

Dissertationes Forestales 213

Animal-vehicle collisions – from knowledge to
mitigation

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Academic dissertation

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public criticism in lecture room B2, B-building (Viikki Campus, Latokartanonkaari 7, Helsinki) on April 1st 2016, at 12 o'clock noon.

Title of dissertation: Animal-vehicle collisions – from knowledge to mitigation

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Dissertationes Forestales 213

<http://dx.doi.org/10.14214/df.213>

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ISSN 1795-7389 (online)

ISBN 978-951-651-516-1 (pdf)

ISSN 2323-9220 (print)

ISBN 978-951-651-517-8 (paperback)

Publishers

Finnish Society of Forest Science

Natural Resources Institute Finland

Faculty of Agriculture and Forestry at the University of Helsinki

School of Forest Sciences of the University of Eastern Finland

Editorial Office

The Finnish Society of Forest Sciences

P.O. Box 18, FI-01301 Vantaa, Finland

<http://www.metla.fi/dissertationes>

Niemi, M. 2016. Animal-vehicle collisions – from knowledge to mitigation. *Dissertationes Forestales* 213. 35 p.

<http://dx.doi.org/10.14214/df.213>

Road networks and traffic cause worldwide environmental and ecological problems, and collisions with large animals are an increasing traffic safety issue. There is thus a continuous need to improve our understanding of the factors affecting the controversial relationship between nature, traffic, and human welfare, and to develop efficient mitigation measures.

In this thesis, I found that population size is the most important factor explaining the yearly variation in the number of moose-vehicle collisions (MVCs) in Finland. The monthly number of MVCs peaked in autumn with a secondary peak in early summer. This pattern differed from Sweden and Norway where the peak occurred in winter. In contrast, the relative risk of personal injuries was highest during summer in each country.

Spring weather was found to affect the detailed timing of spring MVCs in Finland: collisions occurred earlier during warm springs. In addition, as the beginning of the growing season has moved to an earlier date in the last two decades, so has the spring MVC peak.

In addition to MVCs, several thousand collisions involving deer species other than moose annually occur on Finnish roads. White-tailed deer was found to suffer highest traffic mortality rates in relation to population size, followed by moose, roe deer, and fallow deer. Among the studied species, moose has the largest and roe deer the smallest probability of surviving a collision.

The adverse impacts of traffic on animals could be mitigated for example by constructing wildlife passages. Dry paths under road bridges proved to be an effective mitigation measure for reducing the traffic mortality of small and medium-sized terrestrial animals.

The results of this thesis underline that different mitigation measures from population management and driver education to structural solutions are needed when trying to reduce the number and consequences of animal-vehicle collisions.

Keywords: moose-vehicle collision, deer-vehicle collision, ungulates, traffic safety, road kills, wildlife passages, collision mitigation

ACKNOWLEDGEMENTS

My work with animal-vehicle collisions began more than a decade ago when I monitored fauna pipes as a trainee. Afterwards, I have crawled under numerous road bridges in Finland and even climbed inside one in Hungary. During my PhD-studies, I have been lucky to catch rock ptarmigans in Svalbard – no traffic mortality issue there – and shared a campfire with animal movement researchers in Germany. These moments have been the salt and pepper of my work; most days I have been locked up in the office with my laptop and cursed at my badly behaving data. OK, granted, I have enjoyed the computer-part, too...

The journey has been long but I haven't had to travel it alone. First of all, I am grateful for my supervisors Petri Nummi and Jyrki Pusenius. They gave me freedom to make my own choices, but supported me when I needed it. I am acknowledged for all of my co-authors and other people without whom our manuscripts would never have been published. Especially Niina Jääskeläinen has shared her time and interests with me, and Tiina Mäkelä conducted excellent fieldwork in our dry path study. Hannu Rita, Jarkko Isotalo and Mikko Vastaranta helped with study designs and data handling. Next I present my warmest thanks to my custodian Kari Heliövaara, and Atle Mysterud and Anthony P. Clevenger who kindly reviewed my thesis. Stella Thompson corrected my language mistakes and Paavo Ojanen helped with the layout, thank you for that.

Riikka Rajamäki and Seppo Sarjamo helped me gain and understand the moose collisions data over the years. In addition, voluntary hunters from Hyvinkää Game Management Association were kind enough to give their own dataset for scientific purposes. Again, it was a great example of the precious work performed by Finnish hunters.

Although I haven't been a member of a research group, I have felt part of one. This is because of the great "moose team" from Joensuu and Jyväskylä. Thank you Juho Matala, Markus Melin, Raisa Tiilikainen and Tuomas Kukko for being there. I really hope that our cooperation will continue in the future. Wiebke Neumann and Göran Ericsson from Sweden and Christer M. Rolandsen and Erling J. Solberg from Norway took a fresh PhD-student seriously enough to propose collaboration. A special thanks to Christer and Erling, who kindly hosted me during my visit to Trondheim.

Our department has been a great place to work because of all the marvelous people around. Thank you for sharing the office and (the extra long) lunch breaks with me: Abbot, Elina, Heidi, Liisa, Mia, Risto, Sanna B., Sanna V., Stella, and others. Besides of all those funny moments, some of you have had a notable role in my thesis and other projects during my years at the University. Antti Nykänen performed excellent work with his master's thesis and our cooperation has continued afterwards. We are a great team! Veli-Matti Väänänen has been always ready to provide his support. No questions have been too small or too big to ask. I strongly recommend that he buy a comfortable sofa for his office – there will always be a new generation of frustrated students waiting for encouraging discussion sessions with him. Jani Pellikka and I have worked together on several occasions. Our cooperation projects have not been related to my thesis, but our long conversations have taught me critical thinking and increased my willingness to try to break some of the inflexible structures of research. We have also had fun. Thank you all. It has been great to work with you.

This thesis would have never been completed without a three-year grant provided by the Finnish Cultural Foundation. The Finnish Society of Forest Science, Haavikko-säätiö, and

University of Helsinki supported the finalizing process. My very first grant, given by Suomen Riistanhoito-Säätiö, was small in euros but high in importance. Besides these, I have been lucky to receive several traveling grants. Our department paid for my participation in excellent courses organized in Svalbard and Germany, and my doctoral program AGFOREE made it possible for me to conduct a research visit to Norway. Furthermore, several foundations have provided traveling grants to conferences held across Europe. These visits have promoted my journey to an independent researcher and made it possible to join the international network of scientists.

Finally, I wish to thank all my friends who have shared their joys and sorrows with me. Tuomas, you have a bigger role in my thesis than you probably realize – you have always provided me a peaceful hiding place and good company (and excellent food!) when I have needed it. And last, but definitely not least, my family has always supported me and I know there is no situation that I couldn't run to them. Especially I wish to acknowledge my dad who has shared his enthusiasm for wildlife and the outdoor life with me. I have learnt a lot from you.

