Evaluation of the Efficacy of Wildlife Warning Reflectors to Mitigate Wildlife -Vehicle Collisions on Roads

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Around here, however, we don’t
look backwards for very long.

We keep moving forward, opening up new doors and
doing new things, because we’re curious…
And curiosity keeps leading us down new paths.

Walt Disney

Table of Contents

List of Figures

List of Tables

Abbreviations

BA	before-after
BACI	before-after control-impact
BRT	boosted regression tree model
CI	control-impact
WVC	wildlife-vehicle collisions
WWR	wildlife warning reflectors

Summary

Wildlife-vehicle collisions cause human fatalities as well as economic and ecological losses on roads worldwide. Multiple mitigation measures have been developed over the past decades, while wildlife warning reflectors for preventing animals from entering the road when vehicles approach enjoy great popularity due to their commendableness, manageability and comprehensive applicability. However, their efficacy is still in question because of contradictory study outcomes and also behavioral studies could not find any long-term reaction of animals in the presence of the reflectors that would reduce the number of collisions. The task of this thesis, within the framework of a large-scale project initiated by the Germany Insurance Association (GDV), was to objectively analyze contradictions in literature, to evaluate the influence of modern reflectors on collisions with wildlife and on wildlife behavior.

In a first study, a comprehensive literature survey was carried out to evaluate disaccords in previous studies as well as other methodological differences that might explain the variation in study outcomes. The effect size of wildlife warning reflectors on the frequency of wildlife-vehicle collisions across all available data was assessed within a meta-analysis. The meta-analysis on literature data revealed that only studies applying a before-after design, effective study duration of < 12 months and considerably short testing site lengths of < 5 km found an effect of the reflectors.

Our second and main study focuses on the efficacy of modern wildlife warning reflectors to mitigate wildlife-vehicle collisions on roads. Three different optic reflector types that are most widely spread in Germany, as well as one opto-acoustic model were tested on 151 testing sites of approximately 2 km each in a prospective, randomized non-superiority cross-over study design for 24 months. Our results show that wildlife warning reflectors did not lower the number of collisions with ungulates by a relevant amount.

Finally, since few studies as well as hunters and manufacturers have reported a potential short-term effect of the reflectors on animal and driver behavior, we tested the reaction of ungulates towards oncoming vehicles and drivers to animals near the road considering a potential habituation effect in a third study. We could not find any behavioral response of ungulates or humans with reflectors present that would have lowered the risk of a collision, as the devices did not influence the reaction of animals to oncoming vehicles or motorists to wildlife near roads from the very beginning.

Considering the results of our first study, applying study designs without controlling for other, confounding factors such as a before-after study design, is not appropriate for evaluating the impact of an intervention due to the lack of independence from different levels of single treatments and true replications. A potential change after the implementation of a treatment cannot simply be assigned to that impact but to other factors as well. Moreover, the constant frequency of wildlife-vehicle collisions and the invariable responses of wildlife to approaching vehicles in the presence of the reflectors in our second and third study might be caused by the visual abilities of non-human mammals as well as the reflective properties of the reflectors. It has been shown for crepuscular and nocturnal animals that they are dichromatic, i.e. they cannot perceive long-wave light, and visual adaptations to rapid increases in light intensity such as headlights of approaching is considerably slow. Additionally, the light reflected from wildlife warning reflectors is already very low at close distances near the devices and overlaid by the headlights of approaching vehicles. Under these conditions, a potential efficacy of the reflectors is questionable anyway. Based on our results, we conclude that wildlife warning reflectors are not effective for mitigating wildlife-vehicle collisions on roads.

Zusammenfassung

Wildunfälle verursachen nicht nur menschliche Todesfälle, sondern auch einen hohen wirtschaftlichen und ökologischen Schaden. In den vergangenen Jahrzehnten wurden verschiedene Gegenmaßnahmen entwickelt, wobei sich insbesondere Wildwarnreflektoren aufgrund ihrer Handhabung, Preiswürdigkeit und umfangreichen Anwendbarkeit großer Beliebtheit erfreuen. Ihre Wirksamkeit steht jedoch noch immer in Frage, da verschiedene Untersuchungen zu widersprüchlichen Ergebnissen kommen und auch keine Verhaltensänderung von Tieren in Anwesenheit der Reflektoren gefunden wurden, die die Anzahl an Wildunfällen langfristig reduzieren würde. Das Ziel dieser Arbeit bestand daher darin, im Rahmen eines vom Gesamtverband der Deutschen Versichererungswirtschaft (GDV) initiierten Großprojektes, Widersprüche in der Literatur objektiv zu analysieren, den Einfluss moderner Wildwarnreflektoren auf Wildunfälle zu bewerten und eine kurzfristige Verhaltensänderung von Wildtieren in Anwesenheit der Reflektoren zu untersuchen.

In einer ersten Studie wurde eine umfassende Literaturrecherche durchgeführt, um Widersprüche aus früheren Untersuchungen sowie methodische Unterschiede zu bewerten. Die Wirksamkeit von Wildwarnreflektoren auf die Häufigkeit von Wildunfällen wurde im Rahmen einer Meta-Analyse unter Einbezug aller verfügbaren Daten untersucht. Dabei wurde gezeigt, dass nur Studien, die einen Vorher-Nachher Vergleich, eine kurze Studiendauer < 12 Monaten und kurze Teststreckenabschnitte < 5 km vorwiesen, einen Einfluss der Reflektoren feststellten.

Unsere zweite und gleichzeitige Hauptstudie konzentrierte sich auf die Wirksamkeit moderner Wildwarnreflektoren auf die Wildunfallhäufigkeit auf Straßen. Drei verschiedene optische Reflektortypen, die in Deutschland am häufigsten verbreitet sind, sowie ein opto-akustischer Reflektor wurden an insgesamt 151 Teststrecken von jeweils etwa 2 km Länge in

einem randomisierten non-superiority cross-over Versuch über 24 Monate getestet. Die Ergebnisse zeigten, dass Wildwarnreflektoren die Anzahl an Wildunfällen nicht beeinflussten.

Da einige Studien sowie Jäger und Hersteller von einer möglichen kurzfristigen Wirkung der Reflektoren auf das Tier- und Fahrerverhalten berichten, wurde die Reaktion der Tiere auf herannahende Fahrzeuge und die Reaktion von Fahrzeugführern auf Tiere in Straßennähe unter Berücksichtigung eines möglichen Gewöhnungseffektes in einer abschließenden dritten Untersuchung getestet. Dabei wurde keine Verhaltensänderung der Tiere und Fahrzeugführer in Anwesenheit von Wildwarnreflektoren festgestellt, unabhängig von der Dauer ihrer Anwesenheit, die das Risiko eines Wildunfalls verringert hätten.

Unter Berücksichtigung der Ergebnisse unserer ersten Studie ist die Anwendung von Studiendesigns ohne die Kontrolle anderer erklärender Einflussfaktoren, wie etwa eines Vorher-Nachher-Vergleichs, nicht geeignet, um die Auswirkungen eines Eingriffs auf die Umwelt zu erfassen. Eine mögliche Veränderung nach Durchführung der Maßnahmen kann nicht diesem Eingriff, sondern auch anderen Faktoren zugeordnet werden. Die Ergebnisse unserer zweiten und dritten Studie, die unveränderte Häufigkeit von Wildunfällen und die gleichbleibende Reaktion von Wildtieren auf Fahrzeuge und Fahrern auf Wildtiere in Anwesenheit der Reflektoren, liegt vermutlich in den physiologischen Eigenschaften von nicht-menschlichen Säugetieren sowie in den reflektierenden Merkmalen der Reflektoren begründet. Dämmerungs- und nachtaktive Tiere sind dichromatisch, d. h. sie können kein langwelliges Licht wahrnehmen, und visuelle Anpassungen an schnelle Lichtänderungen, z.B. das Annähern von Scheinwerfern, geschehen langsam. Zudem ist das reflektierte Licht in unmittelbarer Nähe der Reflektoren bereits sehr gering und wird darüber hinaus von den Scheinwerfern der herannahenden Fahrzeuge überlagert. Unter diesen Voraussetzungen ist eine mögliche Wirksamkeit der Reflektoren ohnehin fragwürdig. Auf der Grundlage unserer Ergebnisse kommen wir daher zu dem Schluss, dass Wildwarnreflektoren nicht geeignet sind Wildunfälle zu vermeiden.

Chapter 1

Introduction

1.1 Global traffic network

The global traffic network is constantly growing and terrestrial transport systems have already reached a total length of more than 64,285,000 km (CIA, 2017), influencing our environment in direct and indirect ways. While 1 - 2% of the landscape are covered with roads, resulting in a direct loss of habitat as well as changes of microclimate due to alterations of wind, air/ soil temperature and water runoff, the road-effect zones even cover 15 - 20% of the terrestrial surface (Forman and Alexander, 1998, Forman et al., 2003). These are further affected by pollutants, salts as well as light and noise emissions (Forman and Deblinger, 2000, Biglin and Dupigny-Giroux, 2006, Jordaan et al., 2009). Thus, roads alter abiotic and biotic processes (Honu and Gibson, 2006, Delgado et al., 2007). The effects and their pathways are very diverse and the evaluation strongly depends on the considered subject of protection or species; effects might be positive or negative.

Roads may provide new corridors or create new habitats and retreats (Dar et al., 2015, Abrahms et al., 2016). Since many insects are attracted by roads, e.g. due to light pollution, several predator species, such as bats, benefit from more abundant foraging habitats (Myczko et al., 2017). Moreover, constructing roads increases open areas, thus attracting light-demanding species concomitant with the displacement of other species, i.e. the edge effect (Vos and Chardon, 1998, Ortega and Capen, 1999). However, the negative effects of roads on the environment outnumber the positive effects up to five-fold (Fahrig and Rytwinski, 2009). For instance roads favor the spreading of invasive alien species and diseases to remote areas (Porembinski et al., 1996, Goosem and Turton, 2006). Furthermore, roads allow easier access to previously untouched parts of extensive forests (e.g. Geist and Lambin, 2002, Perz et al., 2008) and exert a strong impact on biodiversity loss due to deforestation (Fearnside, 2005, Finer et al., 2008). Thus, the physical presence of roads destroys habitats, increases fragmentation and interrupts ecological processes (cf. Forman and Alexander, 1998).

Additionally, for most non-airworthy terrestrial animals roads present a barrier that limits free movement of individuals, thus causing fragmentation and isolation of populations (Mader, 1984, D'Amico et al., 2016, Van der Ree et al., 2007). Animals that overcome these barriers are exposed to run overs, which threatens the existence of rare species and, of course, impairs road safety (Beben, 2012). Collisions with wildlife are probably one of the most considered effects of infrastructure and traffic on the environment, as signified by remnants commonly found alongside roads (Santos et al., 2011).

1.2 Wildlife-vehicle collisions

Since the beginning of the automobile era wildlife-vehicle collisions have strongly determined the environmental impact of road traffic and thus increasingly threatened both humans and wildlife (Stoner, 1925). So far, reliable data on economic and ecological costs are given only for few countries over the past decades (cf. Langbein et al., 2011). The number of collisions with wildlife seems to rise consistently, as both traffic and global road network continue to increase. Forman and Alexander (1998) already resumed 20 years ago that "sometime during the last three decades, roads with vehicles probably overtook hunting as the leading direct human cause of vertebrate mortality on land." Estimated numbers of road-killed animals have already been high in the past decades, for example 4 million estimated annual road-killed birds in the 1960s in the UK, 1.5 million mammals in Denmark every year in the 1980s, 2 million annual road-killed birds in the Netherlands and 4 million vertebrates in Belgium per year in the 1990s (Hodson, 1966, Hansen, 1982, van den Tempel, 1993, Rodts, 1998). More recent numbers estimate 10 million dead mammals, birds, reptiles and amphibians on roads in Spain every year (Mata et al., 2005). In Germany, 263,000 traffic collisions with ungulates were officially reported in 2016 (GDV, 2017).

Even if people are rarely killed or injured by such accidents, the economic costs are enormous. Recently reported collisions with wildlife in Germany are associated with an economic loss of almost 0.7 billion Euros (GDV, 2017). In addition, it is assumed that a great amount of collisions with wildlife remains unreported. The actual number of wildlife-vehicle collisions is estimated to be three-fold higher than the number of officially reported collisions, as reported for the US and Canada (Huijser and Kociolek, 2008, Snow et al., 2015, Hesse and Rea, 2016). Ecological consequences of collisions with wildlife depend on species, their population size and growth rate. For rare species, collisions with vehicles may cause a serious threat (Harris and Gallagher, 1989). For example, 50% of the endangered Florida panther (*Puma concolor coryi*) and Florida Key deer (*Odocoileus virginianus clavium*) were found to be killed by road traffic (Harris and Scheck, 1991, Forman ad Alexander, 1998, Braden et al., 2008). Analogously, 10% of the Iberian lynx (*Lynx pardinus*) and 20% of the Dutch badger population (*Meles meles*) are known to be lost by traffic collisions ((Rodriguez and Delibes, 1992, Broekhuisen and Derckx, 1996). Other species, such as the European hare (*Lepus europaeus*), Red foxes (*Vulpes vulpes*), House sparrows (*Passer domesticus*) or crows (*Corvus corone*) are affected with less than 5% of their population (Bennett, 1991, Rodts, 1998, Cederlund, 1998, Mysterud, 2006, Massai, 2015). The same amount accounts for ungulates such as roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), which are widespread in Europe (Cederlund, 1998) and mainly involved in wildlife-vehicle collisions in Germany (GDV, 2017).

Wildlife-vehicle collision hotspots depend on species and cluster in space and time (cf. Gunson et al., 2011, Bíl et al., 2016). For low-mobility species, such as amphibians, animals are mainly killed where roads pass close to hatcheries, wetlands and food supply. Moreover, most amphibians are run over during migration to and from the breeding grounds (cf. van Gelder, 1973, Ashley and Robinson, 1996). Other species, especially large mammals, are less dependent on a specific habitat and utilize landscapes at a different spatial scale. The spatio-temporal distribution of collisions with such species is well analyzed by ecologists (Gundersen and Andreassen, 1998, Ramp, 2005, Litvaitis and Tash, 2008, Hothorn et al., 2012, Bíl et al., 2013, Visintin et al., 2016). Local factors, such as land-use patterns, forest coverage and agricultural fields influence the occurrence of collisions with wildlife (Malo et al., 2004, Seiler, 2005, Gunson et al., 2011). Other temporal patterns such as time of the day animals’ and species’ activity phase or phase of the moon also play a role in the occurrence of wildlife accidents (Peris et al., 2005, Langbein et al., 2011, Hothorn et al., 2015, Colino-Rabanal et al., 2018). Thus, identifying time and place of increased risks for collisions with wildlife improves the implementation of suitable countermeasures.

1.3 Mitigation measures to reduce collisions with wildlife

Nowadays, over 40 different types of mitigation installations exist like fencing, warning signs and odor repellents to reduce wildlife-vehicle collisions (Hedlund et al., 2004, Rytwinski et al., 2016). The choice of measures, however, is still in question because sufficient information on the efficacy in reducing collisions with wildlife is missing. Moreover, the associated costs for different mitigation measures have a wide range (Glista et al., 2009, Rytwinski et al., 2016). Mitigation measures are either aimed (1) to separate traffic and wildlife, (2) to warn humans against frequent movements of animals, and/ or (3) to alter wildlife behavior by reducing the attractiveness of roads or by warning and if necessary, scaring away animals from roads and approaching vehicles.

(1) Reducing the coincidence of traffic and wildlife includes the reduction of population densities of species with enhanced risk for wildlife-vehicle collisions by trapping and resettlement, increased hunting pressure or by separating traffic and animals through fencing (DeNicola and Williams, 2008, Rutberg and Naugle, 2008, Huijser et al., 2007, Rytwinski et al., 2016). Trapping and resettlement are not feasible due to excessive costs, the risk of transmitting diseases, the lack of suitable resettlement areas or due to ethical reasons considering the high stress for animals (Conover, 1997, Conover, 2002). Thus, lethal regulation might be more applicable to reduce the number of individuals near roads and is

accompanied by some positive effects such as a reduction of ticks, tick-born encephalitis and Lyme disease or a reduction in browsing damage in managed forest areas (Conover, 1997, Stafford et al., 2003, DeNicola and Williams 2008). However, other studies could not find any correlation between the population density of target species and the risk of wildlife-vehicle collisions (Case, 1978, Waring et al., 1991). Moreover, a reduction of wildlife density is controversial, assuming that the effect occurs locally only, and because lethal regulation is often rejected by the public (Conover, 1997, Hedlund et al., 2004, Storm et al., 2007). Similarly, measures of traffic density regulation are only rarely tolerated by the public. Thus, the number of vehicles is difficult to control, especially in regions with regular traffic, i.e. commuter traffic (Storm et al., 2007).

Accordingly, separating traffic and animals primarily means making roads inaccessible for wildlife via fences, with or without crossing possibilities (Falk et al., 1978, Putman, 1997, Clevenger et al., 2001, Huisjer et al., 2007). Negative effects such as disrupting landscape permeability or migration routes should be counteracted to avoid isolation of populations (as reviewed in Rytwinski et al., 2016). Alternatively, crossing structures can be implemented as over- or underpasses such as landscape bridges, greens bridges, small bridges, tunnels or drainage channels, depending on target species (Forman et al., 2003, Knapp et al., 2004, Beben, 2016, Van der Ree et al., 2015). Although the efficacy of fencing with and without crossing structures has been documented in several studies, including meta-analyses of road mitigation measures, construction and maintenance are highly cost- and time-consuming (Falk et al., 1978, Putman, 1997, Clevenger et al., 2001, Bissonette et al., 2008, Mastro et al., 2008, Huijser and McGrowen, 2010, Rytwinski et al., 2016). Thus, fencing cannot be implemented when the budget is low, besides the fact that comprehensive installations of fences are unrealistic and would increase the barrier effect without implementing a big number of crossing structures.

