attempts to explain changes in game species activity on Kolu overpass (**IV**). For example, a total decline in wild boar crossings (**IV**) was primarily attributed to a significant population collapse driven by African swine fever (ASF) and increased hunting pressure (**I**). This reduction in overpass use directly mirrors broader national trends reported by the Estonian Environment Agency (2024), which documented a sharp decrease in wild boar numbers across the country due to the disease.

As the number of vehicles and the traffic volumes on major roads continue to increase, the role of wildlife overpasses and other crossing structures in providing movement corridors for wildlife, thus contributing to biodiversity conservation and climate adaptation as well as ensuring traffic safety, becomes ever more important.

4.6. Conclusions

Road ecology has evolved significantly over the last century, moving from observations of animal carcasses – pioneered by the Stoners in 1925 – to a formalized, multi-disciplinary science. Modern road ecology no longer views roads merely as a human safety issue but as a primary driver of global biodiversity loss, focusing on complex concepts like habitat fragmentation, ecological barriers, and the long-term functioning of natural ecosystems. The trajectory of road ecology in Estonia mirrors global trends and has matured rapidly since the 1980s. What began as scattered data collection on large ungulate species like roe deer and moose has evolved into a standardized professional procedure. Wildlife impact studies and the design of mitigation measures (such as ecoducts and tunnels) are now integrated requirements for all major Estonian road construction and reconstruction projects.

This thesis investigated different factors influencing the occurrence and reporting of wildlife-vehicle collisions and the performance of wildlife crossing structures as primary mitigation measures. The main conclusions are as follows.

1. Research on wildlife-vehicle collisions (WVCs) indicates that these incidents are governed by complex interactions between animal behaviour and other biological factors, environmental conditions, traffic dynamics, and legal liability and reporting frameworks (**I–III**). Analysis of temporal patterns of WVC reveals that collisions are non-uniformly distributed, with seasonal peaks occurring from October to December but also in May, and weekly peaks on weekends, specifically Fridays. Diurnal patterns are closely tied to light levels, showing a sharp increase in collision frequency during twilight, with high risk persisting throughout the night (**I**).

2. The COVID-19 pandemic functioned as a unique natural experiment, revealing that abrupt traffic reductions profoundly impact wildlife mortality (**II**). Initial mobility restrictions significantly lowered roadkill on major transit routes – sparing animals that typically perish under standard conditions – even when adjusting for reporting biases. Paradoxically, urban areas saw an increase in WVCs, likely due to altered human movement and behavioural shifts in less-stressed animals. While natural population buffers may absorb the impact of a single-year anomaly, the ecological consequences of recurring or sustained restrictions remain uncertain. Consequently, there is an urgent need for high-quality, comprehensive WVC and roadkill data to refine future conservation strategies.

3. The reporting of WVCs is strongly influenced by varying liability protocols. In numerous countries liability is conditional, depending on factors such as road class, presence of fencing, driver compliance, and the species involved (**III**). This legal disparity often leads to the underrepresentation of WVCs in official databases. The quality of collected WVC and roadkill data is further affected by the challenges of reporting, such as the inability of distressed drivers to accurately identify species or locations. These inconsistencies often lead to datasets filled with duplicates or vague entries, particularly when multiple agencies record the same incident (**I–III**). Furthermore, collisions involving smaller mammals and birds remain almost entirely undocumented because they rarely cause vehicle damage and their carcasses may be quickly removed by scavengers.

   To address these issues, the involvement of local hunters is essential; their expertise allows for the identification of species, sex, and approximate age, which provides the necessary data for effective wildlife management (**III**). Given their role in carcass disposal, wounded game tracking and euthanasia, implementing a compensation scheme for hunters could further benefit this response system. Improving the accuracy of WVC records will depend on supporting more efficient reporting process and launching public awareness efforts to remove the fear of punishment, ensuring that the reporting system is seen as a helpful management tool rather than a legal risk.

4. High-trafficked roads function as severe barriers to wildlife movement, a risk that becomes absolute when combined with safety fencing. To counteract this

fragmentation, wildlife crossing structures are essential for maintaining ecological connectivity and assisting species in adapting to climate change by ensuring access to critical resources. The success of these measures depends on specific design criteria: structures must be tailored to the biological needs of target species, prioritized for exclusive wildlife use to minimize human disturbance, and integrated with natural vegetation to encourage use even by more cautious animals.