LIST OF ORIGINAL ARTICLES

This thesis is based on the following articles, which are referred to in the text by their Roman numerals. Articles II–IV are reprinted with the kind permission of the publishers, while article I is the author’s version of the submitted manuscript.

I Niemi M., Rolandsen C.M., Neumann W., Kukko T., Tiilikainen R., Pusenius J., Solberg E.J., Ericsson G. Temporal patterns of moose-vehicle collisions with and without personal injuries. Manuscript.

II Niemi M., Tiilikainen R., Nummi P. (2013). Moose-vehicle collisions occur earlier in the summer. *Acta Theriologica* 58: 341–347.
<http://dx.doi.org/110.1007/s13364-013-0151-z>

III Niemi M., Matala J., Melin M., Eronen V., Järvenpää H. (2015). Traffic mortality of four ungulates in southern Finland. *Nature Conservation* 11: 13–28.
<http://dx.doi.org/110.3897/natureconservation.11.4416>

IV Niemi M., Jääskeläinen N., Nummi P., Mäkelä T., Norrdahl, K. (2014). Dry paths under roads effectively reduce traffic mortality of terrestrial vertebrates. *Journal of Environmental Management* 144: 51–57.
<http://dx.doi.org/110.1016/j.jenvman.2014.05.012>

Author’s contribution

The contributions of the Author (Milla Niemi) to the papers included in this thesis were as follows:

Milla Niemi (MN) is fully responsible for the summary of this doctoral thesis and she is the main author of all the included papers. In manuscript **I**, she was responsible for the original idea and planning of the study along with Christer M. Rolandsen (CMR), Wiebke Neumann (WN), and Raisa Tiilikainen (RT). The data was analyzed by CMR and MN. Although MN was responsible for writing the manuscript, CMR and WN also participated equally in the writing process. All co-authors commented on the manuscript. In paper **II**, MN was responsible for the original idea and planning of the study with RT and Petri Nummi (PN). She analyzed the data and was responsible for the writing. In study **III**, MN was responsible for the original idea. She planned the study with Juho Matala (JM) and Markus Melin (MM). Data collection was organized by Hannu Järvenpää (HJ). MN analyzed the data and was responsible for writing, although JM and MM also wrote parts of the manuscript. All co-authors commented on the manuscript. In paper **IV**, MN was responsible for the original idea with PN. Planning of the study design and fieldwork was conducted with PN, Niina C. Jääskeläinen (NCJ), and Hannu Rita. Fieldwork was conducted by Tiina Mäkelä (TM). MN analyzed the data with the help of Jarkko Isotalo. Although MN was responsible for writing the manuscript, all co-authors participated in the writing process.

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INTRODUCTION

An expanding road network and increasing traffic volumes pose a worldwide environmental and ecological problem (Forman and Alexander 1998). Collisions with wild animals, especially with ungulates, are concurrently an increasing traffic safety issue (Groot Bruinderink and Hazebroek 1996; Huijser et al. 2007; Langbein 2011). These accidents lead to tens of thousands of personal injuries or even fatalities each year, and cause notable economic losses (Bissonette et al. 2008; Sullivan 2011). Hence, various mitigation measures from driver education campaigns to animal road-crossing structures have been developed (Hedlund et al. 2004; Glista et al. 2009), with the target of reducing the consequences caused by roads on animals and to improve traffic safety.

The controversial and complex relationship between nature, road networks, and human welfare has created a new branch of science: road ecology (defined by Forman 1998). The first road ecology studies (e.g. Huey 1941) were actually conducted more than seven decades ago. Over time, researchers have focused for example on road kill surveys, the barrier effect of roads, and landscape fragmentation (reviewed by Coffin 2007).

In principle, road-related problems may be similar everywhere. However, regional differences in landscapes, environmental factors, and animal populations ensure that national or even local knowledge is also needed when seeking reconciliation between roads and the environment. In Nordic countries researchers have been interested in traffic accidents involving large ungulates in particular (Seiler 2004; Seiler 2005; Rolandsen et al. 2011; Neumann et al. 2012). Surprisingly little is still known of wildlife and traffic interactions in Finland. The few systematic Finnish studies have concentrated on the timing (Haikonen and Summala 2001, Niemi et al. 2013), placement (Krisp and Durot 2007; Niemi et al. 2007), or mitigation (Niemi et al. 2010) of animal-vehicle collisions.

The target of this thesis is to fill the obvious gap in the Finnish field of road ecology by improving our understanding of the complex relationship between roads, traffic, and animals. The main focus of the thesis is on ungulate-vehicle collisions because of their considerable role in traffic safety and their economic consequences (see e.g. Finnish Transport Agency 2015).

The number and consequences of animal-vehicle collisions

Animal-vehicle collisions are unquestionably highly visible consequences that traffic has on animals, and road kills are probably the most important human-induced mortality source of vertebrates on land (Forman and Alexander 1998). The phenomenon has thus been the interest of researchers on practically every continent where road networks exist (Groot Bruinderink and Hazebroek 1996; Forman and Alexander 1998; Saeki and Macdonald 2004; Taylor and Goldingay 2004; Coelho et al. 2008; Collinson et al. 2014). In the United States for example, the daily estimate of road-killed animals is approximately one million individuals (Forman and Alexander 1998); roughly at the same level as an annual estimate made in Finland (Manneri 2002). These numbers are enormous but road kills are not necessarily a threat for the population persistence of common and abundant species (Seiler et al. 2004).

While collisions with small or medium-sized animals usually leads to the death of the animal but are rarely harmful to humans, collisions with large animals such as ungulates are an increasing traffic safety issue (Seiler 2004; Sullivan 2011). Nearly one million ungulate-vehicle collisions occur annually in Europe (Langbein 2011) and even more crashes take place in the United States (Huijser et al. 2007), leading to tens of thousands of personal injuries and notable economic losses yearly (Groot Buinderink and Hazebroek 1996; Bissonette et al. 2008; Sullivan 2011). The total number of ungulate-vehicle collisions has been increasing in many countries (Seiler 2004; Sullivan 2011; Hothorn et al. 2015). Again, future numbers will most likely be higher as the populations of large deer species are increasing in many countries (e.g. Apollonio et al. 2010), leading to the continuously growing importance of these collisions.

Approximately 5000 collisions with wild ungulates are registered every year in Finland. As recently as the beginning of the 21st century, the majority of accidents were crashes involving moose (*Alces alces* L.). Since then the number of deer-vehicle collisions (collisions with white-tailed deer *Odocoileus virginianus* Zimmermann, roe deer *Capreolus capreolus* L., fallow deer *Dama dama* L., and wild forest reindeer *Rangifer tarandus fennicus* L.) has increased steadily while the annual number of moose-vehicle collisions has decreased. Nevertheless, the moose has kept its position as the most hazardous ungulate species on Finnish roads; nearly all ungulate-vehicle collisions leading to personal injuries are accidents involving moose, and the calculated annual economic losses are twice as high as losses incurred from deer crashes (Finnish Transport Agency 2015).