(2) Since animals usually cross roads directly, a common method is to warn people with wildlife warning signs or to implement speed limits in vicinity to wildlife accident hotspots (Marcoux et al., 2005, Sudharsan et al., 2009). Training on the risk factors of wildlife accidents also provides opportunities to take preventative action (Marcoux et al., 2005). Nevertheless, these measures are ineffective on the long run due to habituation to warning signs or ignorance of speed limit signs (Beben, 2012). To avoid habituation, warning signs could be attached seasonally only or animal detection systems could provide information only when animals are approaching certain areas (Sullivan et al., 2004, Mastro et al., 2008, Strein et al., 2008). Studies show that these detection systems might lower collisions with wildlife by 57%, probably because motorists reduce speed and increase attention towards wildlife near the roads (Hammond and Wade, 2004, Huijser et al., 2006, Rytwinski et al., 2016). However, such animal detection systems are also accompanied by high costs for construction, fencing and maintenance (Kruidering et al., 2005, Huijser et al., 2007).

(3) Less cost-intensive measures keep animals away from roads by aiming at altering their behavior. A reduction of food supply in proximity to roads, alternative feeding points, or a reduction of salt-spreading during winter decreased the attractiveness of roads (Forman and Alexander, 1998, Wood and Wolfe, 1988, Donaldson, 2007). Additionally, scaring devices such as deer whistles or olfactory repellents were developed to prevent animals from entering the road when a vehicle is approaching. However, the efficacy of these measures is doubtful as deer was not found to distinguish between cars with and without whistles (Romin and Dalton, 1992). Studies on acoustic warning advices have also not been able to detect a lasting effect on roe deer behavior due to habituation (Ujvári et al., 2004). Furthermore, studies on the efficacy of olfactory repellents are inconsistent. Most studies did not show any influence of repellents on collisions with ungulates (Putman, 1997, Danielson and Hubbard, 1998, Hedlund et al., 2004, Knapp et al., 2004, Elmeros et al., 2011). In addition, the use of repellents did not alter the behavior of red deer (*Cervus elaphus*), sika deer (*Cervus Nippon*),

fallow deer (*Dama dama*), European mouflon (*Ovis orientalis musimon*) or roe deer in captivity that might reduce the chance of collisions (Lutz, 1994). However, a recent study on olfactory repellents indicate a reduction of wildlife-vehicle collisions by up to 43%, although the number of recorded collisions (*N* = 201) was rather low (Bíl et al., 2018). Finally, optic scaring devices, so-called wildlife warning reflectors, are supposed to reflect the headlight of an approaching vehicle to the road shoulder, potentially deterring wildlife from entering the road when a vehicle is passing by.

1.4 Wildlife warning reflectors

While most other mitigation measures are accompanied by high costs for construction and maintenance wildlife warning reflectors are comparatively cheap to buy, easy to handle, require little effort for maintenance and can be mounted to guidance posts almost comprehensively along roads. The reflectors exist on the market since the early 1960s and are available in a variety of models and colors. They are supposed to defer wildlife from entering the road for the duration of the passing vehicle reflecting the head light radiation of approaching vehicles to the road shoulder or by creating a light fence in front of the driving vehicle (e.g. Beilharz, 2017, Schilderwerk Beutha, 2017).

“Van de Ree” mirrors and “Ruppert” reflectors were among the first models, developed in the Netherlands and the US (McLain, 1964, Queal, 1968). More commonly applied and tested models are “Swareflex” warning reflectors, developed by Swarovski in 1973 in Austria (Rudelstorfer and Schwab, 1975) and “Strieter Lite” reflectors, developed by Strieter Corp. in 1994 in the US (Barlow, 1997). Other, less common reflectors (Bosch, “WEGU” and “AWIWA” reflectors), were developed in Germany (Gladfelter, 1984, Ujvári et al., 1998). Nowadays, more wildlife warning reflector models are available with reflective films in short wavelengths, such as green and blue, due to color sensitivity of ungulates (e.g. Ahnelt et al., 2006, Beilharz, 2017, Brieger et al., 2017a, Brieger et al., 2017b, Kämmerle et al., 2017, Schilderwerk Beutha, 2017). Even though the market offers a broad spectrum of reflector models, their efficacy is still unclear and many different studies comment on contradictory results (cf. Brieger et al., 2016, Rytwinski et al., 2016).

1.5 The dilemma of contradictory studies – the incitation for this thesis

While some studies claimed reflectors would effectively reduce collisions with wildlife (e.g. McLain, 1964, Ladstätter, 1974, Rudelstorfer and Schwab, 1975, Gladfelter, 1984, Schafer et al., 1985, Ingebrigtsen and Ludwig, 1986, Hildebrand and Hodgson, 1995, Pafko and Kovach, 1996, Stoyan, 2000, Grenier, 2002), others did not prove any reduction in wildlife-vehicle collisions when reflectors were present (e.g. Boyd, 1966, Beauchamp, 1970, Barlow, 1997, Jared, 2002). Moreover, wildlife behavior studies and analysis of collision numbers did not find evidence for alternating behavior in response to wildlife warning reflectors across different species, which could reduce wildlife-vehicle collisions in the long term through direct observations (e.g. Lehtimaki, 1979, Zacks and Budde, 1983, Griffis, 1984, Waring et al., 1991, D'Angelo et al., 2006, Gulen et al., 2006, Ramp and Croft, 2006, Brieger et al., 2017a, Kämmerle et al., 2017).

These contradictions gave rise to the initiation of a large-scale project by the German Insurance Association (GDV) in 2013 to finally evaluate the efficacy of wildlife warning reflectors to prevent wildlife-vehicle collisions on roads, which was initiated by T. Vor, T. Hothorn and C. Ammer and includes the thesis at hand. The project "Evaluation of the Efficacy of Wildlife Warning Reflectors to Mitigate Wildlife-Vehicle Collisions on Roads" comprises three largely independent sub-projects on the efficacy of wildlife warning reflectors, focusing on the questions (i) why study results in literature are contradictory, (ii) if modern wildlife warning reflectors can reduce the number of wildlife-vehicle collisions, and (iii) if ungulates or motorists might react to the reflectors, at least in the beginning, but habituate to these devices over time.

1.6 Objectives, approach and hypotheses

The main focus for this doctoral thesis was the underlying question of whether wildlife warning reflectors are a suitable measure to reduce collisions with wildlife (Chapter 3). This analysis was conducted by applying a randomized non-superiority cross-over design with temporal and spatial controls and an extensive sample size. In this context, a thorough literature study was carried out, as already a number of studies on the efficacy of wildlife warning reflectors exist (Table 2.2). Based on the contradicting results provided by previous studies, which have applied a variety of study designs, the influence of certain variables and conditions on the study results was examined in order to explain former contradictions (Chapter 2). Since some studies also implied a temporary influence of the reflectors on animals, an initial reaction of wildlife towards vehicles when reflectors were present that might lower the risk of collisions was evaluated. Moreover, the impact of reflectors on human behavior as well as a potential shift of reaction intensity was examined (Chapter 4).

The main objectives of the dissertation at hand were:

i) to evaluate the contrasting findings on the effectiveness of wildlife warning reflectors in the literature and to identify significant variables on previous study results.

ii) to determine the efficacy of wildlife warning reflectors to mitigate collisions with wildlife.

iii) to analyze the response of ungulates towards oncoming vehicles and the driving behavior of motorists in response to the presence of wildlife warning reflectors.

iv) to ascertain if an initial difference in response to oncoming vehicles diminishes over time when wildlife warning reflectors are present.

The objectives were achieved by:

September 2014 – December 2016

Testing sites were equipped with dark- and light-blue, as well as with opto-acoustic reflectors, while applying a randomized non-superiority cross-over study design.

May 2015 – December 2017

Testing sites were equipped with multi-colored wildlife warning reflectors in accord with a randomized cross over study design.

January 2015 – November 2016

Evaluation of environmental factors, analyzing variables such as sinuosity, surrounding landscape, agriculture, guard rails and signage, height of road side vegetation and completeness of the experimental setup through regular inspections.

August 2015 – September 2016

Wildlife observation videos were taken using two thermal network cameras, which were maintained weekly and relocated every two months.

October 2016 – March 2017

Literature survey and meta-analysis of data in literature.

The following hypotheses were tested:

1a) existing study results can be explained by the specifics of study designs, and

1b) a meta-analysis of previous studies identifies minimal requirements for a successful study design.

2a) Modern wildlife warning reflectors do not reduce wildlife–vehicle collisions by a relevant amount, and

2b) other environmental variables do not influence the inefficacy of the reflectors.

3) If the reflectors would influence the behavior of animals and humans at roads, ungulates

3a) decrease road crossing events,

3b) increase positive compared to negative reactions when vehicles are approaching,

3c) decrease flight events,

3d) decrease flight initiation distance, and

3e) shift their behavioral response to alarm, while

3f) motorists more often slow down or stop due to increased attention to wildlife near roads with reflectors present.

1.7 Materials and methods

A variety of reflector models is available nowadays (Chapter 1.4), but studies on color sensitivity showed that ungulates, just like most other mammals, are dichromatic and cannot perceive light exceeding 540 nm (VerCauteren and Pipas, 2003, Hanggi and Ingersoll, 2007). Therefore, modern reflectors are made in blue or other short wavelengths. With this background, we examined two of the most common blue reflector models in Germany in our study, one dark-blue model by Schilderwerk Beutha Inc. ("semicircle reflector") and one light-blue model by Beilharz Inc. ("the general"). Additionally, a third optic, multi-colored wildlife warning reflector model by Motzener Kunststoff- and Gummiverarbeitung Inc. ("multi-wildlife warner") has recently and successfully conquered the market and was already awarded the Brandenburg Innovation Prize in 2015 (Innovationspreis, 2018). Since opto-acoustic reflector (WEGU GFT and Eurohunt Inc., "opto-acoustic wildlife warner") that emit high-frequency sounds for 1.5 s with 83 dB and 4 kHz when a headlight hits light-sensitive solar panels, are often reported to effectively reduce collisions with animals, we also included a limited number of these reflectors in our evaluation. However, as this model is to be used in small numbers and only in combination with other optical reflectors according to the manufacturer's specifications, we included this model on 5 testing sites a year together with dark- and light blue reflectors. The reflectors have the measurements of 150 mm x 87 mm x 37 mm ("semicircle reflector") 260 mm x 95 mm x 25 mm ("the general"), 175 mm x 55 mm x 35 mm ("the multi-wildlife warner") and 182 mm x 86 mm x 70 mm ("the opto-acoustic wildlife warner") (height x width x depth). The wildlife warning reflectors used in this study (all reflector models in Chapter 2; model (c) in Chapter 3) are illustrated in Figure 1. 1.

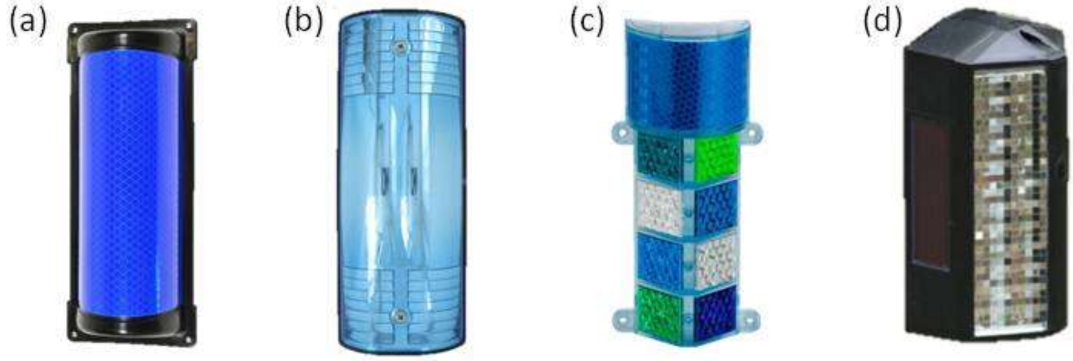

Figure 1. 1. Wildlife warning reflectors that have been evaluated in this thesis. (a) dark-blue "semicircle reflector" by Schilderwerk Beutha Inc. (© Kolosser, S.), (b) light-blue "the general" by Beilharz Inc. ©, (c) "multi-wildlife warner" by Motzener Kunststoff and Gummiverarbeitung Inc. © and (d) "opto-acoustic wildlife reflectors" by WEGU GFT and Eurohunt Inc. ©.

Processed materials are a micro prismatic reflective film by 3M Corporation (Minnesota, USA) ("semicircle reflector"), blue-transparent plastic with aluminum vapor plating ("the general"), a micro prismatic reflective film by 3M with additional eight multi-colored platelets with a honeycomb structure ("the multi-wildlife warner") and transparent mirrors in a 4 mm raster with silver and aluminum vapor plating ("the acoustic wildlife warner"). The reflected vehicle headlight is supposed to either build up a light fence along the road ("semicircle reflector", "the general", "the multi-wildlife warner") or a light fan to the road verge at an angle between 120° and 135° ("the general", "the multi-wildlife warner", "the opto-acoustic wildlife warner"). While both dark- and light-blue reflectors, as well as opto-acoustic wildlife warner, are attached to the guide posts at a height of 55 - 80 cm, multi-colored wildlife warning reflectors are attached at a height of 80 - 100 cm to the guide posts. Testing sites for light-blue (N = 50), multi-colored (N = 50), and dark-blue (N = 51) reflectors were determined by block randomization and divided into two groups (A and B), compliant with a randomized non-superiority cross-over design (Jones and Kenward, 2014), comparing sites before and after installation, as well as controls and impact sites. Details are given in Chapter 3.

For analyzing wildlife near and on roads thermal network cameras (Axis Q1931-E, Axis Communications AB, Inc., Lund, Sweden) were set up at trees outside the forest or forest patches about 3 m height recording approximately 250 m of road sections. Recording public areas, such as roads or road shoulders, is strictly limited by § 25 of the Lower Saxony Data Protection Act. Since thermal cameras do not record personal data and have already proven to be useful for wildlife observations in other research groups (Brieger, pers. comm., 2014) the cameras could be used without any further restrictions. The camera models had a focal lens of 35 mm and a viewing angle of 10.7°. With this, objects of 1.8 x 0.5 m (e.g. humans) can be detected at a distance of 1030 m, recognized at a distance of 260 m and identified at 130 m (Axis Communications AB, Inc., 2017). Testing sites for wildlife observations (N = 13) were recorded from 30 min before dawn until 30 min after dusk. Simultaneously, two testing sites were equipped with one thermal camera each and filmed four weeks without reflectors and hereafter four weeks with reflectors. The sites were prepared with a four-week time offset, so that one testing site was without reflectors while the other testing site had reflectors attached. This allowed us to compare both: the times before and after reflector installations, as well as the same time periods with and without reflectors, i.e. controls and impact. More details are provided in Chapter 4.

1.8 Study area

All research was conducted within a study area of 5,314 km^2 in Central Germany within the counties Göttingen (51°32’ N, 9°56’ E), Kassel (51°19’ N, 9°29’ E), Höxter (51°46’ N, 9°22’ E) and Lahn-Dill (50°34’ N, 8°30’ E), (Fig. 1. 2). The district of Göttingen occupies a natural part of the low mountain threshold of the Central German Triassic Mountain and Hill Country (Gauer and Aldinger, 2005, Bfn, 2015), including the Upper Weser-Mottled Sandstone Anticline, the Dransfelder Shell Limestone surface and the Leine Valley. This area is well-suited for agriculture due to the fertile loess soil. To the east of the Leinegraben runs the shell limestone surface of the Göttingen Forest, which slopes steeply into the Eichsfelder Basin. This region, the Eichsfelder Mottled Sandstone Anticline, consists of larger and smaller basins due to saline leaching (Bfn, 2015) and is characterized by an open cultural landscape (Bfn, 2015), with 32.9% forest share and 54.7% arable land (data provided by the European Environmental Agency, 2013). Spruce, pine, beech and oak dominate over larch, birch and hornbeam in this region. Maple, dewberry and cherry occur occasionally (Gauer and Aldinger, 2005). The climate of the district is both maritime and continental with an annual average temperature of 8.5 °C and an annual mean precipitation of 650 mm (DWD, 2018).

The district of Kassel southwest of Göttingen also belongs to the natural area of the Central German Triassic Mountain and Hill Country in the east. The area is characterized by larger contiguous forest areas that belong to the Weser-Leine Uplands, Reinhardswald, the eastern foothills of the Bramwald and the Kaufunger Forest in the east. In addition to contiguous forest areas, the landscape of the district Kassel is defined by an arable, open cultural landscape (Bfn, 2015), with 39.2% silvicultural and 47.1% agriculture area (data provided by the European Environmental Agency, 2013). Pine and beech dominate in the North Hessian Mountains, while maple, dewberry, cherry and lime trees occur occasionally (Gauer and Aldinger, 2005). The climate is characterized by the North Hessian Mountains and classified as moderately maritime to continental with western winds (ZRK Kassel, 2007). The average annual temperature is 9.1 °C with an annual precipitation of 676 mm (DWD, 2018).

Höxter in the state of North Rhine-Westphalia, northwest of Kassel, is located in the upper Weserbergland with foothills of the Northern Hessian Mountains in the border region to the district of Kassel. The central core area of the district, rich in fertile loess and limestone soils, is framed in the north by the Steinheimer Börde and in the south by the Borgentreicher and Warburger Börde. The fertile soils of the Steinheimer, Borgentreicher and Warbuger Börden as well as the Brakel limestone threshold are predominantly agricultural (Schüttler, 1996). With 25.5% forest share and 61.9% arable land, this county consists mainly of open areas (data provided by the European Environmental Agency, 2013). The small forest share of the Weserbergland is dominated by beech, oak, alder, ash and hornbeam. Cherries are also common (Gauer and Aldinger, 2005). The climate is moderate maritime with beginning transitions to continental conditions. The average annual temperature is 9.1° C, with an annual precipitation of 700 mm (DWD, 2018).