5. Long-term monitoring is absolutely necessary as many species require an extended habituation period; for example, the Kolu overpass in Northern Estonia saw large game activity triple only after a decade of maturation, eventually facilitating the movement of roe deer, moose, red deer and lynx (**IV**). However, crossing data must always be interpreted alongside local population dynamics, as fluctuations in usage – such as the decline in wild boar sightings following an African Swine Fever outbreak – often reflect broader environmental shifts rather than the failure of the mitigation structure itself.

Ultimately, as traffic volumes continue to rise, strategically placed and well-maintained crossing structures remain the primary tool for balancing infrastructure development with biodiversity conservation and road safety.

SUMMARY

While transport infrastructure is a fundamental driver of economic growth and social mobility, its environmental footprint is extensive and enduring. Infrastructure networks act as catalysts for urban sprawl and land-use change, creating cumulative pressures that represent primary drivers of global biodiversity loss.

The scientific origins of road ecology studies field date back a century to a seminal 1925 publication in Science by Dayton and Lillian Stoner. By documenting vertebrate mortality over a 1,017-km journey through Iowa, the Stoners shifted the focus of road impacts from human safety to ecological health. This foundation matured through quantitative studies in Sweden during the 1960s regarding wildlife seasonal mortality and research in the Netherlands that established correlations between traffic volume and roadkill frequency. In the United States, research further linked these impacts to habitat connectivity and ecological barriers. The formal maturation of road ecology as a cohesive discipline was marked by the publication of *Road Ecology: Science and Solutions* (Forman et al., 2003), which provided the conceptual framework necessary to integrate diverse scientific inquiries into a systematic field of study.

In Estonia, systematic research into wildlife-vehicle collisions (WVCs) emerged in the 1980s, led by Jüri Tõnisson and Malle Mardiste at the Estonian Forest Institute. The early 2000s marked a shift from observation to active mitigation. The Estonian Road Administration (now Estonian Transport Administration) began integrating technical solutions, such as amphibian tunnels and the preservation of riparian corridors, into infrastructure planning. Today, wildlife studies and the design of crossing structures have become standardized procedures within Estonian road construction and reconstruction projects, reflecting a mature integration of ecological science and civil engineering.

WVCs constitute a critical intersection of ecological loss and socioeconomic burden, resulting in millions of annual wildlife fatalities across a global road network. While mortality in small-to-medium species primarily threatens population viability and increases extinction risks, collisions with large ungulates pose a severe threat to human safety, causing tens of thousands of injuries and substantial economic costs annually, with incident rates exceeding one million in both Europe and the United States. However, research indicates that official statistics continue to systematically underrepresent the true scale of the issue, with actual accident rates remaining significantly higher than those captured in formal databases.

The purpose of this thesis was to provide empirical data on the dynamics of WVCs in Estonia and, also, on European level and to evaluate critically the factors governing reporting accuracy, the distribution of institutional accountability, and the performance of existing mitigation frameworks. Ultimately, the study posits that as road infrastructure and traffic intensities continue to escalate, the preservation of ecological integrity within natural systems must become a primary driver of transport policy.

To achieve these aims, firstly, the temporal patterns of WVCs within the Estonian road network, with a specific focus on characterizing seasonal, weekly, and diurnal fluctuations were studied (**I**). To quantify the relationship between WVC frequency and traffic density by utilizing the unique "anthropause" conditions created by COVID-19 movement restrictions, we succeeded to show the decline of WVCs due to decrease of road traffic volumes at both the national (Estonia) and continental (Europe) scales (**II**). We analysed the legal and financial liabilities shared among stakeholders – including motorists, emergency services, hunters, and transport authorities – and evaluated how the distribution of these responsibilities may influence the transparency and accuracy of collision reporting in Estonia and across Europe (**III**). Additionally, we managed to demonstrate empirically, through Estonian case study, the "adoption curve" of wildlife crossing structures, built to mitigate the barrier effect and reduce WVCs. We illustrated how even cautious large game species successfully utilize these passages as the structures transition toward a more naturalized ecological state (**IV**).