Collisions with ungulates can be seen not only as a traffic safety problem but also as a management challenge: to keep hunting at a sustainable level, road-killed animals should be taken into account when defining annual harvest quotas. The road kills of game species concurrently mean the loss of hunting opportunities and meat (Romin and Bissonette 1996; see also Storaas et al. 2001 for the economic valuation of moose). In Sweden, the number of road-killed moose is ca. 10% of the annual harvest or 4% of the total population size (Seiler et al. 2004). In Finland, the proportion of road-killed moose has been slightly over 3% of the annual harvest (years 1990–2011; calculated from data provided by the Finnish Wildlife Agency and Finnish Transport Agency), but both regional and species-specific variations in road mortality are obviously large (see also Groot Buinderink and Hazebroek 1996; Joyce and Mahoney 2001).

While road kills of common and abundant species do not necessarily pose a threat to their population persistence (Seiler et al. 2004), a considerable number of examples exist of traffic mortality reaching such high levels that it can negatively affect population levels. The European otter (*Lutra lutra*; L., 1758), for example, is known to suffer from notable traffic mortality (Philcox et al. 1999; Guter et al. 2005) and road kills of European badger (*Meles meles*; L., 1758) has been seen as the major reason for their population decline in the Netherlands (van der Zee et al. 1992). Other well-known examples are the endangered Florida panther (*Felis concolor coryi*; Bangs, 1899) and Florida key deer (*Odocoileus virginianus clavium*; Barbour and G. M. Allen, 1922): approximately half of their documented mortality is found to be due to traffic (Maehr et al. 1991; Lopez et al. 2003). Nevertheless, amphibians are possibly the most vulnerable species group suffering from traffic mortality and other road-related disturbances. Traffic can be a considerable source of mortality for them (Hels and Buchwald 2001; Orłowski 2007) and can significantly reduce populations (Carr and Fahrig 2001; Eigenbrod et al. 2008). In conclusion, the importance of traffic-related mortality is not the same for all species or populations and should therefore be evaluated and mitigated case by case.

Variables affecting the number of collisions

The most important factors affecting the number of animal-vehicle collisions are population size and traffic volume (Mysterud 2004; Seiler 2004; Balčiauskas 2009). In principle, the relationship is simple: more animals and more vehicles equal more animal-vehicle collisions. However, even at a large spatial scale, the relationship between these variables is not necessarily linear (Joyce and Mahoney 2001; Seiler 2004). For example, Rolandsen et al. (2011) found that relatively more moose were struck in areas with high versus low moose density. It is also possible that the demographic structure of a population affects the relative number of collisions: both white-tailed deer and mule deer (*Odocoileus hemionus*; Rafinesque, 1817) bucks are more likely to be killed in traffic than females are (Etter et al. 2002; Olson et al. 2014). Male-biased traffic mortality rates have also been found e.g. for the European otter (Philcox et al. 1999). On the other hand, the composition of struck roe deer and wild boars (*Sus scrofa*; L., 1758) appears to reflect their population structure (Groot Buinderink and Hazebroek 1996) and a meta-analysis conducted by Steen et al. (2006) showed that female turtles are more vulnerable to traffic than males. It is thus obvious that the demographic characteristics of traffic-killed individuals and further, the possible importance of road kills on a population level varies among species and even areas.

When moving towards a smaller spatial scale, the relationship between animal-vehicle collisions, population characteristics, and traffic becomes more complex and can be affected by several local-level factors. The number of collisions may actually decrease with increasing traffic (Clevenger et al. 2003; Seiler 2005) if disturbed animals begin avoiding a certain road rather than trying to cross it (see also Gagnon et al. 2007). On the other hand, even low traffic volumes, e.g. 10 cars per hour, can be enough to kill approximately a third of toads (*Bufo bufo*; L., 1758) during their breeding migration (van Gelder 1973). The presence of preferred habitat can increase the probability of animal-vehicle collisions (Grilo et al. 2009), while local-scale mitigation measures such as wildlife fences (Clevenger et al. 2001; Bissonette and Rosa 2012) as well as animal passages (Dodd et al. 2004; Aresco 2005) may reduce the number of road kills. Thus, the factors affecting animal road mortality are at least partly scale-dependent.

More than one party is always concerned in an animal-vehicle collision; not only are factors affecting an animal and its behavior important, but the role of the driver and the driving circumstances should also be considered. Vehicle speed is one of the most important variables affecting local-scale collision probabilities (Seiler 2005). Besides, the risk of human injuries increases with increasing speed (Garret and Conway 1999; Joyce and Mahoney 2001). Limited visibility due to darkness decreased a driver's ability to detect and react to road-crossing animals (Rodgers and Robins 2006; Mastro et al. 2010). Road characteristics have also been found to affect the presence of road kills (Clevenger et al. 2003). Weather can affect both animals and driving behavior (Mysterud 2004; Dussault et al. 2006) and, again, the risk of animal-vehicle collisions. Snow accumulation in particular is known to be a factor potentially affecting not only temporal distribution but also the total number of animal-vehicle accidents. Rolandsen et al. (2011) observed that the annual number of moose-vehicle collisions was positively related to snow amount. Olson et al. (2015) concurrently found that deer crossed high-traffic-volume roads more often during winter with deep snow when they were forced to use habitats adjacent to road areas.

When considering the number of animal-vehicle collisions and their importance, it is good to keep in mind that the numbers of registered collisions are generally underestimates.

Even for species with systematic recordings, such as ungulates (Groot Bruinderink and Hazebroek 1996), official statistics appear to underestimate the actual number of accidents (Almkvist et al. 1980; Seiler et al. 2004; Marcoux and Riley 2010; Snow et al. 2015). The possible reasons for this are numerous. For example, all accidents are not reported to law enforcement or the data handling process may contain shortages (e.g. Niemi et al. 2013). On the other hand, not all collisions lead to the death of the animal. In general, the increasing size of an animal increases its probability of surviving. An estimated 10% of struck moose are uninjured (Almkvist et al. 1980; Joyce and Mahoney 2001), while roe deer are twice as likely to be killed (Almkvist et al. 1980). The consequences of collisions are usually lethal for smaller animals but the data are typically based on specific surveys (e.g. Manneri 2002) rather than a systematic registering system.

Temporal distribution of ungulate-vehicle collisions

The number of ungulate-vehicle collisions displays clear monthly and circadian cycles (reviewed by Steiner et al. 2014). While a large-scale yearly variation in the number of animal-vehicle collisions is highly explained by population size and traffic volume (e.g. Rolandsen et al. 2011), the reasons behind the monthly and circadian distribution of collisions are partly different.