While the previous three counties adjoin each another, the fourth research area, the Lahn-Dill district, is located at a distance of about 150 km in the southwest of Hessia. The core area of the district is characterized by the Lahn- and Dill troughs of the two formative rivers. The soil consists of slate and quartzite in the north and south, of basanite and silt to the west, and along the Lahn- and Dill troughs of tholeiitic metabasalt, alkaline-basaltic pillow fragment breccias and slate (Hessisches Landesamt für Naturschutz, Umwelt und Geologie, 2013). As the agricultural conditions are less favorable, the economic activities are mainly characterized by the reduction of soil resources and forestry (Hessisches Landesamt für historische Landeskunde, 2018). Thus, forest coverage is at 47.5% the highest within the four study areas, while agricultural land-use only covers 21.9% of the region (data provided by the European Environmental Agency, 2013). The Northern Hessian Slate Mountains are characterized by the occurrence of pine and beech with regular occurrences of oak, while the

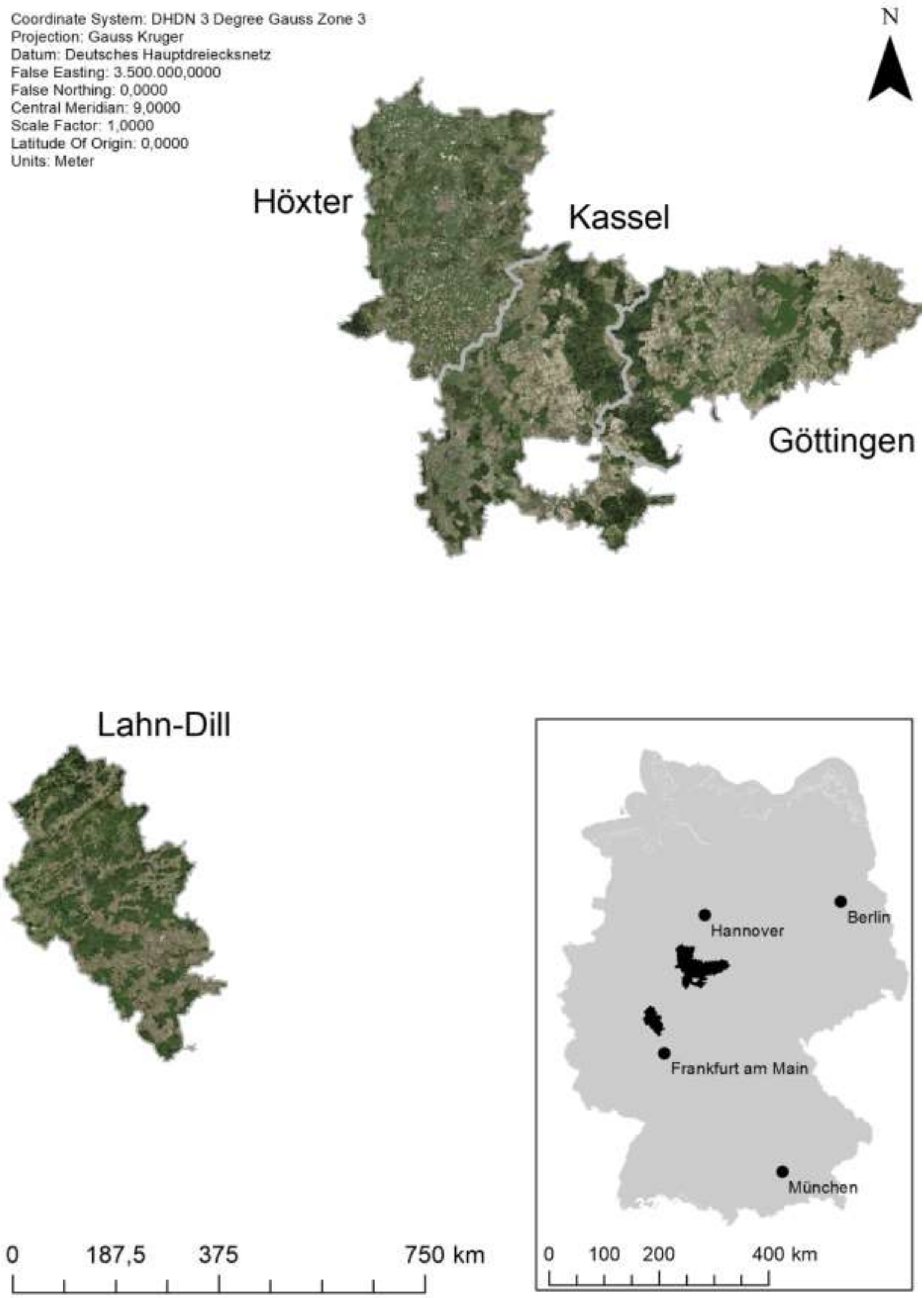

Figure 1. 2. Map of the study area, including the counties Göttingen, Lahn-Dill, Kassel and Höxter. Basemap: Aerial Imagery Basemap (Accessed June 25 2018).

Westerwald is mainly dominated by beech and oak; spruce, maple, ash and larch occur regularly or occasionally (Gauer and Aldinger, 2005). The south of the district, the northern foothills of the Taunus, is dominated by spruce and beech trees with regular occurrences of Douglas fir and oak (Gauer and Aldinger, 2005). The climate of the region is moderately continental with annual precipitation between 650 mm in the southeast and 1000 mm in the Westerwald. The average annual temperature is around 8.5 °C (Regional Development Concept, 2007). All research associated with the influence of wildlife warning reflectors on the number of wildlife-vehicle collisions (Chapter 3) was conducted within these four counties on N = 151 road sections of primary (N = 45), secondary (N = 75) and tertiary (N = 31) roads. Research associated with the reaction of wildlife to oncoming vehicles in relation to wildlife warning reflectors (Chapter 4) was carried out on N = 13 testing sites in the counties Göttingen (N = 10), Kassel (N = 2) and Höxter (N = 1).

1.9. Ungulate species within the study area

Species distributions vary marginally within the study area, roe deer and wild boar being the most abundant ungulate species in all four counties. However, red and fallow deer can also be found throughout the study area. Details on species distribution are given in Table 3.1. Roe deer are solitary and form small groups in winter (Vincent et al., 1995, Mysterud, 1999). They are highly selective feeders, mainly folivorous browsers, but also feed on winter rye and corn (Kaluzinski, 1982, Tixier and Duncan, 1996, Duncan et al., 1998). They frequent open areas and shift between forests and agricultural fields during night for feeding and shelter (Danilkin and Hewison, 1996, Myterud et al., 1999). Hence, road-crossing occurs especially during the dark hours (Hothorn et al., 2015).

Wild boars live in groups of females and juveniles, while adult males are solitary (Briedermann, 2009). They preferably feed on winter rye, oat and especially corn (Dietrich, 1984, Briedermann, 1990, Colino-Rabanal, 2012). Since they are attracted by crop fields for shelter and food sources, agricultural land plays an important role (Briedermann, 1990), and collisions with this species are related to forest cover and maize fields (Colino-Rabanal et al., 2012).

Red deer live in separated groups of adult males and females with their young (Mitchell et al., 1977). They are classified as intermediate feeders, foraging on grass, concentrate foods and sedges depending on the habitat (Hofmann, 1989, Gebert and Verheyden-Tixier, 2001). Fallow deer just like red deer, live in sexually segregated groups and are classified as intermediate feeders (Clutton-Brock et al., 1988, Hofman, 1989). They preferably forage on browse plants and fruits but also use a mixed diet (Putman, 1986). Collision numbers with these species are far lower than for roe deer and wild boar. Annual road kill numbers are estimated between 1 -3% for red deer and 7 - 13% for fallow deer, while about 3% of wild boar and 6% of roe deer spring population fall victim to vehicle traffic (Groot Bruinderink and Hazebroek, 1996, Langbein, 2007). Since roe deer is by far the most abundant ungulate species in Europe, it is involved in most wildlife-vehicle collisions (Groot Bruinderink and Hazebroek, 1996, Apollonio et al., 2010).

1.10 Associated Publications

This doctoral thesis is submitted as a cumulative dissertation consisting of three independent publications. The publications or manuscripts are presented in the Chapters 2 to 4.

Benten, A., Annighöfer, P., & Vor, T. (2018). Wildlife Warning Reflectors' Potential to Mitigate Wildlife-Vehicle Collisions–A Review on the evaluation Methods. Frontiers in Ecology and Evolution, 6, 37

Benten, A., Hothorn, T., Vor, T., & Ammer, C. (2018). Wildlife Warning Reflectors Do not Mitigate Wildlife-Vehicle Collisions on Roads. Accident Analysis & Prevention, 120, 64-73

Benten, A., Hothorn, T., Balkenhol, N., Vor, T., & Ammer, C. (in review). Wildlife Warning Reflectors Do not Alter the Behavior of Ungulates and Motorists even in the Short Term to Reduce the Risk of Wildlife-Vehicle Collisions.

1.11. References

Abrahms, B., Jordan, N. R., Golabek, K. A., McNutt, J. W., Wilson, A. M., & Brashares, J. S. (2016). Lessons from integrating behaviour and resource selection: activity-specific responses of African wild dogs to roads. Anim Cons. 19, 247-255.

Ahmed, S. E., Souza, C. M., Riberio, J., & Ewers, R. M. (2013). Temporal patterns of road network development in the Brazilian Amazon. Reg Environ Change. 13, 927-937.

Ahnelt, P. K., Schubert, C., Kuebber-Heiss, A., Schiviz, A., & Anger, E. (2006). Independent variation of retinal S and M cone photoreceptor topographies: a survey of four families of mammals. Visual Neurosci. 23, 429-435.

Apollonio, M., Andersen, R., & Putman, R. (Eds.). (2010). European ungulates and their management in the 21st century. Cambridge University Press. Cambridge, UK. 618 pp.

Ashley, E. P., & Robinson, J. T. (1996). Road mortality of amphibians, reptiles and other wildlife on the Long Point Causeway, Lake Erie, Ontario. Can Field Nat. 110, 403-412.

Barber, C. P., Cochrane, M. A., Souza Jr, C. M., & Laurance, W. F. (2014). Roads, deforestation, and the mitigating effect of protected areas in the Amazon. Biol Conserv. 177, 203-209.

Barlow, C. (1997). Performance evaluation of wildlife reflectors in British Columbia. In: Proceedings of the second roads, rails and the environment workshop (eds. A.P. Clevenger and K. Wells), pp. 62-67. Revelstoke, BC, Canada.

Beauchamp, D. (1970). Deer Mirror Evaluation. W-51-R-15. California Department of Fish and Game. California. 8 pp.

Beben, D. (2012). Crossings for animals–an effective method of wild fauna conservation. J Environ Eng Landsc. 20, 86–96.

Beben, D. (2016). Crossings construction as a method of animal conservation. Trans Res Proc. 14, 474–483.

Beilharz Straßenausrüstung. (2017). http://www.beilharz.eu/de/wildwarnreflektor.html. Accessed February 8 2017.

Bennett. A. F. (1991). Roads, roadsides and wildlife conservation: a review In: Nature Conservation 2: the role of corridors (eds. D.A Saunders, and R. J. Hobbs), pp. 99-118. Surrey Neatty & Sons Pty Limited, Western Australia.

Bfn. (2015). Landschaften. https://geodienste.bfn.de/landschaften?lang=de. Accessed June 26 2018.

Biglin, K., & Dupigny-Giroux, L. A. (2006). Mapping the road-effect zone to assess impacts of proposed road segments. J Conserv Plan. 2, 1-29.

Bíl, M., Andrášik, & R., Janoška, Z. (2013). Identification of hazardous road locations of traffic accidents by means of kernel density estimation and cluster significance evaluation. Acct Anal Prev. 55, 265–273.

Bíl, M., Andrášik, R., Svoboda, T., & Sedoník, J. (2016). The KDE+ software: a tool for effective identification and ranking of animal-vehicle collision hotspots along networks. Landscape Ecol. 31, 231-237.

Bíl, M., Andrášik, R., Bartonička, T., Křivánková, Z., & Sedoník, J. (2018). An evaluation of odor repellent effectiveness in prevention of wildlife-vehicle collisions. J Environ Manage. 205, 209-214.

Bissonette , R. B., Kassar, C. A. & Cook, L. J. (2008). Assessment of Costs Associated with Deer–Vehicle Collisions: Human Death and Injury, Vehicle Damage, and Deer Loss. Hum-Wildl Interact. 2, 17-27.

Boyd, R. J. (1966). Deer mirrors. Do they work? Outdoor Facts. 6, 44-45.

Braden, A. W., Lopez, R. R., Roberts, C. W., Silvy, N. J., Owen, C. B., & Frank, P. A. (2008). Florida Key deer Odocoileus virginianus clavium underpass use and movements along a highway corridor. Wildlife Biol. 14, 55-163.

Briedermann, L. (2009). Schwarzwild. Franckh-Kosmos Verlags-GmbH & Co. KG, Stuttgart, Germany. 524 pp.

Brieger, F., Hagen, R., Kröschel, M., Hartig, F., Petersen, I., Ortmann, S., & Suchant, R. (2017a). Do roe deer react to wildlife warning reflectors? A test combining a controlled experiment with field observations. Eur J Wildlife Res. 63, 10.1007/s10344-017-1130-5

Brieger, F., Hagen, R., Vetter, D. Dormann, C. F., & Storch, I. (2016). Effectiveness of light-reflecting devices: A systematic reanalysis of animal-vehicle collision data. Accident Anal Prev. 97, 242–260.

Brieger, F., Kämmerle, J.-L., Martschuk, N., Ortmann, S., & Hagen, R. (2017b). No evidence for a ‘warning effect’ of blue light in roe deer. Wildlife Biol. 17. 10.2981/wlb.00331

van Broekhuizen, S., & Derckx, H. (1996). Durchlässe für Dachse und ihre Effektivität. Z Jagdwiss. 42, 134–142.

Case, R. M. (1978). Interstate Highway Road-Killed Animals: A Data Source for Biologists. Wildlife Soc B. 6, 8-13.

Cederlund, G., Bergqvist, J., Kjellander, P., Gill, R., Gaillard, J.M., Boisaubert, B., Ballon, P., & Duncan, P. (1998). Managing roe deer and their impact on the environment: Maximising the net benefits to society. In: The European roe deer: the biology of success (eds. R. Andersen, P. Duncan, J. D. C. Linnell), pp. 189-219. Scandinavian University Press. Oslo, Norway.

CIA. (2017). The World Factbook. Washington DC: Central Intelligence Agency. https://www.cia.gov/library/publications/the-world-factbook/. Accessed July 25 2016.

Clevenger, A. P., Chruszcz, B., & Gunson, K. E. (2001). Highway mitigation fencing reduces wildlife-vehicle collisions. Wildlife Soc B. 29,646–653.

Clutton-Brock, T. H. (1988). Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, London. 538 pp.

Colino-Rabanal, V. J., Bosch, J., Munoz, M. J. & Peris, S. J. (2012). Influence of new irrigated croplands on wild boar (*Sus scrofa*) road kills in NW Spain. Anim Biodiv Conserv. 35, 247-252.

Colino-Rabanal, V. J., Langen, T. A., Peris, S. J., & Lizana, M. (2018). Ungulate-vehicle collision rates are associated with the phase of the moon. Biodivers Conserv. 27, 681-694.

Conover, M. R. (1997). Wildlife management by metropolitan residents in the United States: practices, perceptions, costs and values. Wildlife Soc B. 25, 306-311.

Conover, M. R. (2002). Resolving wildlife conflicts: the science of wildlife damage management. Lewis. Bocca Raton, Florida, 418 pp.

D'Amico, M., Périquet, S., Román, J., & Revilla, E. (2016). Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. J Appl Ecol. 53, 181-190.

D'Angelo, G., D'Angelo, J. G., Gallagher, G. R., Osborn, D. A., Miller, & Warren, R. J. (2006). Evaluation of Wildlife Warning Reflectors for Altering White-Tailed Deer Behavior along Roadways. Wildlife Soc B. 34, 1175–1183.

Danielson, B. J., & Hubbard, M. W. (1998). A literature review for assessing the status of current methods of reducing deer-vehicle collisions. Iowa, The Task Force on Animal Vehicle Collisions, the Iowa Department of Transportation, and the Iowa Department of Natural Resources. 30 pp.

Danilkin, A. & Hewison, A. J. M. (1996). Behavioural Ecology of Siberian and European Roe Deer. Chapman & Hall. London, UK. 278 pp.

Dar, P. A., Reshi, Z. A., & Shah, M. A. (2015). Roads act as corridors for the spread of alien plant species in the mountainous regions: A case study of Kashmir Valley, India. Trop Ecol. 56, 183-190.

Delgado, J. D., Arroyo, N. L., Arévalo, J. R., & Fernández-Palacios, J. M. (2007). Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). Landscape Urban Plan. 81, 328-340.

DeNicola, A. J., & Williams, S. C. (2008). Sharpshooting suburban white-tailed deer reduces deer–vehicle collisions. Hum-Wildl Conflicts. 2, 28-33.

Dietrich, U. (1984). Ergebnisse und Tendenzen der Forschung am Wildschwein *Sus scrofa* in den Jahren 1975-1983. Säugetierkd. Mitt. 31, 223-237.

Donaldson, B. M. (2006). Use of highway underpasses by large mammals and other wildlife in Virginia and factors influencing their effectiveness. In: Proceedings of the 2005 International Conference on Ecology and Transportation, (eds. C. L. Irwin, P. Garrett, and K. P. McDermott), pp. 433-441. Center for Transportation and the Environment. North Carolina State University, Raleigh, NC, USA.

Duncan, P., Tixier, H., Hoffman, R. R. & Lechner-Doll, M. (1998). Feeding strategies and the physiology of digestion in roe deer. In: The European roe deer: the biology of success (eds. R. Andersen, P. Duncan, and J. D. C. Linnell), pp. 91-117. l. Scandinavian University Pres Oslo, Norway.

DWD. (2018). Deutscher Wetterdienst Klimaatlas. https://www.dwd.de/DE/klimaumwelt/klimaatlas/. Accessed June 26 2018.

Elmeros, M., Winbladh, J.K., Andersen, P.N., Madsen, A.B., & Christensen, J.T. (2011). Effectiveness of odour repellents on red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*): A field test. Euro J Wildlife Res. 57, 1223–1226.

European Environmental Agency, 2013. CORINE Land Cover (CLC) 2006. https://www.eea.europa.eu/data-and-maps/data/clc-2006-raster. Accessed December 5 2016.

Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: an empirical review and synthesis. Ecol Soc. 14, 21.

Falk, N. W., Graves, H. B., & Bellis, E. D. (1978). Highway right-of-way fences as deer deterrents. J Wildlife Manage. 3, 646–650.

Fearnside, P. M. (2005). Deforestation in Brazilian Amazonia: history, rates, and consequences. Conserv Biol. 19, 680-688.