Wildlife collision trends exhibit significant spatial variability, thus identifying high-risk periods within specific local contexts is critical, as broad regional data may fail to capture localized ecological nuances. According to paper **I**, the monthly distribution of collisions for the three local common ungulate species revealed distinct seasonal patterns. Roe deer collisions exhibited a bimodal distribution, with a primary peak in November and a secondary surge in May. The spring increase is likely attributable to the fawning period and the subsequent dispersal of yearlings. The pronounced autumnal peak may be driven by heightened juvenile activity or the onset of the collective hunting season – commencing October 1st in Estonia – which serves as a significant anthropogenic stimulus for animal movement. Incident rates for moose peaked during June-July and September-October. Similarly to roe deer, the summer increase aligns with the dispersal of yearlings following maternal abandonment. The autumn surge coincides with the rutting season and seasonal migration toward winter habitats. Furthermore, collective hunting pressure likely intensifies road-crossing frequency by disrupting established movement patterns. The highest frequency of wild boar collisions occurred between September and December. Such incidents typically correlate with intermediate traffic volumes and peak activity periods for female wild boar. These factors converge during the extended nocturnal periods of late autumn and winter. Furthermore, the elevated risk during this season is likely exacerbated by environmental variables, including diminished visibility and hazardous road surface conditions such as rain, snow, and ice.

Weekly analysis indicated that the frequency of ungulate-vehicle collisions (UVCs) peaked during the weekend, with a distinct maximum recorded on Fridays (**I**; see Fig. 2, subchapter 3.1). This trend was consistent across all three studied species. Given that there are no known biological, ecological, or behavioural rhythms in wildlife that adhere to a seven-day cycle, this temporal pattern is presumably driven by anthropogenic factors – specifically, the intensified traffic volumes associated with weekend travel.

The diurnal distribution of UVCs revealed a bimodal pattern, with two distinct peaks occurring in the morning and evening (**I**; see Fig. 3, subchapter 3.1). These results indicate that ungulate activity is strongly synchronized with crepuscular periods (dawn and dusk). The observation that roe deer and moose collisions predominantly occur around sunrise and sunset is well-supported by extensive literature, whereas the temporal distribution of wild boar incidents reflects the species' primarily nocturnal behavioural patterns.

While existing literature has long established that traffic density is a primary driver of WVCs, standard operational conditions rarely offer the controlled parameters required to precisely quantify this relationship. The spring of 2020, however, provided an unprecedented "natural experiment" as the COVID-19 pandemic induced a global contraction in mobility. Although the most pronounced reductions in WVC frequency were recorded during the initial phases of COVID-related traffic reduction (CRTR), these ecological outcomes were heterogeneous and closely correlated with the stringency of local lockdown measures (**II**). Despite these regional variations – and even when accounting for potential under-reporting due to a reduced observer base – the overall decline in traffic volume facilitated the survival of significant number of wildlife, that would have otherwise succumbed to vehicle strikes under typical traffic conditions.

WVCs are traumatic incidents that frequently result in animal mortality or severe injury, often leaving even uninjured motorists in a profound state of shock. Establishing unambiguous regulations regarding the management of collision aftermath is essential for providing driver support and ensuring an efficient emergency response. However, such regulatory frameworks are often inconsistent and exhibit significant cross-national variation (**III**). Furthermore, the quality of collision data is heavily influenced by the reporting source and methodology. Disoriented drivers may struggle to accurately identify animal species or precise geographical coordinates, particularly at night. The psychological distress following a WVC can also deter individuals from exiting their vehicles to assess the animal's condition. Consequently, the integration of local hunters into the reporting process is highly advantageous for large game management. Hunters ensure the verification of the incident location, and their specialized expertise allows for the accurate identification of species, sex, and age cohorts – data that are fundamental to effective wildlife management. Given that hunters are responsible for carcass disposal, tracking wounded game, and performing necessary euthanasia, the implementation of a compensation scheme should be evaluated to cover the operational costs of these specialized services.

Roads with average daily traffic volumes exceeding 10,000 vehicles present a lethal risk to wildlife and function as formidable barriers to movement. When integrated with exclusion fencing, these corridors are transformed into nearly impermeable barriers for the majority of species. Consequently, the primary objective of wildlife passages is to restore or enhance connectivity between habitats fragmented by intensive traffic and physical infrastructure. However, even when designed according to contemporary best practices, several species may require an extended habituation period – often spanning years – before incorporating these new landscape features into their movement patterns. This necessitates long-term monitoring to verify the successful adoption of these structures by target species. Comparative data from the initial (2015–2016) and follow-up (2020–2022) monitoring projects of Estonia's first wildlife overpass reveal a significant evolution in usage patterns (**IV**). The proportion of large game crossings nearly tripled, ultimately accounting for 58% of all crossing events. In contrast, domestic animal activity declined sharply, and small game activity experienced a marginal decrease. While the roe deer remained the most frequent large game species across both periods, the follow-up study documented the successful adoption of the overpass by moose, red deer, and brown bear – species that were notably absent during the initial survey period.