In Nordic countries, the number of moose-vehicle collisions peaks in autumn or early winter (Lavsund and Sandegren 1991; Haikonen and Summala 2001). The autumn peak exists concurrently with the moose rutting period (Lavsund and Sandegren 1991) and is probably fed by the darkness and otherwise adverse driving conditions (Neumann et al. 2012), and possibly by hunting. The winter peak is at least partly related to snow accumulation: when snow reaches a certain level, moose are forced to move from mountains to valleys where the majority of road networks run. Moose are additionally more attracted to using roads as their movement routes during deep snow periods (Bunnefeld et al. 2011; Lavsund and Sandegren 1991; Rolandsen et al. 2011), resulting in an increased risk of collisions.

The seasonal pattern of moose-vehicle collisions in some – but not all – areas of North America differs from the one observed in northern Europe. The number of moose accidents in North America is typically at its highest level during the summer (Joyce and Mahoney 2001; Dussault et al. 2006; Danks and Porter 2010). According to Dussault et al. (2006), this summer peak is a result of moose seeking sodium sources such as sodium-rich ponds in early summer. A secondary summer peak of moose-vehicle collisions has also been found in Finland (Haikonen and Summala 2001), but it is commonly believed to be due to the erratic movements of yearlings after weaning. This explanation is supported by the observation made by Niemi et al. (2013), who studied the monthly distribution of deer collisions in southern Finland and found that collisions with yearling white-tailed deer and roe deer peaked in June. The pattern is similar for moose (Niemi et al., unpublished data).

A strong autumn-centered pattern has been observed in ungulate-vehicle collisions in Finland not only for moose but also for white-tailed deer as well. Niemi et al. (2013) found that ca. half of the annual crashes occurred between October and December i.e. during rutting time. The pattern is similar to that found in North America (Allen and McCullough 1976; Iverson and Iverson 1999, but see Hubbard et al. 2000 concerning the additional spring peak). Interestingly, collisions with roe deer strongly peak in spring in southern

Finland (Niemi et al. 2013), when bucks begin occupying and defending their territories (see also Hothorn et al. 2015; Putzu et al. 2015).

Although the seasonal distribution of ungulate-vehicle collisions is somewhat species- and/or area-specific, it is relatively well known (reviewed by Steiner et al. 2014). However, information is still missing on the detailed timing of documented collision peaks, i.e. it is not known whether the small-scale timing of these peaks is the same year by year or whether it is affected by annually varying environmental conditions. Temperature has been found to affect the habitat selection of moose (van Beest et al. 2012; Melin et al. 2014), which could potentially affect the detailed timing and placement of moose-vehicle collisions. More systematic trends may also exist in the timing of collisions over time. Long-term changes in climate could produce a behavioral response of ungulates, which again could be reflected in the collision statistics. Thus, the detailed seasonal patterns of collisions are not necessarily unchangeable and possible changes should be taken into account when planning and evaluating mitigation measures.

Mitigation measures

The societal expenses of animal-vehicle accidents are enormous. However, human injuries and direct economic losses are not the only consequences of these collisions; the traffic mortality of animals is sometimes a conservation challenge and always an animal welfare issue. A great deal of effort has thus been used when developing and implementing various mitigation measures to prevent these collisions (Hedlund et al. 2004; van der Grift et al. 2013). Mitigation measures can be categorized in several different ways (see e.g. Mastro et al. 2008). One option is to separate measures modifying driving behavior from measures preventing the presence of animals on roads.

Possibly the most widely used mitigation measure aiming to affect motorist behavior is to mark collision “hotspots” or known animal road-crossing sites with warning signs (e.g. Krisp and Durot 2007). Although some promising trials have been conducted using temporary signs equipped with flashing lights (Sullivan et al. 2004) and dynamic message signs (Hardy et al. 2006), the long-term effectiveness of static warning signs is questionable (Al-Kaisy et al. 2008; see also Found and Boyce 2011). Establishing public awareness campaigns are another widely used method supposed to affect driving behavior, but their effectiveness has generally been poorly evaluated (Hedlund et al. 2004). Interestingly, Gkritza et al. (2010) found that the frequency of deer-vehicle collisions involving personal injuries was lower in autumn when the overall number of deer accidents was at its highest level. The authors suggested that the lower injury percent could be attributed to drivers’ increased awareness as a result of safety campaigns.

One extensively used and accepted mitigation method with proven efficiency is to limit the number of ungulate and other large mammal road-crossings and further, decrease the risk of encounters between animals and vehicles by fencing (Lavsund and Sandegren 1991; Clevenger et al. 2001; Bissonette and Rosa 2012). However, fences should not be used alone, i.e. without a combination of wildlife passages or escape routes such as jump-outs, because of the increasing barrier effect and the loss of landscape connectivity. Besides, if no alternative means of crossing roads is available, collisions may aggregate near fence ends (Clevenger et al. 2001) or, in some cases, move to secondary road networks (Niemi et al. 2010).

Wildlife passages such as green bridges and various underpasses are a commonly recommended solution for preventing encounters between cars and animals (reviewed by Glista et al. 2009). Passages may concurrently help maintain landscape connectivity by decreasing the barrier effect (Soanes et al. 2013) and secure the gene flow between subpopulations divided by roads. The usage of wildlife passages is well monitored and documented, and several vertebrate groups are known to utilize these structures (Hunt et al. 1987; Rodríguez et al. 1996; Ng et al. 2004). Although passage structures have been shown to potentially reduce the traffic mortality of animals (Dodd et al. 2004; Aresco 2005) and potentially enhance the gene flow (Sawaya et al. 2013), knowledge concerning the effectiveness of passages is still limited (van der Ree et al. 2007; Corlatti et al. 2009; Lesbarrères and Fahrig 2012). So far, only a few studies have shown the population-level effect of wildlife passages (Mansergh and Scotts 1989; van der Ree et al. 2009).

When considering animal-vehicle collisions from purely a traffic safety perspective, population control or hunting can also be seen as collision mitigation measures. This is true especially for abundant species with high population growth rates and a low risk of becoming threatened. For example, of the large ungulates the white-tailed deer and moose are heavily managed in many countries (e.g. Lavsund et al. 2003) along with other measures to control collision numbers. Since population size is known to be the most important factor affecting the number of ungulate-vehicle collisions (Seiler 2004; Rolandsen et al. 2011), it is not a surprise that systematic population reductions have been found to decrease the number of deer-vehicle collisions (DeNicola and Williams 2008).