Finer, M., Jenkins, C. N., Pimm, S. L., Keane, B., & Ross, C. (2008). Oil and gas projects in the western Amazon: threats to wilderness, biodiversity, and indigenous peoples. PloS one. 3, e2932.

Forman, R. T. & Alexander, L. E. (1998). Roads and Their Major Ecological Effects. Annu Rev Ecol Syst. 29, 207-31.

Forman, R. T., & Deblinger, R. D. (2000). The ecological road-effect zone of a Massachusetts (USA) suburban highway. Conserv Biol. 14, 36-46.

Forman, R. T. T., Sperling, D., Bissonette, J. A., Clevenger, A. P., Cutshall, C. D., Dale, V. H., Fahrig, L., France, R., Goldman, C. R., Heanue, K., Jones, J. A., Swanson, F. J., Turrentine, T. & Winter, T. C. (Eds.). (2003). Road Ecology: Science and Solutions. Island Press, Washington, USA. 481 pp.

Gauer, J. & Aldinger, E. (2005). Waldökologische Naturräume Deutschlands: forstliche Wuchsgebiete und Wuchsbezirke. Mitteilung des Vereins für Forstliche Standortskunde und Forstpflanzenzüchtung. 43. 324 pp.

GDV. (2017). http://www.gdv.de/2016/11/wildunfaelle-erreichen-hoechststand-alle-zwei-minuten-kracht-es/. Accessed February 8 2017.

Gebert C., & Verheyden-Tixier H. (2001). Variations of diet composition of red deer (*Cervus elaphus* L.) in Europe. Mammal Review. 31, 189–201.

Geist, H. J., & Lambin, E. F. (2002). Proximate Causes and Underlying Driving Forces of Tropical Deforestation. Tropical forests are disappearing as the result of many pressures, both local and regional, acting in various combinations in different geographical locations. BioScience. 52, 143-150.

Gladfelter, L. (1984). Effect of wildlife highway warning reflectors on deer-vehicle accidents. Iowa Highway Research Board Project HR-210. Iowa Department of Transportation, Ames, Iowa, USA. 16 pp.

Glista, D. J., DeVault, T. L., & DeWoody, J. A. (2009). A review of mitigation measures for reducing wildlife mortality on roadways. Landscape Urban Plan. 91, 1-7.

Goosem, M. W. & Turton, S. M. (2006). Weed Incursions along Roads and Powerlines in the Wet Tropics World Heritage Area: The Potential for Remote Sensing as an Indicator of Weed Infestations. Rainforest CRC, Cairns, Australia. 190 pp.

Grenier, R. H. (2002). A study of the effectiveness of Strieter-Lite® wild animal highway warning reflector systems. Commissioned report for Strieter Corporation. 19 pp.

Griffis, J. L. (1984). Effects of Swareflex wildlife highway warning reflectors on behavior and mortality of white-tailed deer. Master thesis. Southern Illinois University at Carbondale, USA. 71 pp.

Groot Bruinderink, G. W. T. A. & Hazebroek, E. (1996). Ungulate Traffic Collisions in Europe. Conserv Biol. 10, 1059-1067.

Gulen, S., McCabe, G., Rosenthal, I., Wolfe, S. E., & Anderson, V. L. (2006). Evaluation of Wildlife Reflectors in Reducing Vehicle Deer Collisions on Indiana Interstate 80/90. FHWA/IN/JTRP-2006/18. West Lafayette, Indiana Department of Transportation and the U.S. Department of Transportation. 43 pp.

Gundersen, H., & Andreassen, H. P. (1998). The risk of moose *Alces alces* collision: A predictive logistic model for moose-train accidents. Wildlife Biol. 4, 103–110.

Gunson, K. E., Mountrakis, G., & Quackenbush, L. J. (2011). Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. J Environ Manage. 92, 1074–1082.

Hammond, C., & Wade, M. G. (2004). Deer avoidance: the assessment of real world enhanced deer signage in a virtual environment. Report No. 2004-13. Minnesota Department of Transportation, USA. 5 pp.

Hanggi, E. B., Ingersoll, J. F., & Waggoner, T. L. (2007). Color vision in horses *(Equus caballus*): Deficiencies identified using a pseudoisochromatic plate test. J Comp Psychol. 121, 65-72.

Hansen, L. (2009). Oh deer! Whitetail-vehicle accidents. Mo Med. 106, 412-412.

Harris, L. D., & Gallagher, P. B. (1989). New initiatives for wildlife conservation: The need for movement corridors. In: Preserving communities and corridors. Defenders of Wildlife (ed. G. Mackintosh), pp. 11-34. Washington, D. C, USA.

Harris, L.D., & Scheck, J. (1991). From implications to applications: The dispersal corridor principle applied to the conservation of biological diversity. In: Nature conservation the role of corridors (eds. D. A. Saunder and R. J. Hobbs), pp. 189-220. Surrey Beatty and Sons, Chipping Norton, Australia.

Hedlund, J. H., Curtis, P. D., Curtis, G., & Williams, A. F. (2004). Methods to reduce traffic crashes involving deer: what works and what does not. Traffic Inj Prev. 5, 122-131.

Hesse, G., & Rea, R.V. (2016). Quantifying wildlife vehicle collision underreporting on northern British Columbia highways (2004-2013): Unpublished report prepared for the BC Ministry of Transportation and Infrastructure, Canada. 53 pp.

Hessisches Landesamt für historische Landeskunde. (2018). https://www.lagis-hessen.de/de/subjects/browse/district/532/sn/ol. Accessed June 26 2018.

Hessisches Landesamt für Naturschutz, Umwelt und Geologie. (2018). http://atlas.umwelt.hessen.de/servlet/Frame/atlas/naturschutz/naturraum/karten/34_36.htm. Accessed June 26 2018.

Hildebrand, E., & Hodgson, K. (1995). Effectiveness of Optical Fences in Reducing Vehicle-Deer Collisions in New Brunswick. In: Proceedings of the Canadian Multidisciplinary Road Safety Conference IX. pp. 131-144. Quebec, Canada.

Hodson, N. L. (1962). Some Notes on the Causes of Bird Road Casualties. Bird Study. 9, 168-173.

Hofmann, R. R. (1989). Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia. 78, 443-457.

Honu, Y. A. K., & Gibson, D. J. (2006). Microhabitat factors and the distribution of exotic species across forest edges in temperate deciduous forest of southern Illinois, USA. J Torrey Bot Soc. 133, 255-266.

Hothorn, T., Brandl, R., & Müller, J. (2012). Large-scale model-based assessment of deer-vehicle collision risk. PLoS one. 7, e29510.

Hothorn, T., Müller, J., Held, L., Möst, L., & Mysterud, A. (2015). Temporal patterns of deer–vehicle collisions consistent with deer activity pattern and density increase but not general accident risk. Accident Anal Prev. 81, 143–152.

Huijser, M., McGowen, P. T., Camel, W., Hardy, A., Wright, P., & Clevenger, A. (2006). Animal Vehicle Crash Mitigation using advanced technology. Phase I: Review, Design and Implementation. Oregon Department of Transportation. Washington, D.C., USA. 292 pp.

Huijser, M. P., Kociolek, A., McGowen, P., Hardy, A., Clevenger, A.P., & Ament, R. (2007). Wildlife-vehicle collision and crossing mitigation measures: A toolbox for the Montana Department of Transportation. Bozeman: Western Transportation Institute, Montana, USA. 123 pp.

Huijser, M. P., & Kociolek, A. V. (2008). Wildlife-vehicle collision and crossing mitigation measures: A literature review for Blaine County, Idaho. Western Transportation Institute, Montana State University, Bozeman, Montana, USA. 106 pp.

Huijser, M. P., & McGowen, P. T. (2010). Reducing wildlife–vehicle collisions. In: Safe Passages: Highways, Wildlife, and Habitat Connectivity (eds. J. P. Beckman, A. P. Clevenger, M. P. Huijser, and J. A. Hilty.), pp. 51-74. Island Press, Washington, DC, USA.

Ingebrigtsen, D. K., & Ludwig, J. R. (1986). Effectiveness of Swareflex Wildlife Warning Reflectors in reducing deer-vehicle collisions in Minnesota. St. Paul, MN: Department of Natural Resources, USA. 6 pp.

Innovationspreis. (2018). http://innovationspreis.kunststoffe-chemie-brandenburg.de/preistraeger-2015/. Accessed June 26 2018.

Jared, D. (2002). Evaluation of Wild Animal Highway Warning Reflectors. Office of Materials and Research, Georgia Department of Transportation, USA. 10 pp.

Jordaan, S. M., Keith, D. W., & Stelfox, B. (2009). Quantifying land use of oil sands production: a life cycle perspective. Environ Res Lett. 4, 024004.

Kaluzinski, J. (1982). Composition of the food of Roe deer living in fields and the effect of their Feeding on Plant Production. Acta Theriol. 27, 457-470.

Kämmerle, J.-L., Brieger, F., Kröschel, M., Hagen, R., Storch, I., & Suchant, R. (2017). Temporal patterns in road crossing behaviour in roe deer (*Capreolus capreolus*) at sites with wildlife warning reflectors. PLoS one 12, e0184761.

Jones, B., & Kenward, M. G. (2014). Design and analysis of cross-over trials. CRC Press. 438 pp.

Knapp, K. K., Yi, X., Oakasa, T., Thimm, W., Hudson, E., & Rathmann, C. (2004). Deer-vehicle crash countermeasure toolbox: a decision and choice resource (No. DVCIC-02,). Midwest Regional University Transportation Center, Deer-Vehicle Crash Information Clearinghouse, University of Wisconsin-Madison, USA. 263 pp.

Kruidering A. M., Veenbaas, G., Kleijberg, R., Koot, G., Rosloot, Y., & van Jaarsveld, E. (2005). Leidraad faunavoorzieningen bij wegen. Delft, Nl: Rijkswaterstaa, Netherlands. 122 pp.

Ladstätter, K. (1974). Wildwarnreflektoren. Der Anblick. 29, 378.

Langbein, J. (2007). National deer-vehicle collisions project: England 2003–2005. Final report to the Highways Agency. The Deer Initiative, Wrexham, UK. 94 pp.

Langbein, J., Putman, R., Pokorny, B. (2011). Traffic collisions involving deer and other ungulates in Europe and available measures for mitigation. In: Ungulate management in Europe: problems and practices (eds. R. Putman, M. Apollonio, and R. Andersen), pp 215–259. Cambridge University Press, Cambridge, USA.

Lehtimaki, R. (1979). Elk mirrors and traffic. Deer and Traffic. Ministry of Agriculture and Forestry. Liikenneturva, Finland. 22 pp.

Litvaitis, J. A., & Tash, J. P. (2008). An approach toward understanding wildlife-vehicle collisions. Environ Manage. 42, 688-697.

Lutz, W. (1994). Ergebnisse der Anwendung eines sogenannten Duftzaunes zur Vermeidung von Wildverlusten durch den Straßenverkehr nach Gehege-und Freilandorientierungen. Z Jagdwiss. 40, 91-108.

Mader, H.-J. (1984). Animal habitat isolation by roads and agricultural fields. Biol Conserv. 29, 81-96.

Malo, J. E., Suarez, F., & Diez, A. (2004). Can we mitigate animal-vehicle accidents using predictive models? J Appl Ecol. 41, 701–710.

Marcoux, A., G. J. Hickling, S. J. Riley, & S. R. Winterstein. (2005). Situational and driver characteristics associated with deer–vehicle collisions in southeastern Michigan. In: Proceedings of the Wildlife Damage Management Conference 11 (eds. D. L. Nolte, & K. A. Fagerstone), pp. 246–255. National Wildlife Research Center, Fort Collins, USA.

Mastro, L. L., Conover, M. R., & Frey, S. N. (2008). Deer–vehicle collision prevention techniques. Hum-Wildl Conflicts. 2, 80–92.

Mata, C., Hervás, I., Herranz, J., Suarez, F., & Malo, J. E. (2005). Complementary use by vertebrates of crossing structures along a fenced Spanish motorway. Biol Conserv. 124, 397-405.

McLain, P.D. (1964). The story of the deer mirrors on the parkway. New Jers Outdoors. 15, 13–18.

Mitchell, B., Staines, B. W., & Welch, D. (1977). Ecology of red deer: a research review relevant to their management in Scotland. Institute of Terrestrial Ecology, Cambridge, UK. 102 pp.

Myczko, Ł., Sparks, T. H., Skórka, P., Rosin, Z. M., Kwieciński, Z., Górecki, M. T., & Tryjanowski, P. (2017). Effects of local roads and car traffic on the occurrence pattern and foraging behaviour of bats. Transport Res D-Tr E., 56, 222-228.

Mysterud, A., Larsen, P. K., Ims, R. A., & Østbye, E. (1999). Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Can J Zool. 77, 776–783.

Mysterud, A., Tryjanowski, P., & Panek, M. (2006). Selectivity of harvesting differs between local and foreign roe deer hunters: Trophy stalkers have the first shot at the right place. Biol Letters. 2, 632–635.

Ortega, Y. K., & Capen, D. E. (1999). Effects of forest roads on habitat quality for ovenbirds in a forested landscape. The Auk. 116, 937-946.

Pafko, F., & Kovach, B. (1996). Experience with deer reflectors. Trends in addressing transportation-related wildlife mortality. Minnesota Department of Transportation, Office of Environmental Services, Minnesota, USA. 10 pp.

Peris, S., Baquedano, R., Sánchez, A., & Pescador, M. (2005). Mortalidad del jabalí (*Sus scrofa*) en carreteras de la provincia de Salamanca (NO de España): ¿Influencia de su comportamiento social? Galemys. 17, 13–23.

Perz, S., Brilhante, S., Brown, F., Caldas, M., Ikeda, S., Mendoza, E., Overdevest, C., Reis, V., Reyes, J. F., Rojas, D., Schmink, M., Souza, C., & Walker, R. (2008). Road building, land use and climate change, prospects for environmental governance in the Amazon. Philos Trans R Soc B. 363, 1889–1895.

Porembinski, S., Szarynski, J., Mund, J. P. & Bartholt, W. (1996). Biodiversity and vegetation of small-sized inselbergs in a West African rain forest (Tal, Ivory Coast). J. Biogeogr. 23, 47– 55.

Putman, R. J. (1997). Deer and Road Traffic Accidents: Options for Management. J Environ Manage. 51, 43–57.

Putman, R. J. (1986). The Grazers: Ecology and Behaviour of the Common Stock. In Grazing in Temperate Ecosystems Large Herbivores and the Ecology of the New Forest (ed. R. J. Putman), pp. 27-59. Coorm Helm, London, UK.

Queal, L. M. (1968). Effectiveness of roadside mirrors in controlling deer-car accidents. Research and Development Report No. 137. Michigan Department of Conservation, USA. 9 pp.

Ramp, D., Caldwell, J., Edwards, K.A., Warton, D., & Croft, D.B. (2005). Modelling of wildlife fatality hotspots along the snowy mountain highway in New South Wales, Australia. Biol Conserv. 126, 474–490.

Ramp, D., & Croft, D. B. (2006). Do wildlife warning reflectors elicit aversion in captive macropods? Wildl Res. 33, 583–590.

Thomas, F., Schekahn, A., & Denzel, K. (2007). Regionales Entwicklungskonzept. Kasseler Institut für ländliche Entwicklung e.V. Wetzlar, Germany. 142 pp.

Riginos, C., Graham, M. W., Davis, M., Smith, C., & Johnson, A. (2015). Effects of Wildlife Warning Reflectors (“Deer Delineators”) on Wildlife-Vehicle Collisions in Central Wyoming. FHWA-WY-15/03F. Teton Research Institute, Jackson, WY, USA. 93 pp.

Riginos, C., Graham, M. W., Davis, M. J., Johnson, A. B., May, A. B., Ryer, K. J. & Hall, L. E. (2018). Wildlife warning reflectors and white canvas reduce deer–vehicle collisions and risky road-crossing behavior. Wildl. Soc. 42, 119-130.

Rodriguez, A., & Delibes, M. (1992). Current range and status of the Iberian lynx *Felis pardina* Temminck, 1824 in Spain. Biol Conserv. 6, 189-196.

Rodts, J., Holsbeek, L., Muyldermans, & S., België, V. (1998). Dieren onder onze wielen: Fauna en wegverkeer. Vubpress. Brüssel, Belgium. 190 pp.

Romin, L. A., & Dalton, L. B. (1992). Lack of response by mule deer to wildlife warning whistles. Wildlife Soc B. 20, 382-384.

Rudelstorfer, K., & Schwab, K. (1975). Optische Einrichtungen im Dienste der Verkehrssicherheit. University of Innsbruck, Austria. 57 pp.

Rutberg, A. T., & Naugle, R. E. (2008). Deer–vehicle collision trends at a suburban immunocontraception site. Hum-Wildl Conflicts. 2, 60-67.

Rytwinski, T., Soanes, K., Jaeger, J. A., Fahrig, L., Findlay, C. S., Houlahan, J., & van der Grift, E. A. (2016). How effective is road mitigation at reducing road-kill? A meta-analysis. PLoS one. 11, e0166941.

Santos, P., Mexia-de-Almeida, L. & Petrucci-Fonseca, F. (2004). Habitat selection by wild boar *Sus scrofa* L. In Alentejo, Portugal. Galemys. 16, 167-184.

Schafer, J. A., Carr, W. P., & Penland, S. (1985). Effectiveness of wildlife warning reflectors in reducing deer-vehicle accidents in Washington State. J Wildlife Manage. 19, 99–100.

Schilderwerk Beutha Inc. (2017). Der Wildwarnreflektor. http://www.halbkreisreflektor.de/. Accessed December 12 2017.

Schüttler, A. (1996). Der Kreis Höxter - eine Einführung. In: Der Kreis Höxter (ed. Mayr, A). pp. 1-13. Höxter, Germany.

Seiler, A. (2005). Predicting locations of moose–vehicle collisions in Sweden. J Appl Ecol. 42, 371–382.

Snow, N. P., Porter, W. F., & Williams, D. M. (2015). Underreporting of wildlife-vehicle collisions does not hinder predictive models for large ungulates. Biol Conserv. 181, 44–53.

Stafford, K. C., DeNicola, A. J., & Kilpatrick, H. J. (2003). Reduced abundance of Ixodes scapularis (*Acari Ixodidae*) and the tick parasitoid Ixodiphagus hookeri (*Hymenoptera Encyrtidae*) with reduction of white-tailed deer. J Med Entomol. 40, 642–652.