As traffic volumes on major road networks continue to escalate, the strategic role of wildlife overpasses and other crossing structures becomes increasingly vital. These structures serve as essential movement corridors that not only enhance traffic safety by reducing collisions but also contribute significantly to biodiversity conservation and climate adaptation by maintaining landscape connectivity.

SUMMARY IN ESTONIAN

Metsloomadega juhtuvate liiklusõnnetuste toimumist ja nendest teatamist mõjutavad tegurid ning ulukipääsude kui peamiste leevendusmeetmete toimivus

Kuigi transporditaristu on majanduskasvu ja ühiskonna liikuvuse tagamisel äärmiselt oluline, on selge, et sellel on ulatuslik ja püsiv keskkonnajalajälg. Teedevõrgustiku arendamine on eelduseks linnade laienemisele ja maakasutuse muutustele, mis üheskoos toimivad paraku ülemaailmse elurikkuse vähenemise peamiste põhjustajatena.

Teedeökoloogia valdkonda kuuluvate uuringute ajalugu ulatub sajandi taha, Dayton ja Lillian Stoneri 1925. aasta olulise publikatsioonini ajakirjas *Science*. Dokumenteerides selgroogsete hukkumist 1017 km pikkusel teekonnal läbi Iowa, nihutasid Stonerid teede ja liikluse negatiivsete mõjude fookuse liiklusohutuselt keskkonnamõjudele, ehk senisele ainuüksi antropotsentristlikule lähenemisele lisandus ka teisi elusolendeid väärtustav vaatepunkt. Teedeökoloogia areng jätkus jõulisemalt 1960. aastatel Rootsis läbi viidud kvantitatiivsete uuringute kaudu metsloomade hooajalise hukkumise kohta ja Hollandis tehtud tööde kaudu, mis tuvastasid seoseid liiklussageduse ja ulukiõnnetuste arvu vahel. Ameerika Ühendriikides hakati neid mõjusid seostama elupaikade ühenduvuse ja ökoloogiliste barjääridega. Teedeökoloogia küpsemist iseseisvaks teadusharuks tähistas raamatu „*Road Ecology: Science and Solutions*“ (Forman jt, 2003) avaldamine. See siiani teedeökoloogia tüviteoseks peetav mahukas kogumik pakkus kontseptuaalse raamistiku, mis on vajalik mitmekesiste teaduslike uuringute integreerimiseks valdkonda. Eestis alustati süstemaatiliste ulukiõnnetuste uuringutega 1980. aastatel Eesti Metsainstituudis Jüri Tõnissoni ja Malle Mardiste juhtimisel. 2000. aastate alguses toimus nihe olukorra analüüsilt reaalsete leevendusmeetmete planeerimise ning kasutuselevõtuni. Maanteeamet (nüüdne Transpordiamet) hakkas maanteeprojektidesse integreerima tehnilisi lahendusi, alustades tunnelite rajamisega kahepaiksetele ja väikeulukitele ning sillaaluste kallasradade säilitamisega. Tänapäeval on eluslooduse uuringud ja ulukiläbipääsude ning seonduvate rajatiste planeerimine ning ehitamine Eesti teedeehitus- ja rekonstrueerimisprojektide elementaarne osa, mis näitab ökoloogia ja teedeehituse sidususe arengut ning väga olulist suhtumise muutust.

Maailmas juhtub igal aastal ulukitega miljoneid liiklusõnnetusi, mis ohustavad liiklejate elu ja tervist, tekitavad märkimisväärset majanduslikku kahju ning põhjustavad loomade asjatu hukkumise. Kuigi väikese ja keskmise kehasuurusega loomade hukkumine ohustab peamiselt populatsioonide elujõulisust ja suurendab väljasuremisohtu, kujutavad kokkupõrked suuremate ulukitega, näiteks suursõralistega tõsist ohtu liiklejate turvalisusele, põhjustades igal aastal kümneid tuhandeid inimvigastusi ja märkimisväärseid majanduslikke kulusid. Samas näitavad uuringud, et ametlik statistika alahindab süstemaatiliselt probleemi tegelikku ulatust ning tegelik õnnetuste arv on andmebaasides kajastatust oluliselt kõrgem.