Knowledge concerning the effectiveness of implemented mitigation measures is a key factor when planning future solutions. However, little is known about the effectiveness of the various implemented methods (van der Grift et al. 2013), partly because environmental issues, such as landscape connectivity, often have low priority in road planning and construction processes (Lesbarrères and Fahrig 2012, but see also van der Grift et al. 2013). Research and researchers should therefore become involved in the mitigation planning process during its early stages (Rytwinski et al. 2015) and the cooperation between road planners and scientists should be seen as a standard in future road projects.

AIMS OF THE THESIS

The main aim of this thesis was to improve the basic understanding of the factors affecting the number and timing of ungulate-vehicle collisions in Finland. The consequences of these collisions, both for human and animals, were additionally studied. Finally, the effectiveness of dry paths (dry land connections under road bridges) in preventing the road kills of small and medium-sized animals was measured. The results can be used as management tools when defining annual ungulate hunting quotas and especially when planning mitigation measures targeted to reduce the number and severity of animal-vehicle collisions.

Population density and traffic volume are the most important factors affecting the number of ungulate-vehicle collisions (Seiler 2004; Rolandsen et al. 2011). In paper **I**, our first aim was to study to what extent these variables explained the annual changes in the number of MVCs with and without personal injuries in Finland. We additionally analyzed the monthly distribution of MVCs – again with and without personal injuries – and examined whether the monthly pattern of these collisions differs among Fennoscandian countries.

The number of MVCs occurring in Finland is at its highest level during autumn, with a secondary peak in late spring or early summer (Haikonen and Summala 2001), and public traffic safety campaigns are timed concurrently with these peak times. However, it is not known whether the accurate timing of collision peaks is stable from year to year or if it is related for example to weather factors. The aim of paper **II** was therefore to investigate whether the timing of the MVC spring peak varies in relation to annual temperatures, i.e. whether MVCs peak earlier during early springs.

Although population size is a major factor affecting the annual number of ungulate-vehicle collisions (e.g. Rolandsen et al. 2011, **I**), relative traffic mortality (percent of population) can differ among species. In paper **III**, we calculated the traffic mortality rate of four ungulate species living in the same area in relation to species population sizes and tested whether it differs among species.

Knowledge of the factors affecting animal-vehicle collisions is essential when developing and choosing the optimal measures to reduce the number and consequences of these accidents. However, it is not enough: effectiveness of the implemented measures should also be tested and documented. Wildlife passages are a widely accepted method to reduce the road kills of animals (reviewed by Glista et al. 2009), although the real effectiveness of these structures is currently not very well known. The aim of paper **IV** was to improve the understanding concerning the effectiveness of wildlife passages and, to be more specific, to investigate whether dry paths under road bridges could reduce the traffic mortality of small and medium-sized vertebrates.

MATERIALS AND METHODS

Study area and spatial scale

The study areas as well as the spatial scale of the studies presented in this thesis varied paper by paper. In study **I**, we evaluated the large-scale patterns of MVCs at the country level (Finland) and used supplementary nationwide datasets from Sweden and Norway. In paper **II**, the study area covered the entire country (Finland) although analyses were conducted at the region level. Study **III** was carried out at a local scale, in the Hyvinkää Game Management Association. The design of study **IV** differed from the previous studies: data were collected from 20 study-reference pairs located in southern Finland.

Collision data and supportive datasets

The main dataset used in this thesis (studies **I** and **II**) was a nationwide moose-vehicle collision data (Accident register). In Finland, it is obligatory to call the emergency number after an ungulate-vehicle collision occurs, and all reported accidents are registered by the police. Statistics Finland annually collects the data from the law enforcement database and generates the Accident register, which is maintained by the Finnish Transport Agency (FTA). The Accident register contains the timing and locations of collisions that have occurred on public roads (from 2009 onwards data of collisions on private roads have also been collected, but these were omitted from analyses, see details in Finnish Transport

Agency 2015), and provides additional information e.g. on driving conditions. Possible personal injuries or fatalities due to collisions are also presented.

However, not all reported accidents prior to 2012 ended up in the final register because of technical reasons (Finnish Transport Agency 2014; Niemi et al. 2013). Luckily, there was no reason to expect anything other than a random temporal distribution of these dropouts, giving that the data were usable for the temporal analyses conducted in papers **I** and **II**. However, with the purpose of keeping the years in the used time series comparable, only the 22-year-long dataset collected between 1989 and 2011 (i.e. before 2012) was used in the analyses. Shorter but otherwise corresponding datasets from Sweden and Norway were also used in study **I** in addition to the Finnish MVC data, to enable comparison between the Fennoscandian countries.

Collisions with moose are registered at the species level in the Accident register, but crashes with other wild ungulates (white-tailed deer, roe deer, fallow deer, wild forest reindeer) are unfortunately merged as deer-vehicle collisions regardless of species. It was thus not possible to use the present register when studying species-specific differences related to deer-vehicle collisions. A smaller unofficial collision dataset, collected by local hunters who provide executive assistance to law enforcement and visited nearly every collision site, was used in study **III**. In this 12-year (2001–2012) voluntary-based dataset, all ungulates hit by cars were defined to the species level.

Although ungulate-vehicle collisions are relatively well documented in Finland, no systematic road-kill data of small and medium-sized animals is available. Hence, the data used in paper **IV** were collected specifically for that study. Collection was performed during the summer of 2008 by walking along 400-m-long study sections in the vicinity of our study bridges and their control road segments. The survey was repeated ten times, once each during ten consecutive weeks, and all vertebrate carcasses found on the road area were identified to the species level.

In addition to the animal collision data, different supportive datasets (Table 1) were used in this thesis.

Table 1. Supportive datasets used in the thesis.

Data	Spatial scale	Source	Used in paper
Annual traffic volume	Country	Finnish Transport Agency (FTA)	I
Moose observation index	Country (averaged)	Natural Resources Institute Finland	I
The number of harvested moose	Country	Finnish Wildlife Agency	I
The beginning of the growing season	Road district (N = 9)	Finnish Meteorological Institute	II
Population size	Game Management Association	Finnish Wildlife Agency	III
Land-use data	Raster size 25 square meters; proportions calculated for buffers with a radius of 1 km	CORINE Land Cover 2006	IV
Speed limit	Studied road section (400 m)	Finnish Road Administration (part of FTA since 2015)	IV
Daily traffic volume	Studied road section (400 m)	Finnish Road Administration	IV

MAIN RESULTS

This thesis (I) confirmed that moose population size is the most important factor affecting the number of MVCs. When used together, the moose observation index (used as a measure for the yearly variation in population size) and traffic volume explained approximately 60% of the annual variation in the number of MVCs in Finland. The final model suggested that a doubling of moose density could result in a nearly threefold increase in MVCs while an increase in traffic volume returned a proportional increase in collision numbers. As well as the annual number of all MVCs, MVCs involving personal injuries was also related to moose population size. However, the proportion of injury collisions decreased during our 22-year study period.