Stoner, D. (1925). The toll of the automobile. Science. 61, 56–57.

Storm, D. J., Nielsen, C. K., Schauber, E. M., & Woolf, A. (2007). Deer–human conflict and hunter access in an exurban landscape. Hum-Wildl Conflicts. 1, 53-59.

Stoyan, D. (2000). Gutachten zur Wirksamkeit des AWIWA-Sytems. Gutachten, Institut für Stochastik, Technical University Bergakademie Freiberg, Germany. 2 pp.

Strein, M., Burghardt, F., Haas, F. & Suchant, R. (2008). Pilotprojekt Elektronische Wildwarnanlage B292 bei Aglasterhausen. Forestry Research Institute Baden-Württemberg. Freiburg, Germany. 41 pp.

Sudharsan, K., Riley, S. J., & Winterstein, S. R. (2006). Relationship of autumn hunting season to the frequency of deer-vehicle collisions in Michigan. J Wildlife Manage. 70, 1161–1164.

Sullivan, T. L., Williams, A. F., Messmer, T. A., Hellinga, L. A., & Kyrychenko, S. Y. (2004). Effectiveness of temporary warning signs in reducing deer-vehicle collisions during mule deer migrations. Wildlife Soc B. 32, 907–914.

Tixier, H. & Duncan, P. (1996). Are European roe deer browsers? A review of variations in the composition of their diets. Rev Ecol. 51, 3-17.

Ujvári, M., Baagøe, H. J., & Madsen, A. B. (1998). Effectiveness of wildlife warning reflectors in reducing deer-vehicle collisions: a behavioral study. J Wildlife Manage. 62, 1094–1099.

van den Tempel, R. (1993). Vogelslachtoffers in het wegverkeer. Vogelbescherming Nederland, Ministerie van Verkeer en Waterstaat, Directoraat-Generaal Rijkswaterstaat. Netherland. 103 pp.

van der Ree, R., van der Grift, E., Gulle, N., Holland, K., Mata, C., & Suarez, F. (2007). Overcoming the barrier effect of roads–how effective are mitigation strategies? An international review of the use and effectiveness of underpasses and overpasses designed to increase the permeability of roads for wildlife. In: International Conference on Ecology and Transportation (eds. C. L. Irwin, P. Garrett, and K. P. McDermott), pp. 20-25. Arkansas, USA.

van der Ree, R., Smith, D. J., & Grilo, C. (Eds.). (2015). Handbook of road ecology. John Wiley & Sons, Ltd. New Jersey, USA.

van Gelder, J. J. (1973). A quantitative approach to the mortality resulting from traffic in a population of *Bufo bufo* L. Oecologia. 13, 93–95.

VerCauteren, K. C., & Pipas, M. J. (2003). A review of color vision in white-tailed deer. Wildlife Soc B. 31, 684–691.

Vincent, J. P., Bideau, E., Hewison, A. J. M., & Angibault, J. M. (1995). The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (*Capreolus capreolus*). J Zool. 236, 371-382.

Visintin, C., Van Der Ree, R., & McCarthy, M. A. (2016). A simple framework for a complex problem? Predicting wildlife–vehicle collisions. Ecol Evol. 6, 6409-6421.

Vos, C. C., & Chardon, J. P. (1998). Effects of habitat fragmentation and road density on the distribution pattern of the moor frog Rana arvalis. J Appl Ecol. 35, 44-56.

Waring, G. H., Griffis, J. L., & Vaughn, M. E. (1991). White-tailed deer roadside behavior, wildlife warning reflectors, and highway mortality. Appl Anim Behav. Sci. 29, 215–223.

Wood, P., & Wolfe, M. L. (1988). Intercept feeding as a means of reducing deer-vehicle collisions. Wildlife Soc B. 16, 376–380.

Zacks, J. L., & Budde, W. (1983). Behavioral investigations of color vision in the white-tailed deer, *Odocoileus virginianus*. Invest Ophthalmol Vis Sci Suppl. 24, 183.

ZRK Kassel. (2007). Landschaftsplan. http://www.zrk-info.de/zrk/index.php/lp?id=100. Accessed June 26 2018.

Chapter 2

Wildlife Warning Reflector's Potential to Mitigate Wildlife-Vehicle Collisions on Roads – A Review on the Evaluation Methods

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REVIEW
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Wildlife Warning Reflectors' Potential to Mitigate Wildlife-Vehicle Collisions—A Review on the Evaluation Methods

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Wildlife-vehicle collisions (WVC) produce considerable costs in road traffic due to human fatalities as well as ecological and economic losses. Multiple mitigation measures have been developed over the past decades to separate traffic and wildlife, to warn humans, or to prevent wildlife from entering roads. Among these, wildlife warning reflectors (WWR) have been frequently implemented, although their effectiveness remains a subject of discussion due to conflicting study results. Here we present a literature review on the effectiveness of WWR for $N = 76$ studies, including their methodological differences, such as the type of WWR (model and color), study conditions, and study designs. We used boosted regression trees to analyse WVC-data addressed in the literature to compare WWR effectiveness depending on the study design, study conditions, effective study duration, length of the tested sections, time period of the study, data source, reflector type, and animal species. Our analyses revealed no clear evidence for the effectiveness of WWR in preventing WVC. Instead, our meta-analysis showed that most studies indicating significant effects of WWR on the occurrence of WVC may be biased due to insufficiencies in study design and/or the approach of WVC data acquisition. Our computation of log response ratios (LRR_{WVC}) showed that only studies applying a before-after (BA) design concluded that WWR were effective. Moreover, BRT modeling revealed that only studies of <12 months effective study duration and <5 km test site length indicated that WWR might lower WVC. Based on the vulnerability to confounding factors of WWR-study designs applied in the past, this review suggests the standardization of study conditions, including a before-after control-impact (BACI) or a cross-over study design with spatial and temporal control sections, a minimum test site length and a minimum study duration.

Keywords: animal-vehicle collisions, deer-vehicle collisions, wildlife mirrors, roadside reflectors, deer mirrors, swareflex, strieter lite, van de ree

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INTRODUCTION

Since the beginning of the automobile era, wildlife-vehicle collisions (WVC) have strongly influenced the environmental impact of road traffic and have increasingly threatened both humans and wildlife (Stoner, 1925). Reliable data on economic and ecological costs is available to date for only a few European countries over the past three decades (cf. Langbein et al., 2011). For the year

1996 alone, in Europe 500,000 collisions with ungulates, 300 human fatalities and an economic loss of ca. one billion US dollars were estimated by Bruinderink and Hazebroek (1996). Two decades later, 263,000 officially reported WVC and an economic loss of almost 0.7 billion Euros were reported for Germany alone (GDV, 2017)[1]. The total damage in Europe overall can therefore be assumed to be far larger than in 1996. At present, a total of 800,000 WVC with ungulates is estimated for Germany, given that likely more than two-thirds of all collisions remain unreported, as reported for the US and Canada (Huijser and Kociolek, 2008; Snow et al., 2015; Hesse and Rea, 2016). However, WVC are not randomly distributed, but tend to accumulate in certain areas as a result of spatial and temporal factors (Gunson et al., 2011; Bíl et al., 2013). The duration of temporary WVC-hotspots is determined by diurnal and seasonal changes depending on species and climate conditions (Madsen et al., 2002; Compare et al., 2007). Furthermore, local differences in WVC-hotspots usually depend on species' habitat characteristics (Malo et al., 2004), type of road, and traffic volume (Clarke et al., 1998; van Langevelde and Jaarsma, 2009; Langbein et al., 2011; Beben, 2012). As mammals utilize landscapes at a different spatial scale than, for example, amphibians, predicting exact WVC-hotspots for these species is difficult (van Gelder, 1973; Ashley and Robinson, 1996; Madsen et al., 1998). Deer-vehicle collisions are the most common type of reported WVC in northern Europe (DeNicola et al., 2000; Rutberg and Naugle, 2008) and involve ~6% of the roe deer (*Capreolus capreolus*) spring population (Bruinderink and Hazebroek, 1996); or up to 264,000 animals in Germany every year (GDV, 2017)[2]. WVC-hotspots and temporal aggregations for this species are potentially due to habitat structure (Finder et al., 1999; Nielsen et al., 2003; McShea et al., 2008), seasonality (Hubbard et al., 2000), and perhaps lunar cycles (Steiner et al., 2014; Colino-Rabanal et al., 2018). Although WVC depend on both human and deer activities (Mysterud et al., 2004), deer-vehicle collisions have increased by 25% over the past decade, whereas all non-deer-vehicle collisions have decreased by 5–10% (Hothorn et al., 2015). The overall increase in WVC may therefore be due to an increase in deer population density rather than an increase in human activity or traffic intensity.

Mitigation measures (cf. Iuell et al., 2003; van der Ree et al., 2015) to reduce WVC on roads are often accompanied by high costs for construction and maintenance, including fencing, green bridges, or electric warning signs (Kruidering et al., 2005; Huijser et al., 2007a). Other, less costly measures (e.g., olfactory repellents, wildlife warning signs, speed limit reductions, or specific training to warn humans) have been shown to be ineffective in the long term, partly due to habituation (Elmeros et al., 2011; Beben, 2012). So far, only optical alarm devices, such as wildlife warning reflectors (WWR) have been occasionally reported to reduce WVC, but their effectiveness remains in question, as findings are mixed and concomitant conclusions are highly contradictory (cf. Brieger et al., 2016). Previous reviews have surveyed outcomes on the effectiveness of WWR and have sometimes conducted meta-analyses to include national and international published studies (D'Angelo and van der Ree, 2015: $N = 13$ studies; Brieger et al., 2016: $N = 23$ directly available studies, $N = 18$ indirectly available studies, $N = 12$ newspaper articles and $N = 37$ not accessible studies). However, we identified a considerable number of additional peer-reviewed studies which have not been evaluated, and which also focus on the effectiveness of WWR (Supplementary Table 1).

In this review we provide an extensive summary of research findings on the effectiveness of WWR ($N = 65$ directly available studies, $N = 13$ indirectly available studies); and excluded non-scientific public articles as sources. As far as we know, this is to date the most comprehensive review on the effectiveness of WWR, with almost twice as many studies than the next comprehensive review [cf. (D'Angelo and van der Ree, 2015) ($N = 13$ studies), and (Brieger et al., 2016) ($N = 41$ studies, 12 newspaper articles)]. In addition, we focused on methodological differences due to the variability in WWR models, such as manufacturer, reflector color, as well as study approaches, such as study designs and collision reports. This is the first study testing WWR, of which we are aware, that examines the relationship between study approaches and study results. We also aimed to identify minimal requirements for a successful study design in order to make further recommendations for effective studies on WWR efficiency. Consequently, we tested the hypotheses that: (H1) existing study results can be explained by the specifics of study designs, and (H2) a meta-analysis of previous studies identifies minimal requirements for a successful study design.

FUNDAMENTALS

Wildlife Warning Reflectors

Optical warning devices, such as WWR, are mounted along the road on guideposts oriented toward the road verge. WWR are intended to prevent wildlife from entering a road when a vehicle passes at night, its headlights reflecting off the WWR toward the road verge. The reflections from several WWR are supposed to create a "fence of light" in front of animals in close proximity to the moving vehicles. This is believed to alter the behavior of animals and interrupt their movement toward the road (e.g., Beilharz, 2017[3]; Schilderwerk Beutha, 2017). WWR have been distributed since the early 1960s and are now available in diverse construction types and in a variety of colors. Among the first models were the "Van de Ree" mirrors, developed in the Netherlands (McLain, 1964; Nettels, 1965), followed by the "Ruppert" reflectors (Queal, 1968). More commonly applied and tested are the models "Swareflex," developed by Swarovski in 1973 in Austria (Rudelstorfer and Schwab, 1975) and "Strieter Lite," developed by Strieter Corp. in 1994 in the United States (Barlow, 1997). Other WWR were developed by Bosch and GFT (Bosch, "WEGU," and "AWIWA" reflectors), both in Germany (Gladfelter, 1984; Ujvari et al., 1998).

[1] http://www.gdv.de/2016/11/wildunfaelle-erreichen-hoechststand-alle-zwei-minuten-kracht-es/. *Accessed* 08.02.2017.

[2] http://www.gdv.de/2016/11/wildunfaelle-erreichen-hoechststand-alle-zwei-minuten-kracht-es/. *Accessed* 08.02.2017.

[3] http://www.beilharz.eu/de/wildwarnreflektor.html. Accessed 08.02.2017.

Color Vision

WWR are most commonly produced in red, but also in white or amber colors (D'Angelo et al., 2006). Whereas humans are trichromatic and perceive red as a warning signal (Goldstein, 1942; Elliot et al., 2007), most mammals, including ungulates, are dichromatic with a high density of rods (Witzel et al., 1978; Jacobs et al., 1994, 1998). Thus, ungulates have one photo-pigment associated with a cone mechanism for short wavelengths with a peak between 450 and 460 nm (S-cone), and a second photo-pigment associated with a cone mechanism 167 for middle wavelengths with a peak of 537 nm (M/L-cone) (e.g., Carroll et al., 2001). Therefore, red light with a wavelength of 650 nm exceeds the visible range of ungulates (Jacobs et al., 1994; Yokoyama and Radlwimmer, 1998; Pürstl, 2006). Thus, recently developed WWR models have been adjusted accordingly, and are now produced in colors of shorter wavelengths, such as green and blue (e.g., Beilharz, 2017[4]; Brieger et al., 2017a,b; Kämmerle et al., 2017; Schilderwerk Beutha, 2017).

MATERIALS AND METHODS

Literature Survey and Study Selection

The available literature was surveyed systematically using the online databases ISI Web of Knowledge (webofknowledge.com) and Google Scholar (scholar.google.de). The search was conducted by combining the terms ("wildlife" OR "deer" OR "roadside" OR "animals") AND ("reflectors" OR "mirrors") using multiple languages (Dutch, Danish, German, Norwegian, Swedish, and Spanish). We additionally tested the names of various manufacturers of WWR (cf. Supplementary Table 1). All studies (including empirical studies and reviews) were filtered for their relevance regarding the effectiveness of WWR. Subsequently, we surveyed the reference lists of relevant studies for additional older studies which had not been recorded. In total, we found 76 publications evaluating the effectiveness of WWR between 1964 and 2017 (cf. Supplementary Table 1). Twelve of these studies were not accessible, but relevant information is presented indirectly through later studies in which they were cited.

Data Extraction and Data Processing

Each study was scanned for information on the reflector, reflector color, and manufacturer. If available, the respective species was documented and classified as cervid species, marsupial species, or other. All information on study duration (length in months), study location (e.g., field, enclosure, or laboratory) as well as the number and length in road distance of test- and control sites was listed. Additionally, we captured the effective study duration, which quantifies the effective duration of a test or control period, including or precluding the use of reflectors, respectively. Furthermore, the applied study design was identified [e.g., before-after (BA), control-impact (CI), before-after control-impact (BACI), cover/uncover(C/U), behavior, other) and, finally, the number of WVC was documented. We also collected information on the data source for counts of WVC (e.g., police, transportation administrations, research group or hunters) and the statistics used for analyzing the data (e.g., *t*-test, chi-square). To make possible an adequate comparison of observed occurrences between studies, we normalized each count of WVC to 1 year each of the effective study duration (time period of a test or control measurement) and 1 km of road distance (WVC_{norm}, $year^{-1}$ km^{-1}). In total, 41 sets of WVC data with and without reflectors were considered for our analysis (Supplementary Table 1). Using WVC_{norm}, we calculated the log response ratio (LRR) as an effect size measure of WWR-effectiveness, thus quantifying the effect of the mean outcome in the experimental group (i.e., with WWR) in comparison to the control (i.e., without WWR) as described by Hedges et al. (1999).The LRR represents a suitable metric for meta-analysis of count data, which can be easily compiled without knowledge of data variances and sample sizes of single studies (Borenstein et al., 2009).

Statistical Analysis

Statistical analyses were performed using the R system for statistical computing (R Core Team, 2018, version 3.4.3). The response variables WVC_{norm} and LRR_{WVC} were tested for normal distribution and homoscedasticity of variances (Zuur et al., 2010; Fox, 2015). Depending on the data structure of WVC_{norm}, we applied parametric (paired student's *t*-test) or non-parametric statistics (Mann-Whitney U-test) to test for mean differences between each test- and control- group (WWR vs. no WWR). In the case of LRR_{WVC}, we used a one-sample *t*-test to analyze whether the mean effect size was different from zero. Each time multiple comparisons were conducted we additionally implemented a Bonferroni correction. To model the significance of the study design and site conditions on the effect size of WWR, we applied a boosted regression tree (BRT) analysis. This machine learning procedure combines the regression tree approach (De'ath and Fabricius, 2000) with a boosting procedure aimed at achieving optimized model accuracy (Schapire, 2003). BRT analysis is suitable for the interpretation of ecological data as it can combine analysis of nominally and metrically-scaled data, and due to its robustness with respect to unbalanced designs, can accommodate missing data and implement interaction effects of independent variables. The interpretation of the model output is straightforward since the relative importance as well as fitted functions for each predictor variable in use can be computed (Elith et al., 2008). For this analysis we used the R package *gbm* in combination with BRT function *gbm.step*() as developed by Elith et al. (2008).We aimed to explain the variance in LRR_{WVC} and we therefore tested the importance of various possible predictors: (i) study design (BA, CI, BACI, CU); (ii) test road distance; (iii) effective study duration; (iv) data source for counts of WVC (authorities, hunters, scientists, others); (v) age of publication (1970s, '80s, '90s, 2000s, '10s); (vi) study region (North America, Europe, Australia); (vii) type of wildlife (cervids, marsupials, others); (viii) reflector type (Strieter, Swareflex, etc.); and (ix), reflector color (red, white, etc.,). Since the number of observations was too small to run a BRT model testing the importance of all possible predictors simultaneously [$N = 9$, reflector type, reflector color, study design, species, length of testing sites, study period, data source, effective study duration

[4] http://www.beilharz.eu/de/wildwarnreflektor.html. Accessed 08.02.2017

(i.e., times reflectors are "active") and study region], we applied a core model using study design, effective study duration and test distance as permanent predictors. To additionally select the most influential predictors from these three, we implemented a series of BRT models, in each case adding the two other possible predictors in all possible combinations. Variables were considered as predictors for the final model only when their relative importance was not below 5%. The final model was fitted as 10-fold replication and the results were averaged to present a mean outcome of the partially stochastic procedure.