Selle väitekirja eesmärk oli pakkuda empiirilisi andmeid Eestis suurulukitega juhtuvate liiklusõnnetuste ajaliste mustrite kohta ning hinnata kriitiliselt aruandluse täpsust, institutsioonilise vastutuse jaotust ja olemasolevate leevendusmeetmete toimimist mõjutavaid tegureid. Lõppkokkuvõttes jõudsin järelduseni, et kuna teedevõrgustiku ulatus ja liiklusintensiivsus jätkuvalt kasvavad, peab ökoloogilise terviklikkuse säilitamine looduslikes süsteemides saama transpordipoliitika üheks peamistest prioriteetidest.

Doktoritöö eesmärkide saavutamiseks analüüsisime esiteks suursõralistega juhtunud liiklusõnnetuste ajalist sagedust, keskendudes eelkõige aastaajaliste, nädalaste ja ööpäevaste mustrite iseloomustamisele (**I**). Näitamaks ulukiõnnetuste seost liiklussagedusega, kasutasime ära 2020. aasta kevadel COVID-19 tõttu kehtestatud liikumispiirangute põhjustatud ainulaadseid tingimusi. Meil õnnestus näidata ulukiõnnetuste arvu vähenemist tingituna väiksematest liiklussagedustest nii riigi kui ka Euroopa tasandil (**II**), samas erines olukord riigiti märgatavalt, olenedes konkreetses piirkonnas kehtestatud piirangute rangusastmest. Edasi analüüsisime ulukiõnnetustega seotud erinevate osapoolte – sealhulgas autojuhtide, päästeteenistuste, jahimeeste, transpordiametite – vahel jaotunud õiguslikke ja rahalisi kohustusi, mis võimaldas mul hinnata, kuidas praegune vastutuse jagunemine ning teadlikkus võib mõjutada õnnetuste kohta käivate andmete ning aruandluse läbipaistvust ja täpsust Eestis ning Euroopas laiemalt (**III**). Lisaks näitasin Eesti juhtumiuuringu kaudu empiiriliselt ulukiõnnetuste vähendamiseks ning barjääriefekti leevendamiseks rajatud suurulukipääsu „omaksvõtukõverat“. Nimelt Eesti esimese, Kolu ökodukti seire tõestas, et isegi ettevaatlikud suurulukiliigid asusid rajatist kasutama, kui ökodukt omandas aastate möödudes looduslikuma väljanägemise (**IV**).

Ulukiõnnetuste trendid näitavad märkimisväärset ruumilist varieeruvust, seega on oluline kõrge riskiga perioodide kindlakstegemine konkreetses piirkonnas. Laiemad üldistatud andmed ei pruugi lokaalseid nüansse tabada. **I** uuringu tulemused näitasid kolme Eestis levinud suursõralise – põdra, metssea ja metskitse – osalusel aset leidnud liiklusõnnetuste toimumissageduses selgelt eristuvaid aastaajalisi mustreid. Metskitsedega toimusid õnnetused kõige sagedamini novembris; veidi madalam tõus oli mais. Kevadine õnnetuste arvu kasv on tõenäoliselt tingitud metskitsede poegimisperioodist ja aastaste loomade hajumisliikumistest. Märkimisväärne sügisene tippaeg võib olla tingitud noorloomade suurenenud aktiivsusest või ajujahi hooajast – see algab Eestis 1. oktoobril. Ajujahi pidamine on oluline häiring, mis ajab metsas liikvele ka need ulukid, keda jahi käigus ei kütita. Põdraõnnetuste arv saavutas haripunkti juunis-juulis ja septembris-oktoobris. Sarnaselt metskitsedega langeb suvine haripunkt kokku aastaste mullikate hajumisliikumisega. Põdralehmad poegivad harilikult mais ning peletavad eelmise aasta järeltulijad eemale. Sügisene õnnetuste kasv langeb kokku jooksuajaga ja hooajalise liikumisega talvistesse elupaikadesse. Lisaks suurendab ajujaht tõenäoliselt teedeületuste sagedust, häirides väljakujunenud liikumismustreid. Metssigadega toimus kokkupõrkeid kõige enam septembrist detsembrini, tõenäoliselt eelkõige seetõttu, et suur osa liiklust toimub sügistalvel pimedal ajal, metssead on aga pimeduses aktiivsemad. Lisaks tõstavad talve hakul õnnetuste riski halvenenud nähtavus ja kehvemad sõidutingimused, näiteks vihm, lumi ja jää.