The observed monthly pattern of MVCs (I) differed between Finland, Sweden, and Norway. In Finland, the relative number of MVCs peaked in autumn with a secondary peak during the summer. In Sweden and Norway, most accidents occurred in early winter. Interestingly, the monthly pattern of MVCs involving personal injuries differed from the overall distribution of MVCs: in each of the three countries, sustaining an injury was more likely in a single MVC occurring between late spring and early autumn.

The presence of the secondary spring MVC peak in Finland was confirmed in paper I, but, interestingly, the beginning of the growing season was found (II) to affect the detailed timing of annual springtime MVCs. More specifically, the date when half of the collisions between April and July had occurred positively correlated with the first day of the growing season. Thus, moose-vehicle collisions appeared to occur earlier during warm springs. The pattern was similar in all studied road districts (N = 9), although statistical significance was only confirmed in six out of nine districts. The onset of the growing season has additionally moved to an earlier date during our study period, meaning that the detailed timing of springtime MVCs has also shifted to an earlier date.

As already shown in this thesis (I), population size and the number of ungulate-vehicle collisions are related. However, the relationship is not necessarily equal for all species even within the same area (III): as a species, white-tailed deer appears to suffer the highest collision rate, i.e. individuals were struck more often than moose, roe deer, and fallow deer in relation to their population sizes.

Although collisions are nearly always fatal for ungulates, the increasing size of an animal appeared to increase its survival probability: while only 1% of struck roe deer were uninjured, the corresponding proportion was 10% for moose (III). The total traffic mortality (animals struck and died) of small deer species was thus more or less equal to their collision rate, while the total mortality for moose due to traffic was slightly lower than the number of collisions. We calculated the total traffic mortality (percent of wintering population) in our study area with a relatively high traffic volume to be 6.5% for white-tailed deer, 4.5% for moose, 3.7% for roe deer, and 2.1% for fallow deer. We next compared these numbers with the annual harvest and found that the number of road-killed fallow deer was almost as large as the hunting bag. Traffic mortality for roe deer was 30.9% of the annual harvest, while the ratio was lower for white-tailed deer (10.3%) and moose (6.9%).

In study IV, we showed that the presence of dry paths under road bridges reduced the traffic mortality of small and medium-sized animals. When comparing the number of road-killed terrestrial vertebrates in the vicinity of our study bridges equipped with dry paths (N = 10) and their dry land reference road sections, less carcasses were observed near bridges

in eight out of ten study-reference pairs. Contrastingly, we found more road-killed animals in the vicinity of bridges without dry paths than in their reference sections in nine pairs out of ten. These observations were confirmed by models containing landscape- and road-related explanatory variables; the effect of dry paths was evident for the entire data (mammals, amphibians, and reptiles combined) and for amphibians alone. We calculated a theoretical effectiveness for dry paths and found it to be 88% for amphibians and 70% for mammals, i.e. the presence of dry paths prevented ca. four out of five animal road kills. The use of dry paths was confirmed by track observations we made during the study: a total of 15 species or species groups had utilized dry paths.

DISCUSSION

The role of population

Population size is a key factor in moose-vehicle collisions

This thesis (I) confirmed the positive relationship between moose population size, traffic volume, and collisions (see also Lavsund and Sandegren 1991; Seiler 2004; Rolandsen et al. 2011): population density and traffic volume explained ca. 60% of the yearly variation in the number of MVCs in Finland. However, our results suggest that the relationship between moose population size and the number of collisions is not necessarily proportional: based on our model, it appears that a doubling of the population size index (moose observation index) produces a nearly threefold increase in MVCs. Still, it is possible that the true relationship between moose population and collisions is closer to the proportional than observed by us (see also Rolandsen et al. 2011); the moose observation index tends to underestimate population growth, probably because of a decreasing hunters' searching efficiency with increasing moose density (Ueno et al. 2014).

However, although more than a third of the yearly variation in MVCs remained unexplained, the obvious relationship between population size and collision statistics suggest that future nationwide collision trends will more or less follow population development. Thus, when defining the optimal size of the country-level moose population (and hunting quotas), policymakers and wildlife managers also define the acceptable level of MVCs.

Collision data as a population estimation tool

Because collision statistics represent an independent source of the data (Ueno et al. 2014), they can be used – with care – as a supportive tool when defining population estimates. The estimation of moose population size and structure has long traditions in Finland. Collision data are used when estimating the directions of population development, but not in modeling processes because this would mean the loss of the independent reference data source (Researcher Jyrki Pusenius, Natural Resources Institute Finland, pers. comm. in 2015). However, there is a need to also develop better population estimates and more effective tools for small ungulate species, especially for the white-tailed deer, and collision statistics are one potential data source for this.

Unfortunately, crashes involving deer are treated collectively as “deer collisions” in the Finnish collision statistics regardless of species. This obvious lack in data management means that the data in their present form are not usable when constructing population estimates for small ungulates: if the proportion of accidents involving for example white-tailed deer to the total number of collisions is unknown, it is not possible to evaluate the strength and shape of the relationship between collision numbers and population size.

Traffic as a mortality source for ungulates

In paper **III**, we used an unofficial collision register collected by local hunters, which contained information concerning the ungulate species involved in collisions. By combining this species-specific collision statistics with annual local-level population estimates based on snow track censuses, we were able to calculate how large a proportion of various deer species were involved in collisions and further, died in traffic. We found that an average 6.5% of white-tailed deer (wintering population) are killed by traffic, while this proportion is only 3.7% for roe deer. A crude ratio based on these numbers means that the relative road mortality of white-tailed deer was approximately 1.7 times higher than that of roe deer. In other words, white-tailed deer appear to be nearly twice as likely to end up in the collision statistics than roe deer. This observed difference could be explained by the behavioral differences between species: monthly home ranges are smaller and daily movements shorter for roe deer than for white-tailed deer (Saari 2011; Honzová 2013), possibly leading to a lower road-crossing rate and again, a lower collision risk for roe deer.

Naturally, it should be noted that our study was conducted at a small spatial scale (in one Game Management Association) and therefore our results might not reflect the overall situation. For example, the areal differences in population age and sex ratios may affect the relative road mortality of ungulates: different demographic groups may be more likely to be killed in traffic than others (e.g. Etter et al. 2002; Olson et al. 2014). Some evidence additionally suggests that the relative number of collisions may be higher with high population density (Rolandsen et al. 2011; **I**). Thus, the relationship between population structure, density and the number of collisions and further, road mortality, needs to be studied in more detail in the future.