RESULTS

Behavioral, Physiological, and Spectrometric Studies on the Effectiveness of WWR

Behavioral studies of the reactions of animals to WWR ($N = 10$) did not show any effect that would lower WVC or any reaction of animals that would decrease the risk of WVC. The reactions of different deer or marsupial species were examined mainly for Swareflex and Strieter Lite Warning Reflectors (e.g., Griffis, 1984; Zacks, 1985; D'Angelo et al., 2006; Ramp and Croft, 2006). No study found any flight behavior or increased vigilance of animals when WWR or other light sources were activated (e.g., Sheridan, 1991; Norman, 2001). If anything, D'Angelo et al. (2006) showed that deer were more likely to be involved in negative deer-vehicle interactions, i.e. that the chance of a collision between deer and approaching vehicles increased, when WWR were installed than in periods without reflectors. Moreover, spectrometric analyses of WWR showed that the reflected light intensity was infinitesimal even at short distances from the reflectors and was additionally diminished by the headlights of approaching vehicles (Sivic and Sielecki, 2001; Schulze and Polster, 2017).

Methodological Differences and Results of WWR Studies

In total, we found 76 publications evaluating the effectiveness of WWR between 1964 and 2017 (62 directly and 14 indirectly accessible, cf. Supplementary Table 1). Most studies ($N = 51$) conducted analyses of WWR in the field using either a before-after ($N = 29$), control-impact ($N = 5$), BACI ($N = 8$), or cover/uncover ($N = 10$) study design. Of these, 39 studies provided 41 data sets which could be standardized to WVC year^{-1} km^{-1} with and without reflectors. Information on study duration and road length of the study sites was available in 42 and 43 studies, respectively. Behavioral analyses of wildlife and WWR were conducted in 10 studies (e.g., Ujvari et al., 1998). Additionally, four studies analyzed optical response measures of cervids with respect to WWR effectiveness, but reflectors were not tested directly in these studies (Almkvist et al., 1980; Zacks and Budde, 1983; Martschuk, 2014; Brieger et al., 2017b), thus these studies were not considered further. Other studies used spectrometric ($N = 2$), physiological ($N = 1$), or meta- ($N = 1$) analyses to evaluate the efficacy of WWR (cf. Supplementary Table 1). Twenty studies concluded that WWR reduce WVC and 18 studies found no effect or no conclusion was provided (**Figure 1**), while only 15 datasets showed a decline in WVC. Moreover, 26 data sets demonstrated (and 38 studies concluded) that there was an increase in WVC after WWR implementation.

Wildlife warning reflector models evaluated in the literature were mainly Swareflex reflectors ($N = 39$). A slightly different model (Sivic and Sielecki, 2001), the Strieter Lite WWR, was tested in 16 studies (e.g., Barlow, 1997; Riginos et al., 2015, 2018). Other reflectors evaluated were WEGU ($N = 2$, e.g., Olbrich, 1984), AWIWA ($N = 2$, e.g., Voß, 2007), Bosch ($N = 2$, e.g., Gladfelter, 1984), Ruppert ($N = 1$, Queal, 1968), ITEK ($N = 1$, van den Berk, 2017), and Beutha reflectors ($N = 3$, Pluntke, 2014; Brieger et al., 2017a; Kämmerle et al., 2017) (cf. Supplementary Table 1). Study duration testing the effectiveness of WWR varied from 0.75 months (Ujvari et al., 1998) to 300 months (Sielecki, 2001), depending on the study approach (e.g., behavioral observations of Ujvari et al., 1998 compared to a before-after study design of Sielecki, 2001; cf. Supplementary Table 1). In summary, the majority of authors concluded that WWR were either ineffective ($N = 19$) or even (marginally) increasing WVC with WWR ($N = 26$). Other authors resumed that an effect remained undetected ($N = 7$). In contrast, twenty studies indicated a decreasing trend in WVC with WWR (**Figure 1**, Supplementary Table 1). All the studies differed greatly in their methodologies (**Table 1**). It is notable that statistical analyses comparing WVC with and without reflectors applying a before-after design led to a significant reduction in WVC after implementation of reflectors ($p < 0.05$). Other study approaches revealed a tendency toward increases in WVC (e.g., behavioral studies, BACI, cover/uncover, **Figure 1**) or at least no reductions in WVC after installation of WWR (**Figure 2**). Only 14 publications that included information on WVC year^{-1} km^{-1} concluded that WWR reduce WVC ($N = 13$ before-after, $N = 1$ control-impact) (cf. Supplementary Table 1).

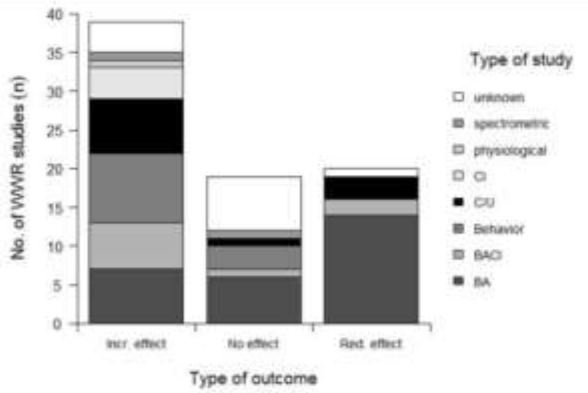

FIGURE 1 | Findings of the effectiveness of Wildlife Warning Reflectors (WWR) to reduce Wildlife-Vehicle collisions (WVC). Study designs included before-after (BA), control-impact (CI), before-after-control-impact (BACI), or cover/uncover (C/U) study approaches, as well as behavioral, physiological, and spectrometric evaluations. Unknown study designs ($N = 12$) did not provide information on the applied design or the information was not accessible.

TABLE 1 | Studies evaluating the effectiveness of wildlife warning reflectors (WWR) to reduce wildlife-vehicle collisions (WVC) on roads.

Study design	Statement	References
Before-after	–	Howe, 1967; Rudelstorfer and Schwab, 1975; Lück, 1977; Johnson, 1981; Paxson, 1981; Olbrich, 1984; Ingebrigtsen and Ludwig, 1986; Hildebrand and Hodgson, 1995; Pafko and Kovach, 1996; Schwabe et al., 2000; Stoyan, 2000; Grenier, 2002; Steiner, 2011; van den Berk, 2017
	*	Nettels, 1965; Beauchamp, 1970; O'Rourke, 1990; Johnson et al., 1993; Jared, 2002; Voß, 2007; Christensen, 2016
	+	McLain, 1964; Ladstätter, 1974; Dalton and Stranger, 1990; Waring et al., 1991; Sielecki, 2001; Binetruy and Kenny, 2005; Pluntke, 2014; Riginos et al., 2015
Control-impact	+	Ekblom, 1979; Gilbert, 1982; Reeve and Anderson, 1993; Cottrell, 2003; Bertwistle, 2009
Before-after control-impact	–	Lehtimaki, 1979; Gladfelter, 1984
	*	Boyd, 1966
	+	Queal, 1968; Gordon, 1969; Aspinall, 1994; Rogers and Premo, 2004; Gulen et al., 2006
Cover/uncover	–	Schafer et al., 1985; Fjeld and Antonsen, 1999; Lien Aune, 2004
	*	Barlow, 1997; Riginos et al., 2015
	+	Armstrong, 1992; Ossinger and Schafer, 1992; Ford and Villa, 1993; Libjå and Gundersen, 2001; Woodard et al., 1973; Woodham, 1991; Reeve and Anderson, 1993
Behavior	*	Konings, 1986
	+	Griffis, 1984; Zacks, 1985, 1986; Sheridan, 1991; Ujvari et al., 1998; D'Angelo et al., 2006; Ramp and Croft, 2006; Brieger et al., 2017a; Kämmerle et al., 2017
Physiology	+	Norman, 2001
Spectrometry	+	Sivic and Sielecki, 2001; Schulze and Polster, 2017
No information	*	Müller, 1977; Williamson, 1980; White, 1983; Kofler, 1984; Janssen and Claus, 1996; Pepper et al., 1998
	+	Garver, 1976; Mah, 1989; Scholten et al., 1989; Hester, 1991; Pepper, 1999

Studies are arranged by study design (i.e., before-after, control-impact, before-after control-impact, cover/uncover, behavior, physiology, spectrometry and without information on the study design). Studies were further arranged by the statement of the author on the effectiveness of the reflectors to lower WVC (–), increase WVC (+) or with no conclusion provided or found (*).

Effects of Study Characteristics on the Outcome of WWR Efficiency

Based on 41 datasets presented in 39 studies, a quantitative analysis of the effectiveness of WWR on mitigation of WVC and its dependence on study conditions was applied. With respect to BRT modeling, the pre-selection of predictors revealed insignificance of the variables *study region* (mean relative importance: 0.1%), *reflector type* (1.9%), *reflector color* (0.0%), and the considered *species* (0.0%). Accordingly, the final model included five predictor variables and explained, on average, 23.2% of the variance observed in LRR_{WVC} (**Figure 3**). *Study design* was identified as the most influential predictor (mean relative importance: 32.7%) and the BRT revealed considerable differences between fitted values for the class *before-after* design in comparison to other study designs (**Figure 3**). The *time of the study release* as well as the *testing site length* of tested road segments indicated their relative importance for the accurate prediction of LRR_{WVC} observed (22.1% and 23.1%, respectively; **Figure 3**). Fitted values of LRR_{WVC} were generally higher using data from earlier published studies (1970–1990) and lower for more recent studies. With respect to *effective testing site length*, the fitted function showed a peak for the short road lengths studies (below 5 km) but the explanatory power was inconclusive for distances > ~15 km (**Figure 3**). Finally, the factor *data source* of WVC and *effective study duration* explained marginal degrees of the observed variance (relative importance: 14.0 and 8.2%,

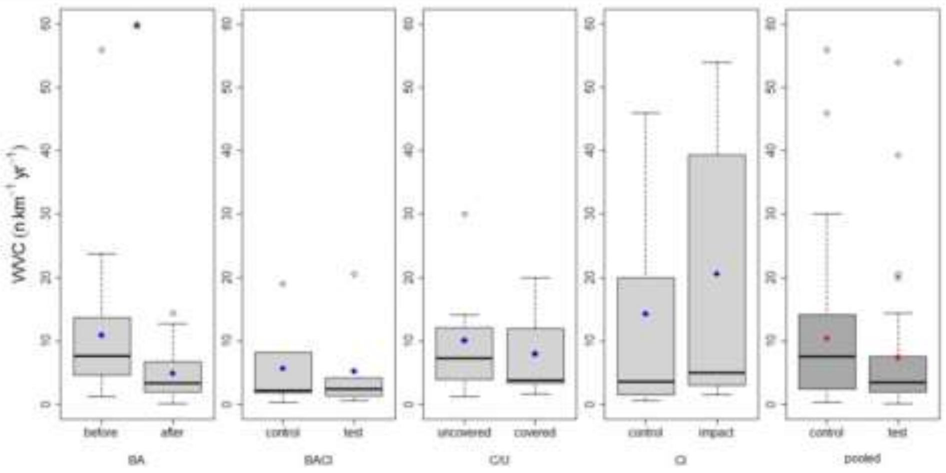

FIGURE 2 | Boxplots showing the influence of Wildlife Warning Reflectors (WWR) on Wildlife-Vehicle collisions (WVC) with respect to the study design. Data was standardized to WVC year^{-1} km^{-1} for both with and without reflectors. Studies performing a before-after (BA) comparison showed a significant reduction in WVC-data ($p < 0.05$). Before-after control-impact (BACI), covered/uncovered studies (C/U), as well as control-impact (CI) studies, did not show any significant effect of WWR on WVC-data. All standardized data comparing WVC year^{-1} km^{-1} for both, with and without reflectors WVC did not show any significant effect of WWR on WVC-data (pooled).

respectively). Fitted values of LRR_{WVC} varied slightly between datasets; for instance, those obtained from authorities, or data collected directly by scientists. The fitted function given for study duration followed the same curve as that of the road distance curve, with a high value plateau for low study durations (below 12 months) and a neutral prediction value above 20 months (**Figure 3**). Our statistical analyses, including BRT modeling, identified *before-after* study design, *effective study duration* <12 months and *effective testing sites length* <5 km as most influential variables on the tested "effectiveness" of reflectors.

DISCUSSION

The results of both the review and the analysis of WVC-data from literature indicated that the effectiveness of WWR remains questionable and that the observed effect of WWR on WVC largely depended on other factors such as study design, effective study duration, and effective testing site length.

According to our meta-analyses the reflector model (1.9%) or the color of the reflectors (0.0%) did not indicate any influence on WWR. However, the risk of WVC varies during the year and the time of day, with high risks during the rutting season, as well as in the morning and first hours of the night (Hothorn et al., 2015). As ungulates, such as roe deer, prefer open areas and agricultural fields during the night (Mysterud et al., 1999a,b), the frequency of road crossings increases during darkness (Hothorn et al., 2015). Therefore, scotopic and mesopic vision play an important role in the life of ungulates with diurnal patterns (Hanggi et al., 2007), concomitant with greater rod density and better light perception in the range of blue and blue-green (Szél et al., 1996; VerCauteren and Pipas, 2003). From this perspective, the value of long-wavelength WWR is questionable and the likelihood of a reduction of WVC can be argued given the lack of animals' ability to perceive colors in these wavelengths (VerCauteren and Pipas, 2003). Modern WWR, produced and marketed in the past decade, are primarily blue (e.g., Brieger et al., 2017a; Beilharz, 2017[5]; Kämmerle et al., 2017; Schilderwerk Beutha, 2017). However, independent studies evaluating the effectiveness of modern WWR in the field as well as the influence of blue light on feeding behavior in roe deer have not found any effect of the reflectors, either in reducing WVC directly or resulting in aversion or increased vigilance in roe deer (Brieger et al., 2017a,b; Kämmerle et al., 2017). Moreover, spectrometric analyses of WWR models have shown that the reflected light intensity is already very low at distances near the devices (Sivic and Sielecki, 2001) and reflector intensity is further overlaid by the headlights of approaching vehicles (Schulze and Polster, 2017). This applies especially to colored WWR (Sivic and Sielecki, 2001). Thus, it is doubtful that the light reflected from WWR has a sufficient intensity to elicit any reaction in animals at all.

Interestingly, some studies as well as observations by local hunters report their positive experiences with various models of WWR, including red models. A temporary reduction in WVC after installation of WWR may be explained by chance or by naturally oscillating fluctuations in population densities related, e.g., to hunting effort and food supply (Fryxell et al., 1991, 2010). Animals may also react aversively to something "new" in their environment (i.e., "novel object," cf. Forkman et al., 2007), so their reaction could be simply to the presence of the posts on which reflectors are mounted. In this case, the color of the reflector would not matter. Riginos et al. (2018) reported that carcass rates decreased by 33% when

[5]http://www.beilharz.eu/de/wildwarnreflektor.html. Accessed 08.02.2017

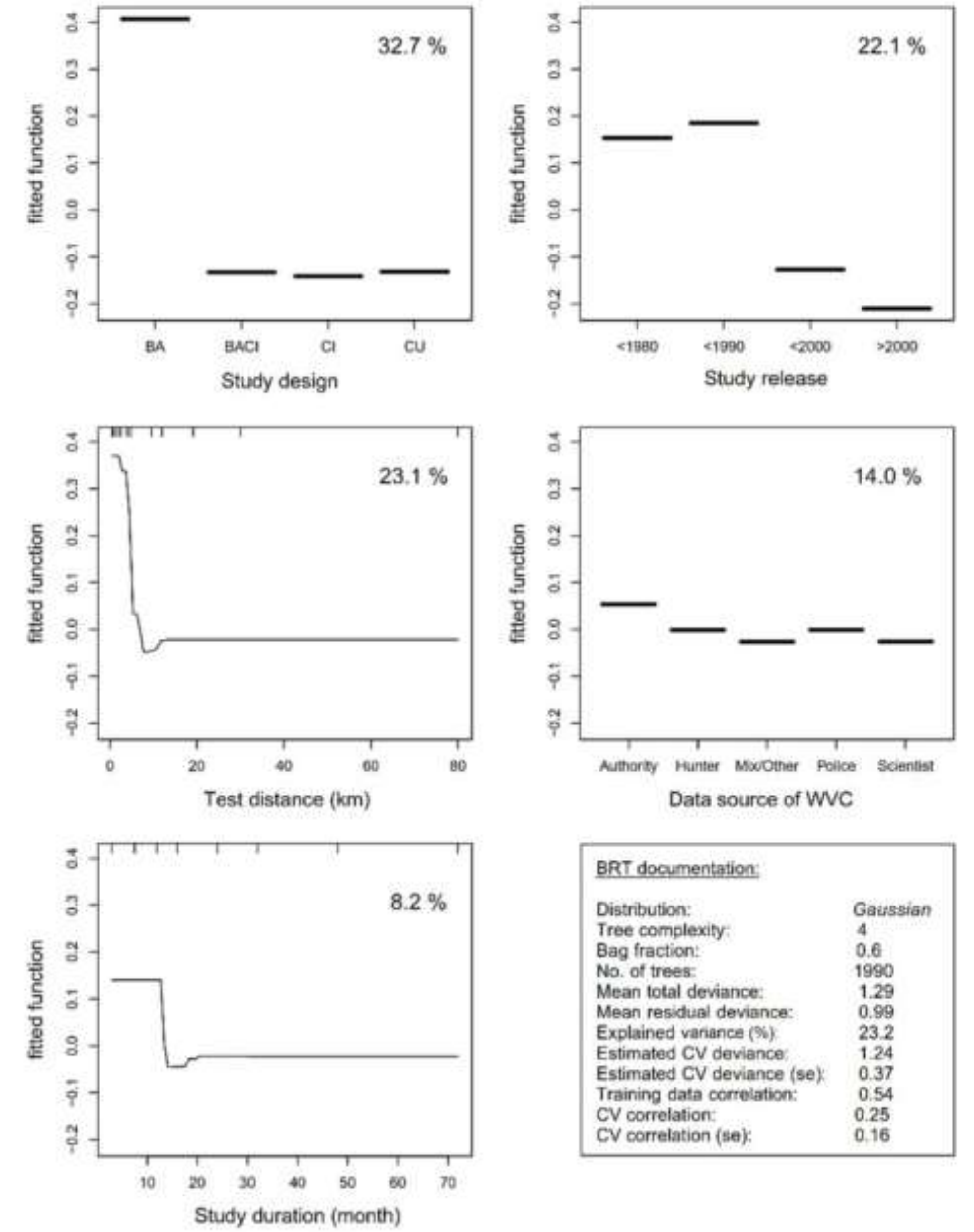

FIGURE 3 | Partial response plots of the five explanatory variables in the boosted regression tree (BRT) model including BRT documentation, such as explanatory variance of the model (23.2%), and values indicating the relative influence of the explained variance in the BRT model, for each variable respectively. Study designs included before-after (BA), before-after control-impact (BACI), control-impact (CI), and cover/uncover (CU) approaches. Data source was separated by authority from which data were obtained, i.e., transportation administration, road authorities), hunters, mix/other (i.e., more than one data source was used), police (i.e., WVC which were officially reported to the local police station) and scientists.

delineator posts were covered with white canvas bags compared to uncovered reflectors, but carcass rates were 32% lower with uncovered reflectors than with posts covered with black canvas bags. Thus, white canvas and reflectors might stand out more from the surrounding landscape than black. However, the animals could be expected to become habituated to the presence of these objects over time, with a resulting decline in their effectiveness. Reduction in WVC may also be due to the influence of the reflectors on the behavior of drivers rather than on the behavior of animals (Zacks, 1985), as the light intensity from the direct reflection to the driver is far larger than the reflection to the surroundings of the road (Schulze and Polster, 2017). An increased attention of drivers to wildlife near the road has been reported for studies testing deer-whistles, resulting in decreasing WVC (Zacks, pers. comm. 2015). However, the response of drivers to WWR has not been evaluated. It is also possible that the reflectors serve as a warning device that influences driver behavior (Rowden et al., 2008), but habituation might be expected as has been shown for wildlife warning signs (Huijser et al., 2007b).