Nädala lõikes saavutasid kokkupõrked haripunkti nädala lõpuosas, kusjuures selgelt eristuv õnnetuste maksimum kõigi kolme uuritud liigi puhul registreeriti reedeti (**I**; vt joonis 2, alapeatükk 3.1). Arvestades, et metsloomadel ei ole teadaolevaid bioloogilisi, ökoloogilisi ega käitumuslikke rütme, mis järgiksid seitsmepäevast tsüklit, on see muster väga tõenäoliselt tingitud inimeste nädalavahetuse sõitudest tulenevatest intensiivistunud liiklusmahtudest.

Suursõraliste kokkupõrgete ööpäevane jaotus näitas bimodaalset mustrit, kus eristuvad tipud esinevad hommikul ja õhtul (**I**; vt joonis 3, alapeatükk 3.1). Sõraliste aktiivsus on tugevalt seotud hämarikuperioodidega (päikesetõusu eelne ning loojangu järgne aeg). Tähelepanekut, et metskitsede ja põtradega toimuvad kokkupõrked peamiselt päikesetõusu ja -loojangu paiku, toetab ulatuslik teaduskirjandus, samas kui metsseaga seotud juhtumite ajaline jaotus peegeldab liigi peamiselt öist aktiivsust.

Kuigi juba varasemalt on teada, et liiklussagedus on ulukiõnnetuste puhul üks olulisemaid faktoreid, pakuvad tavatingimused väga harva võimaluse selle seose demonstreerimiseks. 2020. aasta kevad pakkus aga suurepärast katsekeskkonda, kuna COVID-19 pandeemia tõttu kehtestati üle maailma liikumispiirangud ning sellest tulenevalt vähenes märkimisväärselt ka maanteeliiklus. Kuigi ulukiõnnetuste koguarv kukkus kõige enam COVID-iga seotud liiklussageduse vähenemise (CRTR) algfaasis, oli selle ulatus erinevates riikides erinev ning sõltus kohalike piirangute rangusastmest (**II**). Vaatamata piirkondlikele erinevustele – ja isegi arvesse võttes potentsiaalset õnnetuste alaraporteerimist väiksema liiklejate arvu tõttu – oli selge, et tänu liiklussageduse üldisele vähenemisele jäi ellu märkimisväärne arv metsloomi, kes tavapärastes tingimustes oleks tõenäoliselt maanteeliikluses hukkunud.

Otsasõidud metsloomadele on traumaatilised intsidendid, mis enamasti lõppevad looma hukkumise või raskete vigastustega, põhjustades sageli isegi füüsiliste vigastusteta autojuhtidel šokiseisundi. Seega on väga oluline ühtne reeglistik ja eri osapoolte vastutuse selge jagunemine, mis tagab õnnetusjuhtumi tagajärgede kiire ja tõhusa lahendamise ning juhi toetamise. Sellised regulatsioonid on aga sageli omavahel ebakõlas; lisaks näitas analüüs, et olukorra reguleerimises on olulised riikidevahelised erinevused (**III**). Lisaks mõjutavad ulukiõnnetuste statistika kvaliteeti suuresti infoallikas ja info edastamise viis. Segaduses ja stressis autojuhtidel võib olla keeruline looma liiki või täpseid geograafilisi koordinaate tuvastada, eriti öösel. Õnnetusega kaasnev šokk võib takistada inimestel sõidukist väljumist, et looma seisundit hinnata. Seetõttu on väga tähtis, et olukorra lahendamisse on kaasatud kohalikud jahimehed, kes suudavad määrata intsidendi toimumise täpse asukoha ning tuvastada õnnetusse sattunud uluki liigi, soo, vanuseklassi ning teatud juhtudel tervisliku seisundi – jätkusuutliku ulukimajanduse jaoks üliolulised andmed. Arvestades, et jahimehed vastutavad korjuse teisaldamise, haavatud suuruluki jälitamise ja vajadusel hädatapu läbiviimise eest, tuleks kaaluda hüvitusskeemi rakendamist, et jahiseltsile tasuda kaasnevad aja- ja tegevuskulud.