All ungulate species studied in paper **III** were game species, meaning that their population sizes are regulated by hunting (hunting roe deer does not require a hunting license in Finland). However, the traffic mortality of fallow deer was nearly as high as the hunting bag and approximately one third of the annual harvest of roe deer was killed in traffic. Our results concerning fallow deer may be partly explained by the limited amount of data, but the most feasible explanation for roe deer is the self-regulation of hunters (see also Niemi et al. 2011); the past decade has been difficult for roe deer and it appears that hunters have adapted their behavior by reducing the harvest (about the game bag: Finnish Wildlife Agency and Finnish Game and Fisheries Research Institute). Thus, despite the ratios we calculated being noteworthy, they do not necessarily mean that traffic mortality is threatening the populations we studied but rather reflected the adaptation of wildlife managers and individual hunters to current population levels.

The traffic mortality of white-tailed deer was 10.3% of the annual harvest in the area. For moose, the corresponding percentage was 6.9, which was comparable with the ratio found in Sweden (Seiler et al. 2004). However, this was ca. twice as high as the country-level ratio in Finland: during the last decade, the number of moose-vehicle collisions has averaged approximately 3% of the number of shot moose (calculated based on the data

provided by the Finnish Wildlife Agency and the Finnish Transport Agency). This observed difference is most likely due to the location of our study area – we conducted the study in a densely populated part of the country where traffic volume, also known to affect the number of collisions (Seiler 2004, **I**), was high.

Although it seems unlikely that traffic mortality is a threat to our study populations (see also Seiler et al. 2004), the observed traffic mortality compared with population sizes and the annual number of harvested individuals was high. Wildlife managers should thus take the local traffic mortality of ungulates into account when defining annual hunting quotas (or the number of licenses). In addition, our results underlined the importance of species-specific collision registering practices; a great deal of useful information is lost when combining several species in the same category.

Temporal patterns of MVCs

MVCs peak in autumn with a secondary peak in summer

The monthly distribution of MVCs in Finland, which was observed in studies **I** and **II**, was congruent with previous studies (e.g. Haikonen and Summala 2001): we found that MVCs peaked during the autumn months with a secondary peak in late spring/early summer.

The timing of the autumn peak is consistent with the rutting time of moose (September–October) and increased moose movements have therefore been suggested to explain the high number of collisions during the autumn months (Lavsund and Sandegren 1991). Moose concurrently begin moving from summer pastures to wintering areas (Katajisto et al., unpublished data) and the beginning of the hunting season may also increase their movements (for white-tailed deer: see Sudharsan et al. 2006), thereby increasing collision probability. On the other hand, Neumann et al. (2012) suggested that the autumn peak is more likely due to poor driving conditions than the activity of moose. Daylight time decreases dramatically towards winter in the Nordic countries and limited visibility is known to affect a driver's ability to detect and react to road-crossing animals (Rodgers and Robins 2006; Mastro et al. 2010). Thus, the autumn collision peak appears to be the sum of several factors rather than being explained by one or two single variables.

The secondary spring or summer peak examined in detail in study **II** appears to be driven by several factors, just like the autumn MVC peak. Neumann et al. (2012) found that the probability of moose road-crossings peaked not only in autumn but also in early summer (May to June), which was concurrent with the timing of the moose spring migration in Sweden (Singh et al. 2012). Interestingly, the timing of moose spring movements in Finland appears to occur earlier than the secondary MVC peak (Heikkinen 2000; Katajisto et al., unpublished data). This implies that other factors also affect the occurrence of the spring MVC peaks. One possible explanation is the yearlings' erratic movements after weaning; the separation of the yearlings happens in May and the distance between the cow and the yearling increases until mid-June (Cederlund et al. 1987). During this period, young moose seek for their own home ranges and tend to move more or less randomly. The phenomenon is well known in the Finnish media, which annually publishes articles and stories concerning moose visiting city centers and even metro stations. This yearling-related explanation is supported by a study conducted by Joyce and Mahoney (2001), who found that 1-year-old moose were overly represented in June and July collision statistics. Finnish collision data unfortunately do not contain any detailed information

concerning struck animals, so we were unable to test the possible effect of moose age on an individual's probability of being involved in a collision.

One aspect related to the monthly distribution of MVCs that was not studied in this thesis is the effect of a changing moose population size within a year. Moose population size is at its highest level in spring when new calves are born and hits bottom in winter (i.e. after the hunting season). In Finland, the annual harvest can reach up to 40% of the summer population (Finnish Wildlife Agency and Natural Resources Institute Finland 2015), suggesting that at least part of the monthly variation in collision numbers may be explained simply by the number of moose rather than by other variables.

However, while the annual number of MVCs in Finland reached its top in autumn with a secondary peak in summer, we found that the pattern was somewhat different in Sweden and Norway (**I**), where the highest number of collisions took place in early winter (December to February). These country-level differences are likely to reflect the differences in landscape and environmental conditions: snow accumulation in the mountainous areas of Scandinavia forces moose to move from mountain areas to lower altitudes (Rolandsen et al. 2011), where most of the road networks exist. Finland's landscape is relatively flat and the effects of snow are therefore different: moose tend to minimize their movements in deep snow (Katajisto et al. unpublished) to save energy, leading the low movement rates and a low number of MVCs during the winter months.

The observed differences in the monthly distribution of MVCs between countries underline the importance of country-level knowledge. For example, if temporal mitigation measures such as temporary education campaigns in Finland are implemented based on Norwegian MVC statistics, the timing of these measures will most likely be wrong. Even a country-level examination may be too rough because of the large differences in environmental conditions and other variables between regions within countries (see also **II**).

Weather affects the detailed timing of MVCs

Although the secondary spring or summer peak in the number of MVCs is an annual phenomenon in Finland (**I**), the detailed timing of collisions is affected by spring temperature (**II**). In other words, MVCs appear to occur earlier during warm springs. The beginning of the growing season has additionally moved to an earlier date during our 23-year study period, given that spring-time MVCs (median dates) have also shifted towards an earlier date.

Despite several explanations being possible for our observations (the possible changes in the timing of spring migration or in the weaning of calves; increased traffic volumes), we were unable to recognize the ultimate reason behind our findings. Still, these results have a notable practical importance: based on our observations, the timing of temporary collision mitigation measures such as public awareness campaigns should be planned year by year rather than implemented at the same time each year. Our study additionally underlined that the environmental conditions, and again, the timing of MVCs can vary within a country: both the beginning of the growing season and the median dates of MVCs differed between regions. Internal differences should therefore also be taken into account when planning temporary mitigation measures.

Study **II** concentrated on springtime MVCs only, but as we found a systematic relationship between weather and the detailed timing of collisions, testing whether a similar

relation can be found in autumn would also be logical. Our observations can thus be seen as the basis for further research hypotheses.

Temporal distribution of MVCs with and without personal injuries

Possibly the most interesting result in study **I** was that the relative risk of being injured in a single MVC was highest during the summer. This was true not only in Finland, where the total number of MVCs peaked in autumn, but also in Sweden and Norway where the annual collision peak occurred in late autumn or early winter. The systematic difference in the monthly pattern between MVCs with and without personal injuries suggests that different variables at least partly affect the total number and severity of MVCs.