BRT modeling showed that especially short studies, with <12 months of effective study duration and <5 km test sites and a before-after approach, showed a decrease in WVC with WWR. Thus, we could confirm our hypotheses that (H1) study results can rather be explained by the specifics of study designs than by the presence of WWR. Additionally, we can partly confirm our second hypothesis (H2) that examination of previous studies made it possible to infer minimal requirements for a successful study design: before-after study design, effective study duration <12 months and effective testing sites length <5 km as the most influential variables on the tested "effectiveness" of reflectors.

Before-after study designs most often detected a decrease in WVC with WWR, but it is possible that control and testing periods may not have used the same season. Activity patterns of ungulates are reflected in WVC peaks, especially during the rutting season of each species (Allen and McCullough, 1976; Lavsund and Sandegren, 1991; Hothorn et al., 2015). There could be a decrease in animals' vigilance during this period. A WVC peak during dusk and dawn, especially in the darker seasons (Steiner et al., 2014), in which high traffic volumes—such as during rush hours—coincide with an increase in the activity phase of animals. Thus, studies including all activity periods of animals are more likely to include all variables (e.g., mating season or fawning) that may influence the reactions of wildlife to oncoming vehicles. Although Brieger et al. (2016) note that a before-after study design requires at least 8 years of study to gain solid data on the effectiveness of WWR to reduce WVC, a longer study duration could be confounded by environmental changes or population fluctuations over that time period and thus affect the outcome of studies testing the effectiveness of WWR (Fryxell et al., 2010; Brieger et al., 2016).

LRR_{WVC} analyses showed that only studies applying a before-after study design found a decrease in WVC with WWR. When studies that applied the before-after or control-impact designs were omitted, WWR did not lower WVC. Moreover, BRT models showed that the applied study design explains most of the variance (>30%). Studying the impact of a single treatment in a paired study design usually takes the form of studying a population before and after a treatment or by studying two very similar populations or locations (Morrison et al., 2008). However, other potential factors influencing a change may complicate the interpretation of experiments, increasing the Type II error, as heterogeneity results in the confounding of experimental errors (Underwood, 1997; Morrison et al., 2008). Study designs such as before-after or control-impact designs lack the independence of different levels of single treatments and true replication (Morrison et al., 2008). Thus, although there may be no statistical problem with the study and the null hypotheses is rejected, a potential change after the implementation of a treatment cannot simply be assigned to that impact, but may be due to other factors such as weather, crop rotation, etc., (Underwood, 1997; Morrison et al., 2008). Therefore, results comparing the number of WVC before and after the implementation of WWR, as well as comparing test sites with control sites, must be treated with caution due to discontinuity in time or space. In these, BACI and cross-over study designs provide a remedy, as they have the highest inferential strength for assessing impacts on the environment (Green, 1979; Underwood and Chapman, 2003; Roedenbeck, 2007).

In addition to a number of influencing variables such as *reflector model*, *reflector color* or *effective testing site length* in road distance and *effective study duration*, the *type of data collection* also seems to affect the results of studies testing the effectiveness of WWR. BRT analyses showed that data sources influence the variance in the model by 15%. Also, the opinion of the authors can influence study results. While Gladfelter (1984) stated that WWR reduced the number of WVC significantly, he compared test and control sites that differed strongly in WVC numbers, challenging the control-impact approach. Moreover, WVC differed among test sites after installation of WWR; thus not all test sites showed a reduction in WVC after implementation. When his data were standardized, WVC changed only from 1.86 WVC $year^{-1}$ km^{-1} without WWR and 1.39 $year^{-1}$ km^{-1} with WWR (cf. Supplementary Table 1). Similar issues apply to the study conducted by Hildebrand and Hodgson (1995). While WVC were rather low before installation of WWR at two test ($N = 1$ WVC) and control sites ($N = 2$ WVC), numbers increased to 3 WVC $year^{-1}$ at the test sites and 2.75 WVC $year^{-1}$ at the control sites after installation. Standardizing this data to the test site length, WVC actually increased from 0.38 WVC $year^{-1}$ km^{-1} without reflectors to 0.6 WVC $year^{-1}$ km^{-1} with reflectors. With so few observations, a test for significance is not actually possible. However, the authors stated that they found a non-significant reduction in WVC comparing test and control sites, and concluded that WWR are effective in reducing WVC. Olbrich (1984) compared test sites that he maintained. Although WVC differed strongly among test sites after installation and no statistical test was applied, he concluded that WWR reduce WVC. In additional examples of previous study limitations, Pafko and Kovach (1996) compared data before and after installation of WWR, yet without proper information on WVC before the study and with an invalid type of data collection. However, the authors concluded that WWR effectively reduced WVC. Other studies have also failed to provide data on the numbers of WVC before installation of WWR (e.g., Nettels, 1965). For example Grenier (2002) conducted a meta-analysis including data from different highway and transportation agencies. He concluded that WWR are effective in reducing WVC, although it remains unclear which studies he considered, as studies without any effect of WWR were excluded.

CONCLUSIONS

The effectiveness of WWR remains doubtful, due to conflicting study results and questionable study designs, especially using the before-after approach. BRT modeling indicated that only studies with <12 months effective study duration and <5 km test sites found a decrease in WVC with WWR. Moreover, LRR_{WVC} analyses showed that only studies applying a before-after approach concluded that WWR was effective. This design however, lacks the independence that would accrue from different levels of single treatments and true replication (Morrison et al., 2008). Thus, a potential change after the implementation of a treatment cannot simply be assigned to that impact, but to other factors as well. (Underwood, 1997; Morrison et al., 2008). Additionally, analyses of physiological abilities and spectrometric requirements in the literature provide evidence that most mammals cannot effectively perceive red light and that reflected light has insufficient intensity to elicit any reaction in animals that would lead to a decreased risk of WVC. Thus, to include as many explanatory variables, but also to exclude as many confounding factors (environmental biases) as possible, a BACI or cross-over design (Roedenbeck, 2007; Morrison et al., 2008) is advisable. Furthermore, predictive variables such as test site length, effective study duration, and data source influenced the variance observed in LRR_{WVC}. Additionally, behavioral observations of animals reacting to WWR including all activity periods, especially WVC-peak seasons, are recommended for further studies testing the effectiveness of modern WWR.

AUTHOR CONTRIBUTIONS

AB: Idea for this publication, Literature Survey, Data Collection, Data Analyses, Statistics, Writing the manuscript; PA: Statistics, comments on the manuscript; TV: Project idea, Organization of funding, comments on the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00037/full#supplementary-material

REFERENCES

Alfreider, M., and Mühlegger, S. (2010). *Konstruktion einer Wildwarner-Messanlage.* Diploma thesis, Höhere technische Bundeslehranstalt Jenbach.

Allen, R. E., and McCullough, D. R. (1976). Deer-car accidents in southern Michigan. *J. Wildl. Manage.* 40, 317–325. doi: 10.2307/3800431

Almkvist, B., André, T., Ekblom, S., and Rempler, S. A. (1980). *Slutrapport Viltolycksprojekt. Swedish National Road Administration, TU146:1980-05.* Borlänge.

Armstrong, J. J. (1992). *An Evaluation of the Effectiveness of Swareflex Deer Reflectors.* Downsview, CA: Ontario Ministry of Transportation. 18.

Ashley, E. P., and Robinson, J. T. (1996). Road mortality of amphibians, reptiles and other wildlife on the Long Point Causeway, Lake Erie, Ontario. *Can. Field Nat.* 110, 403–412.

Aspinall, I. (1994). *Evaluation of Wildlife Warning Reflectors.* Kew Victoria: VicRoads. 39.

Barlow, C. (1997). "Performance evaluation of wildlife reflectors in British Columbia," in *Proceedings of the Second Roads, Rails and the Environment Workshop*, eds A. P. Clevenger, K. Wells, and B. C. Revelstoke (Victoria, BC), 62–67.

Beauchamp, D. (1970). *Deer Mirror Evaluation. W-51-R-15. California Department of Fish and Game.* California. 8.

Beben, D. (2012). Crossings for animals – an effective method of wild fauna conservation. *J. Environ. Eng. Landsc.* 20, 86–96. doi: 10.3846/16486897.2012.662753

Bertwistle, J. (2009). *An Assessment of Strieter Lite Reflectors.* Jasper Alberta, AB. 9.

Bil, M., Andrášik, R., and Janoška, Z. (2013). Identification of hazardous road locations of traffic accidents by means of kernel density estimation and cluster significance evaluation. *Acct. Anal. Prev.* 55, 265–273. doi: 10.1016/j.aap.2013.03.003

Binetruy, L., and Kenny, B. (2005). *Animal Collision Countermeasures on rural Alberta Highways.* Calgaray, AB: EBA Engineering Consultans Ltd. 24.

Borenstein, M., Hedges, L. V., Higgins, J. P. T., and Rothstein, H. R. (eds.). (2009). "Effect sizes based on means," in *Introduction to Meta-Analysis* (Chichester: John Wiley & Sons, Ltd.). doi: 10.1002/9780470743386.fmatter

Boyd, R. J. (1966). Deer mirrors. Do they work? *Outdoor Facts* 6, 44–45.

Brieger, F., Hagen, R., Kröschel, M., Hartig, F., Petersen, I., Ortmann, S., et al. (2017a). Do roe deer react to wildlife warning reflectors? A test combining a controlled experiment with field observations. *Eur. J. Wildlife Res.* 63, 72. doi: 10.1007/s10344-017-1130-5

Brieger, F., Hagen, R., Vetter, D., Dormann, C. F., and Storch, I. (2016). Effectiveness of light-reflecting devices: a systematic reanalysis of animal-vehicle collision data. *Accid. Anal. Prev.* 97, 242–260. doi: 10.1016/j.aap.2016.08.030

Brieger, F., Kämmerle, J.-L., Martschuk, N., Ortmann, S., and Hagen, R. (2017b). No evidence for a "warning effect" of blue light in roe deer. *Wildlife Biol.* 17. doi: 10.2981/wlb.00331

Bruinderink, G., and Hazebroek, E. (1996). Ungulate traffic collisions in Europe. *Conserv. Biol.* 10, 1059–1067. doi: 10.1046/j.1523-1739.1996.10041059.x

Carroll, J., Murphy, C. J., Neitz, M., Hoeve, J. N., and Neitz, J. (2001). Photopigment basis for dichromatic color vision in the horse. *J. Vis.* 1, 80–87. doi: 10.1167/1.2.2

Christensen, K. (2016). *Evaluation of Strieter-Lite Wild Animal Highway Warning Reflector System TM on Reducing Vehicle-Animal Collisions.* Montana Department of Transportation. 9.

Clarke, G. P., White, P. C. L., and Harris, S. (1998). Effects of roads on badger (*Meles meles*) populations in south-west England. *Biol. Conserv.* 86, 117–124. doi: 10.1016/S0006-3207(98)00018-4

Colino-Rabanal, V. J., Langen, T. A., Peris, S. J., and Lizana, M. (2018). Ungulate: vehicle collision rates are associated with the phase of the moon. *Biodivers Conserv.* 27, 681–694. doi: 10.1007/s10531-017-1458-x

Compare, D. L., Sturaro, E., Cocca, G., and Ramanzin, M. (2007). An analysis of roe deer (*Capreolus capreolus*) traffic collisions in the Belluno province, eastern Italian Alps. *Italian J. Anim. Sci.* 6, 848–850. doi: 10.4081/ijas.2007.1s.848

Cottrell, B. H. (2003). *Evaluation of Deer Warning Reflectors in Virginia. Technical Assistance Report.* Virginia Transportation Research Council in cooperation with US Department of Transportation and Federal Highway Administration. VTRC. 21.

Dalton, L. B., and Stranger, M. C. (1990). *Effectiveness of Swareflex Reflectors at Reducing Mule Deer-Vehicle Collisions.* Price, UT: Utah Division of Wildlife Resources. 7.

D'Angelo, G., D'Angelo, J. G., Gallagher, G. R., Osborn, D. A., Miller, and Warren, R. J. (2006). Evaluation of wildlife warning reflectors for altering white-tailed deer behavior along roadways. *Wildlife Soc. B.* 34, 1175–1183. doi: 10.2193/0091-7648(2006)34[1175:EOWWRF]2.0.CO;2

D'Angelo, G., and van der Ree, R. (2015). "Use of reflectors and auditory deterrents to prevent wildlife-vehicle collisions," in *Handbook of Road Ecology*, eds R. van der Ree, D. J. Smith, and C. Grilo (Chichester: John Wiley & Sons, Ltd). 213–218.

De'ath, G., and Fabricius, K. E. (2000). Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology* 81, 3178–3192. doi: 10.1890/0012-9658(2000)081[3178:CARTAP]2.0.CO;2

DeNicola, A. J., VerCauteren, K. C., Curtis, P. D., and Hyngstrom, S. E. (2000). *Managing White-Tailed Deer in Suburban Environments.* Ithaca, NY: Cornell Cooperative Extension.

Ekblom, S. (1979). Undersökning av viltspeglars effect. Viltolycksprojektet (VIOL). Rapport nr 30. Stockholm: Statens Vägverk. 14.

Elith, J., Leathwick, J. R., and Hastie, T. (2008). A working guide to boosted regression trees. *J. Anim. Ecol.* 77, 802–813. doi: 10.1111/j.1365-2656.2008.01390.x

Elliot, A. J., Maier, M. A., Moller, A. C., Friedman, R., and Meinhardt, J. (2007). Color and psychological functioning: the effect of red on performance attainment. *J. Exp. Psychol. Gen.* 136, 154–168. doi: 10.1037/0096-3445.136.1.154

Elmeros, M., Winbladh, J. K., Andersen, P. N., Madsen, A. B., and Christensen, J. T. (2011). Effectiveness of odour repellents on red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*): a field test. *Euro J. Wildlife Res.* 57, 1223–1226. doi: 10.1007/s10344-011-0517-y

Finder, R. A., Roseberry, J. L., and Woolf, A. (1999). Site and landscape conditions at white-tailed deer/vehicle collision locations in Illinois. *Landscape Urban Plan.* 44, 77–85. doi: 10.1016/S0169-2046(99)00006-7

Fjeld, G., and Antonsen, K. (1999). *Viltreflektorers Virkning på Elgens Kryssing av vei.* Master thesis, Høgskolen i Hedmark, Evenstad. 30.

Ford, S. G., and Villa, S. L. (1993). *Reflector Use and the Effect They Have on the Number of Mule Deer Killed on California Highways:* Final Report, Sacramento, CA: California Department of Transportation. 12.

Forkman, B., Boissy, A., Meunier-Salaün, M. C., Canali, E., and Jones, R. B. (2007). A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiol. Behav.* 92, 340–374. doi: 10.1016/j.physbeh.2007.03.016

Fox, J. (2015). *Applied Regression Analysis and Generalized Linear Models.* Thousand Oaks, CA: Sage Publications.

Fryxell, J. M., Hussell, D. J. T., Lambert, A. B., and Smith, P. C. (1991). Time lags and population fluctuations in white-tailed deer. *J. Wildlife Manage.* 3, 377–385.

Fryxell, J. M., Packer, C., McCann, K., Solberg, E. J., and Sæther, B.-E. (2010). Resource management cycles and the sustainability of harvested wildlife populations. *Science* 328, 903–906. doi: 10.1126/science.1185802

Garver, J. (1976). *Report on 1974-1975 roadside mirror study along Illinois Route 148 in Crab Orchard Refuge.* Jonesbro, IL: Illinois Department of Conservation.

Gilbert, J. R. (1982). *Evaluation of Deer Mirrors for Reducing Deer-Vehicle Collisions.* Final Report. Springfield, VA: Federal Highway Administration. 14.

Gladfelter, L. (1984). *Effect of Wildlife Highway Warning Reflectors on Deer-Vehicle Accidents. Project HR-210*, Boone, IO: Iowa Highway Research Board. 11.

Goldstein, K. (1942). Some experimental observations concerning the influence of colors on the function of the organism. *Am. J. Phys. Med. Rehab.* 21, 147–151.

Gordon, D. F. (1969). Deer mirror- a clearer picture. *Outdoor Facts* 6, 77–79.