Maanteed, kus aasta keskmine ööpäevane liiklussagedus on suurem kui 10 000 sõidukit, kujutavad endast metsloomadele surmavat ohtu ja toimivad märkimisväärsete liikumistõketena. Ulukiaedadega eraldatuna muutuvad teedekoridorid enamiku loomaliikide jaoks peaaegu täiesti läbitungimatuteks barjäärideks. Seetõttu on rajatavate ulukipääsude (näiteks ökoduktide, erinevate mõõtmetega ulukitunnelite, sillaaluste kallasradade jm) peamine eesmärk taastada või parandada ühendust teedevõrgu ja intensiivse liikluse poolt killustatud elupaikade vahel. Samas, isegi kui loomaläbipääsud on projekteeritud vastavalt kaasaegsetele normidele ja parimatele teadmistele, võivad mitmed liigid vajada pikemat – sageli aastaid kestvat – kohanemisperioodi, enne kui uued käiguteed oma liikumismustrites omaks võetakse. Nõuab pikaajalist jälgimist, et tuvastada nende rajatiste edukas omaksvõtt sihtliikide poolt. Eesti esimese, 2013. aasta lõpus valminud ning järgmisel suvel haljastatud ökodukti esma- (2015–2016) ja jätkuseire (2020–2022) käigus kogutud andmetele tuginedes näitasime rajatise kasutamises positiivseid muutusi (**IV**). Suurulukite ületuste osakaal peaaegu kolmekordistus, moodustades jätkuseire perioodil ligi kaks kolmandikku kõigist ületusjuhtumitest. Seevastu koduloomade ületuste arv kukkus järsult; väikeulukite ületused omakorda vähenesid marginaalselt. Kuigi metskits jäi mõlemal perioodil kõige sagedasemaks rohesilda kasutavaks suurulukiliigiks, tuvastas jätkuseire ökodukti omaksvõtu põtrade, punahirve ja pruunkaru poolt – ülepääsu asusid kasutama liigid, keda vahetult rajatise valmimise järel ei õnnestunud registreerida.

Kuna liiklussagedus jätkuvalt kasvab, muutub ökoduktide ja teiste ulukipääsude strateegiline roll üha tähtsamaks. Need rajatised kujutavad endast olulisi liikumiskoridore, mis mitte ainult ei paranda liiklusohutust ulukikokkupõrgete vähendamise kaudu, vaid aitavad oluliselt kaasa ka bioloogilise mitmekesisuse säilitamisele ja kliimamuutustega kohanemisele, tagades loomade liikumisteed ja maastiku ühenduvuse.

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Twenty years ago I was invited to join the Estonian Road Administration as a fresh graduate of environmental sciences and that`s where I discovered this massive, complex and dramatic bundle of problems called ‘road ecology’ that has become my lifelong obsession. Two decades later, however, I often still feel like a beginner standing in front of an unfolding mystery.

These have been years of true adventure, defined by a life lived on, under, and alongside the roads of Estonia, action in forests, learning and discussing things in seminar rooms and at conferences, hours spent in front of computer, and all this, depending on the period, both day or night. We have tracked animals with GPS devices and spied on them with trail cameras, followed their tracks and met face to face. Sometimes we tried to attract them and sometimes had to escape from them. Practiced air rifle shooting in the attic of our academic building. Tossed some nice pieces of roadkill into the zoologists’ freezer. Flew by helicopter over remote forest villages and drowned several SUVs in the mud, not to mention a vintage Lexus (happy to announce that they all were pulled out).

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PUBLICATIONS

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1989–2000	Tartu Tamme Gymnasium

Professional employment

2023 –…	The Centre of Estonian Rural Research and Knowledge, Agricultural Research Department; Deputy Head of Agroecology Unit
2020–…	Ulukiuuringud OÜ; founder/owner/CEO/wildlife researcher
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2017–2022	Agricultural Research Centre, Agricultural Research and Monitoring Department, Agri-environmental Monitoring and Research Bureau; Senior Specialist
2015–2016	Estonian Naturalists Society; project leader
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Research

Main research fields

Wildlife-vehicle collisions, including temporal and spatial distribution; wildlife movements near road network, including the barrier effect of traffic; monitoring of wildlife crossings.