Vehicle speed is the single most important factor affecting the risk of personal injuries in ungulate-vehicle collisions (Garret and Conway 1999; Joyce and Mahoney 2001). Interestingly, the risk of being injured in a collision is higher if the road surface is dry, i.e. driving conditions are good (Garret and Conway 1999; Gkritza et al. 2010), and collisions are less severe in winter (Savolainen and Ghosh 2008). This is most likely connected with driving behavior: people generally tend to be more careful if driving conditions are poor (Kilpeläinen and Summala 2007). Thus, it is likely that the temporal pattern of injury risk we observed is related to careless driving behavior during the summer months: the light nights and good driving conditions may attract drivers to speed without considering the collision risk.

Different mitigation measures are needed

From population management to driver education

The results of this thesis underline the need for different mitigation measures to prevent animal-vehicle collisions and to minimize their consequences. As study **I** showed, there is a strong relationship between moose population size and the annual number of collisions. Thus, as the moose is not a vulnerable species but a heavily managed game animal in Finland as well as in other Nordic countries (e.g. Lavsund et al. 2003), population control by hunting is the most important way of reducing the number of collisions at the country level. Reducing the number of moose can concurrently diminish the human consequences of MVCs; the total number of MVCs involving personal injuries was showed to follow the overall moose population trend.

However, population control cannot be the only way of reducing encounters between motorists and animals, even if no conservation issues are related to the target species. Wildlife fences in particular are non-lethal mitigation measures that have been shown to be effective in reducing the number of animal-vehicle collisions (Clevenger et al. 2001; Bissonette and Rosa 2012). The drawback is that they are expensive and can additionally increase the barrier effect of roads (Olsson and Widén 2008). It is thus not feasible to use fences elsewhere than along major roads with heavy traffic loads. Other mitigation measures, also suitable for minor roads, are therefore needed.

As ungulate-vehicle collisions often show a clear temporal pattern (Steiner et al. 2014, **I, II**), different temporal mitigation measures could be used to reduce the risk of collisions. Most of these are targeted to alter driving behavior. For example, it is possible to warn

motorists of an increased collision risk using temporary signs equipped with flashing lights (Sullivan et al. 2004) or launch public awareness campaigns to coincide with a collision peak (Sullivan and Messmer 2003). The problem is that the effectiveness of these campaigns is either poor or not very well known (but see Gkritza et al. 2010).

However, the results of study **I** suggest that the injury risk in MVCs may be partly due to careless driving behavior (i.e. speeding), which indicates that driver education should be developed and evaluated in more detailed in the future. If awareness campaigns are not able to decrease the number or severity of collisions, dynamic speed limit signs may be the next option in altering driving behavior during the riskiest collision season. Technical instruments such as car navigators and smart phone applications could also provide an alternative way in the future of delivering information on increased MVC risk levels and affecting motorist behavior.

Wildlife passages as a solution

The results of study **IV** clearly showed that dry paths under road bridges could reduce the road mortality of small and medium-sized terrestrial vertebrates. The calculated efficiency (how large a proportion of road kills are prevented) of dry paths was 79% for all species, even without guiding fences that are often used to keep animals away from road areas and funnel them towards wildlife passages (e.g. Aresco 2005). Our results thus suggest that dry paths have the potential to offer safe road-crossing options for animals, and they should therefore be taken as standard practice when planning and constructing road bridges.

The structures we studied were not originally planned for animal use but rather to help in bridge maintenance work. However, many species are known to have their own specific demands concerning the structural characteristics of wildlife passages (McDonald and St Clair 2004; Grilo et al. 2008; Mata et al. 2008). The efficiency of dry paths can potentially be improved by taking species-specific needs into account. Of course that would have required more monitoring work than we were able to conduct during our study.

A majority of the wildlife passages we studied were too small for large mammals, such as moose, but a combination of passages and wildlife fences are known to facilitate the movements of large mammals as well (Clevenger and Waltho 2000; Olsson et al. 2008; Sawaya et al. 2013). These could concurrently help to reduce the number of collisions, although an increased barrier effect of roads may be a drawback of fencing – even when used together with passages (Olsson and Widén 2008). Still, carefully planned structures can help to maintain landscape connectivity (e.g. Soanes et al. 2013), reduce the number of road-killed animals (Dodd et al. 2004; Aresco 2005), and enhance traffic safety. Maybe the most remarkable disadvantage of wildlife passages is that they, especially large overpasses, are expensive and therefore often neglected during the road planning process.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

This thesis confirmed the positive relationship between moose population density, traffic volume, and the number of MVCs (**I**). Because traffic volume is more likely to increase rather than decrease in the future, moose population management will play a key role when influencing the overall trend of MVCs. As our findings reflect the country-level

relationship but final management decisions are made at the local scale, future studies should concentrate on the relationship between moose population density and MVCs in smaller spatial units (see also Seiler 2004). Again, the role of population age and sex structure, implemented mitigation measures, and other variables known to affect the number of MVCs should be taken into account.

Interestingly, the monthly distribution of all MVCs and MVCs involving personal injuries were found to differ systematically (**I**), suggesting that partly different factors affect the number and severity of accidents. Thus, not only mitigation measures targeting the reduction of the total number of animal-vehicle collisions, but also those aiming to decrease their severity are needed.

The monthly number of MVCs in Finland was found to peak in autumn with a secondary peak in early summer (**I**, **II**). Temporal mitigation measures, such as drivers' education campaigns, temporary warning signs, and dynamic speed limits, could therefore help to decrease the seasonal collision risk. Although the real effectiveness of these measures is not very well known (Hedlund et al. 2004), the fact that they are implementable on the whole road network supports their use and development. Again, as the detailed MVC peak was found to differ depending on the year and among regions (**II**), mitigation measures need to be adjusted in time and space.

Traffic safety often dominates the discussion of animal-vehicle collisions, but the consequences of these accidents on animals should also be taken into account. Collision registers unfortunately do not always contain species-specific information (e.g. Finnish Transport Agency 2015), which complicates conclusions. Our finding that the traffic mortality rates of ungulates living into the same area differed (**III**) underlines the importance of developing species-specific collision registers. Combining several species in the same category will lead to the loss of information, which could otherwise be used when planning population management and developing more effective mitigation measures.

So far, the most widely accepted method for reducing animal-vehicle collisions and facilitating animal movements across road areas is the construction of wildlife passages (reviewed by Glista et al. 2009). Dry paths under road bridges reduced the traffic mortality of small and medium-sized terrestrial animals (**IV**). Structures equipped with dry paths should therefore be taken as standard practice when planning and constructing road bridges. Well-designed wildlife passages provide a safe road-crossing opportunity for all species regardless of their conservation status and help to concurrently improve traffic safety.

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