Key publications

Kruuse, M., Tull, A., Valdmann, H. 2025. Changes in mammal crossings in less than 10 years after the construction of Estonia's first wildlife overpass. *European Journal of Wildlife Research* 71, 109. https://doi.org/10.1007/s10344-025-01996-3.

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Kruuse, M.*, Adamoviča, A., Tull, A., Valdmann, H. 2024. Large game have found their way to Estonia`s first wildlife overpass. 9th IENE International Conference *"Biodiversity in the headlight of future transport"*, Prague 9.–13.09.2024. Poster presentation.

Kruuse, M.*, Oja, T., Oja, R., Anijalg, P., Saarma, U. 2017. Home ranges and movements of moose *(Alces alces)* in Estonia. X Baltic Theriological Conference, Tartu 27.–30.09.2017. Oral presentation.

Kruuse, M.*, Valdmann, H. 2017. Evidence of utilization of Estonia`s first ecoduct by mammals. 29th International Baltic Road Conference: Technical Tour to South Estonia, Tallinn 27.–30.08.2017. Oral presentation.

Kruuse, M.*, Enno, S.-E., Oja, T. 2017. Using available existing data for analysing temporal patterns of traffic collisions related to large ungulates. ICOET – the 2017 International Conference on Ecology & Transportation, Salt Lake City 14.–18.05.2017. Poster presentation.

Kruuse, M.*, Valdmann, H. 2016. Evidence of usage of Estonia's first ecoduct by mammals. 5th IENE International Conference on Ecology and Transportation, Lyon 30.08.–2.09.2016. Poster presentation.

Kruuse, M.*, Oja, T. 2014. Locations of the registered moose-vehicle collisions and their spatial relations with green network in Estonia. 4th IENE International Conference on Ecology and Transportation. Malmö 16.–19.09.2014. Oral presentation.

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Supervision

Una Adamoviča, Master's Degree. 2025. Moose (*Alces alces*) movements and the impact of barrier effect on roads with different traffic volumes based on GPS positioning data. Estonian University of Life Sciences / University of Tartu. Supervisors: Associate Professor Raivo Aunap (University of Tartu, Institute of Ecology and Earth Sciences, Department of Geography) and MSc Maris Kruuse (Centre of Estonian Rural Research and Knowledge). Available at: https://dspace.emu.ee/items/533b7bf7-e8cb-4ca8-8095-21de4378abff.

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2000–2006	Eesti Maaülikool, põllumajandus- ja keskkonnainstituut, bakalaureusekraad (võrdsustatud magistrikraadiga) maastikukaitse ja -hoolduse erialal.
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Teenistuskäik

2023 –…	Maaelu Teadmuskeskus, põllumajandusuuringute osakond; agroökoloogia valdkonna juhataja asetäitja
2020–…	Ulukiuuringud OÜ; asutaja/omanik/tegevjuht
2022–2022	Põllumajandusuuringute Keskus, põllumajandusseire ja -uuringute osakond; põllumajanduskeskkonna seire ja uuringute büroo juhataja
2017–2022	Põllumajandusuuringute Keskus, põllumajandusseire ja -uuringute osakond; põllumajanduskeskkonna seire ja uuringute büroo peaspetsialist
2015–2016	Eesti Looduseuurijate Selts; projektijuht
2006–2014	Maanteeamet, planeeringute osakond; peaspetsialist keskkonna alal

Teadustegevus

Peamised uurimisvaldkonnad

Ulukitega juhtuvad liiklusõnnetused, sh nii ajaline kui ruumiline jaotus; ulukite liikumine maanteede ümbruses, sh liiklusest tulenev barjääriefekt; ulukiläbipääsude kasutatavus.

Olulisemad publikatsioonid

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*ettekandja

Juhendamine

Una Adamoviča, magistrikraad. 2025. Põtrade (*Alces alces*) liikumised ning barjääriefekti mõju erineva liiklussagedusega maanteedel GPS asukohapunktide andmetel. Eesti Maaülikool/Tartu Ülikool. EMÜ keskkonnakaitse ja maastikukorralduse õppetool. Juhendajad kaasprofessor Raivo Aunap (Tartu Ülikool, loodus- ja täppisteaduste valdkond, ökoloogia ja maateaduste instituut, geograafia osakond) ja MSc Maris Kruuse (Maaelu Teadmuskeskus). Töö on kättesaadav veebiaadressil:
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