Green, R. H. (1979). *Sampling Design and Statistical Methods for Environmental Biologists.* New York, NY; Chichester; Brisbane; Toronto: John Wiley & Sons.

Grenier, R. H. (2002). *A Study of the Effectiveness of Strieter-Lite® Wild Animal Highway Warning Reflector Systems.* Commissioned report for Strieter Corporation. 19.

Griffis, J. L. (1984).*Effects of Swareflex Wildlife Highway Warning Reflectors on Behavior and Mortality of White-Tailed Deer.* Master thesis, Southern Illinois University at Carbondale, USA. 71.

Gulen, S., McCabe, G., Rosenthal, I., Wolfe, S. E., and Anderson, V. L. (2006). *Evaluation of Wildlife Reflectors in Reducing Vehicle Deer Collisions on Indiana Interstate 80/90. FHWA/IN/JTRP-2006/18.* West Lafayette, IN: Indiana Department of Transportation and the U.S. Department of Transportation.

Gunson, K. E., Mountrakis, G., and Quackenbush, L. J. (2011). Spatial wildlife-vehicle collision models: a review of current work and its application to transportation mitigation projects. *J. Environ. Manage.* 92, 1074–1082. doi: 10.1016/j.jenvman.2010.11.027

Hanggi, E. B., Ingersoll, J. F., and Waggoner, T. L. (2007). Color vision in horses (*Equus caballus*): deficiencies identified using a pseudoisochromatic plate test. *J. Comp. Psychol.* 121, 65–72. doi: 10.1037/0735-7036.121.1.65

Hedges, L. V., Gurevitch, J., and Curtis, P. S. (1999). The meta-analysis of response ratios in experimental ecology. *Ecology* 80, 1150–1156.

Hesse, G., and Rea, R. V. (2016). *Quantifying Wildlife Vehicle Collision Underreporting on Northern British Columbia Highways (2004-2013): Unpublished Report Prepared for the BC Ministry of Transportation and Infrastructure.* 53.

Hester, R. A. (1991). *Evaluation of Roadside Reflectors in Preventing Deer-Vehicle Collisions at Bruce Nuclear Power Development.* Report No. CPS-07017-0002. Ontario Hydro. Environmental Prot. Dept.

Hildebrand, E., and Hodgson, K. (1995). "Effectiveness of optical fences in reducing vehicle-deer collisions in new brunswick," in *Proceedings of the Canadian Multidisciplinary Road Safety Conference IX* (Montreal, QC). 131–144.

Hothorn, T., Müller, J., Held, L., Möst, L., and Mysterud, A. (2015). Temporal patterns of deer-vehicle collisions consistent with deer activity pattern and density increase but not general accident risk. *Accid. Anal Prev.* 81, 143–152. doi: 10.1016/j.aap.2015.04.037

Howe, S. (1967). Deer mirrors save deer. . . and cars. *Maine Fish Game* 29–30.

Hubbard, M. W., Danielson, B. J., and Schmitz, R. A. (2000). Factors influencing the location of deer-vehicle accidents in Iowa. *J. Wildlife Manage.* 64, 707–713. doi: 10.2307/3802740

Huijser, M. P., Kociolek, A., McGowen, P. T., Hardy, A., Clevenger, A. P., and Ament, R. J. (2007a). *Wildlife-vehicle Collisions and Crossing Mitigation Measures: a Toolbox for the Montana Department of Transportation.* Helena, MT: Montana Department of Transportation.

Huijser, M. P., and Kociolek, A. V. (2008). *Wildlife-vehicle Collision and Crossing Mitigation Measures: a Literature Review for Blaine County, Idaho.* Bozeman, MT: Western Transportation Institute; Montana State University.

Huijser, M. P., McGowen, P. T., Fuller, J., Hardy, A., and Kociolek, A. (2007b). *Wildlife-Vehicle Collision Reduction Study: Report to Congress.* No. FHWA-HRT-08-034. 251.

Ingebrigtsen, D. K., and Ludwig, J. R. (1986). *Effectiveness of Swareflex Wildlife Warning Reflectors in reducing Deer-Vehicle Collisions in Minnesota.* St. Paul, MN: Department of Natural Resources.

Iuell, B., Bekker, H. G. J., Cuperus, R., Dufek, J., Fry, G., Hicks, C., et al. (2003). "Wildlife and traffic: a European handbook for identifying conflicts and designing solutions," in *COST 341 Habitat Fragmentation due to Transportation Infrastructure.*

Jacobs, G. H., Deegan, I. I., J. F., Neitz, J., Murphy, B. P., Miller, K. V., and Marchinton, R. L. (1994). Electrophysiological measurements of spectral mechanisms in the retinas of two cervids: white-tailed deer (*Odocoileus virginianus*) and fallow deer (*Dama dama*). *J. Comp. Physiol.* 174, 551–557.

Jacobs, G. H., Deegan, J. F., and Neitz, J. A. (1998). Photopigment basis for dichromatic color vision in cows, goats, and sheep. *Vis. Neurosci.* 15, 581–584.

Janssen, L., and Claus, K. (1996). *Wildspiegels: Beheer van Wildspiegels. Vadamecum Natuurtechniek.* Brüssel, BE: Ministerie van de Vlaamse Gemeenschap.

Jared, D. (2002). *Evaluation of Wild Animal Highway Warning Reflectors.* Office of Materials and Research; Georgia Department of Transportation. 10.

Johnson, D. (1981). Deer Reflectors Update. Newsletter Minn. Dept. Transport. *District.* 2, 1.

Johnson, P. M., Nolan, B., and Moore, B. (1993). *The Use of Wildlife Reflectors as a Means of Reducing Kangaroo Road Deaths–the Proserpine Rock-Wallaby*

Experience. Brisbane, QLD: Queensland Department of Environment and Heritage. 18.
Kämmerle, J.-L., Brieger, F., Kröschel, M., Hagen, R., Storch, I., and Suchant, R. (2017). Temporal patterns in road crossing behaviour in roe deer (Capreolus capreolus) at sites with wildlife warning reflectors. *PLoS ONE* 12:e0184761. doi: 10.1371/journal.pone.0184761
Kofler, H. (1984). Aufstellung von Wildwarnreflektoren. *Wildbiolog. Ges. München*. 45, 16–17.
Konings, P. (1986). *Een Onderzoek Naar de Werking en Effectiviteit van Wildspiegels Voor Dassen*. Arnhem, NL: Studentenverslag Rijksinstituut voor Naturbeheer.
Kruidering, A. M., Veenbaas, G., Kleijberg, R., Koot, G., Rosloot, Y., and van Jaarsveld, E. (2005). *Leidraad faunavoorzieningen bij wegen*. Delft: Rijkswaterstaat.
Ladstätter, K. (1974). Wildwarnreflektoren. *Der Anblick* 29, 378.
Langbein, J., Putman, R., Pokorny, B., Apollonio, M., and Andersen, R. (2011). "Traffic collisions involving deer and other ungulates in Europe and available measures for mitigation," in *Ungulate Management in Europe: Problems and Practices*, eds R. Putman, M. Apollonio and R. Andersen (Cambridge: Cambridge University Press), 215–259.
Lavsund, S., and Sandegren, F. (1991). Moose-vehicle relations in Sweden. *Alces* 27, 118–126.
Lehtimaki, R. (1979). *Elk Mirrors and Traffic. Deer and Traffic. Ministry of Agriculture and Forestry*. 22.
Libjå, L. E., and Gundersen, M. (2001). *Viltreflektorers Virkning på Elgens Kryssing av Veg*. Master thesis, Høgskolen i Hedmark, Evenstad. 24.
Lien Aune, L. (2004). *Viltreflektorers Virkning på Elgens Kryssing av vei*. Master thesis, Høgskolen i Hedmark, Evenstad. 30.
Lück, F. W. (1977). *Untersuchung an einer Swareflex-Wildwarnreflektoranlage im Reinhardswald*. Diploma thesis, University of Göttingen, Germany. 101.
Madsen, A. B., Fyhn, H. W., and Prang, A. (1998). *Traffic Killed Animals in Landscape Ecological Planning and Research. Trafikdræbte dyr i Landskabsøkologisk Planlægning og Forskning*. DMU Rapport 228. Århus. 43.
Madsen, A. B., Strandgaard, H., and Prang, A. (2002). Factors causing traffic killings of roe deer Capreolus capreolus in Denmark. *Wildlife Biol.* 8, 55–61.
Mah, L. (1989). *Wildlife Warning Reflectors*. Report No. ABTR/RD-89/08. *Alberta Transportation and Utilities*. 13.
Malo, J. E., Suarez, F., and Diez, A. (2004). Can we mitigate animal-vehicle accidents using predictive models? *J. Appl. Ecol.* 41, 701–710. doi: 10.1111/j.0021-8901.2004.00929.x
Martschuk, N. (2014). *Wirkung von Licht Unterschiedlichen Spektralbereichs auf Rehe (Capreolus capreolus): Ein Beitrag zur Erforschung der Effektivität von Wildwarnreflektoren*. Master thesis, Albert-Ludwigs-University Freiburg, Germany. 54.
McLain, P. D. (1964). The story of the deer mirrors on the parkway. *New Jers Outdoors* 15, 13–18.
McShea, W., Stewart, C., Kearns, L., Licciol, S., and Kocka, D. (2008). Factors affecting autumn deer–vehicle collisions in a rural Virginia county. *Hum. Wildl. Confl.* 2, 110–121. Available online at: http://www.jstor.org/stable/24875111
Morrison, M. L., Block, W. M., Strickland, M. D., Collier, B. A., and Peterson, M. J. (2008). *Wildlife Study Design*. New York, NY: Springer Science & Business Media.
Müller, S. (1977). *Protection des Routes contre le Gibier: Surfaces Reflechissantes*. Rapport intermédiaire *No*. 3. Berne. 26.
Mysterud, A., Langvatn, R., and Stenseth, N. C. (2004). Patterns of reproductive effort in male ungulates. *J. Zool.* 264, 209–215. doi: 10.1017/S0952836904005618
Mysterud, A., Larsen, P. K., Ims, R. A., and Østbye, E. (1999a). Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? *Can. J. Zool.* 77, 776–783.
Mysterud, A., Lian, L. B., and Hjermann, D. Ø. (1999b). Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. *Can. J. Zool.* 77, 1486–1493.
Nettels, K. (1965). Mirrors to reduce deer-auto collisions. *Outdoor Indiana* 8, 22–25.
Nielsen, C. K., Anderson, R. G., and Grund, M. D. (2003). Landscape influences on deer-vehicle accident areas in an urban environment. *J Wildlife Manage.* 67, 46–51. doi: 10.2307/3803060
Norman, P. C. (2001). *Reducing Deer-Vehicle Collisions by the Use of Reflectors: A Summary of Current Research and Literature*. Howard County Department of Recreation and Parks. 8.
O'Rourke, S. (1990). *Report on Effectiveness of 'Swareflex Wildlife Warning Reflectors' After 9 Month Trial on State Highway 18*. North of Coonamble, NSW.
Olbrich, P. (1984). Untersuchung der wirksamkeit von wildwarnreflektoren und der eignung von wilddurchlässen. *Z. Jagdwiss.* 30, 101–116. doi: 10.1007/BF02312729
Ossinger, M., and Schafer, J. A. (1992). *Discovery Bay Deer Reflector Study: Progress Report for May 1992*. Washington State Department of Transportation. 7.
Pafko, F., and Kovach, B. (1996). "Experience with deer reflectors," in *Minnesota Experience with Deer Reflectors* (Minneapolis: Minnesota Department of Transportation), 7.
Paxson, R. (1981). *Flashing Lights Seem to Save Lives of Deer*. Des Moines Sunday Register.
Pepper, H. W. (1999). *Road Traffic Accidents and Deer Reflectors: a Comparative Trial of the Effectiveness of Standard Red and New Blue/Green Roadside Reflectors at Preventing Motor Vehicle and Wild Deer Collisions*. Internal report on Project 257. Forestry Commission, Forest Research, London.
Pepper, H. W., Chadwick, A. H., and Packer, J. J. (1998). Deer *Reflectors and Road Traffic Accidents through Forestry Commission Forests: A Review of Traffic Accident Records of Roads where Deer Warning Reflectors have Been Installed*. Appendix to contract report VC 0317. Ministry of Agriculture Fisheries and Foods, London.
Pluntke, D. (2014). *Halt bei Blau ist Schlau: Auswertung der Wildunfallzahlen im Landkreis Oldenburg sowie Rückschlüsse auf die Wirksamkeit Blauer Wildwarnreflektoren als Präventionsmaßnahme*. Bachelor thesis, Leibniz University Hannover; University of Veterinary Medicine, Hannover, Germany. 31.
Pürstl, A. (2006). *Tierärztliches Gutachten zum Farbsehvermögen von Rot- und Rehwild*. Vienna: Tierambulanz Türkenschanzplatz. 7.
Queal, L. M. (1968). *Effectiveness of Roadside Mirrors in Controlling Deer-Car Accidents*. Research and Development Report No. 137. Michigan Department of Conservation. 9.
R Core Team (2018). *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. Available online at: https://www.R-project.org/
Ramp, D., and Croft, D. B. (2006). Do wildlife warning reflectors elicit aversion in captive macropods? *Wildl Res.* 33, 583–590. doi: 10.1071/WR05115
Reeve, A. F., and Anderson, S. H. (1993). Ineffectiveness of Swareflex reflectors at reducing deer-vehicle collisions. *Wildlife Soc. B.* 21, 127–132.
Riginos, C., Graham, M. W., Davis, M. J., Johnson, A. B., May, A. B., Ryer, K. J., et al. (2018). Wildlife warning reflectors and white canvas reduce deer-vehicle collisions and risky road-crossing behavior. *Wildl. Soc. Bull.* 42, 119–130. doi: 10.1002/wsb.862
Riginos, C., Graham, M. W., Davis, M., Smith, C., and Johnson, A. (2015). *Effects of Wildlife Warning Reflectors ("Deer Delineators") on Wildlife-Vehicle Collisions in Central Wyoming. FHWA-WY-15/03F*. Jackson, WY: Teton Research Institute. 93.
Roedenbeck, I. A. E. (2007). *Landscape-Scale Effects of Roads on Wildlife*. Ph.D. thesis, University of Giessen. 157.
Rogers, E., and Premo, D. (2004). *An Ecological Landscape Study of Deer-Vehicle Collisions in Kent County, Michigan*. Report for the Michigan State Police, Office of Highway Safety and Planning. White Water Associates, Inc, Amasa, MI. 56.
Rowden, P., Steinhardt, D., and Sheehan, M. (2008). Road crashes involving animals in Australia. *Accident Anal. Prev.* 40, 1865–1871. doi: 10.1016/j.aap.2008.08.002
Rudelstorfer, K., and Schwab, K. (1975). *Optische Einrichtungen im Dienste der Verkehrssicherheit*. Innsbruck: University of Innsbruck. 57.
Rutberg, A. T., and Naugle, R. E. (2008). Deer-vehicle collision trends at a suburban immunocontraception site. *Hum. Wildlife Conflicts* 2, 60–67.
Schafer, J. A., Carr, W. P., and Penland, S. (1985). Effectiveness of wildlife warning reflectors in reducing deer-vehicle accidents in Washington State. *J. Wildlife Manage.* 19, 99–100.
Schapire, R. E. (2003). "The boosting approach to machine learning: an overview," in *Nonlinear Estimation and Classification. Lecture Notes in Statistics*, Vol. 171, eds D. D. Denison, M. H. Hansen, C. C. Holmes,

B. Mallick, and B. Yu (New York, NY: Springer). doi: 10.1007/978-0-387-21579-2_9

Schilderwerk Beutha (2017). Available online at: http://www.halbkreisreflektor.de/. (Accessed February 08, 2017).

Scholten, G., Loveland, G., and Spinazole, J. (1989). *Effectiveness of Swareflex Reflectors*. Idaho Department of Fish and Game.

Schulze, C., and Polster, J. U. (2017). "Wirkungsweise von Wildwarnern," in *Forschung Straßenbau und Straßenverkehrstechnik 1127/2017*, ed Bundesministerium für Verkehr und digitale Infrastruktur (Bremen), 96.

Schwabe, K. A., Schuhmann, P. W., Tonkovich, M. J., and Wu, E. (2000). An analysis of deer-vehicle collisions: the case of Ohio. *Hum. Conflicts Wildl. Econ. Considerations*. 91–103.

Sheridan, G. J. (1991). *The Effectiveness of Swareflex and Wegu Brand Wildlife Reflectors in Deterring Perameles gunnii (barred bandicoot) from Crossing a Section of Roadway*. Ballarat, VIC: Ballarat University College. 23.

Sielecki, L. E. (2001). "Evaluating the effectiveness of wildlife accident mitigation installations with the wildlife accident reporting system (WARS) in British Columbia," in *Proceedings of the 2001 International Conference on Ecology and Transportation*, eds C. L. Irwin, P. Garrett, and K. P. McDermott (Raleigh, NC: Center for Transportation and the Environment; North Carolina University), 473–489.

Sivic, A., and Sielecki, L. E. (2001). *Wildlife Warning Reflectors: Spectrometric Evaluation*. Victoria, BC: Ministry of Transportation and Highways. 24.

Snow, N. P., Porter, W. F., and Williams, D. M. (2015). Underreporting of wildlife-vehicle collisions does not hinder predictive models for large ungulates. *Biol. Conserv.* 181, 44–53. doi: 10.1016/j.biocon.2014.10.030

Steiner, W. (2011). "Wildtierbestände und Verkehr-Reduktion von verkehrsbedingtem Fallwild," in *Forschungsarbeiten des Oesterreichischen Verkehrssicherheitsfonds 008*, ed Bundesministerium Für Verkehr (Vienna: Innovation und Technologie), 139.

Steiner, W., Leisch, F., and Hackländer, K. (2014). A review on the temporal pattern of deer–vehicle accidents: impact of seasonal, diurnal and lunar effects in cervids. *Accident Anal. Prev.* 66, 168–181. doi: 10.1016/j.aap.2014.01.020

Stoner, D. (1925). The toll of the automobile. *Science* 61, 56–57. doi: 10.1126/science.61.1568.56

Stoyan, D. (2000). *Gutachten zur Wirksamkeit des AWIWA-Sytems*. Gutachten. Institut für Stochastik; Technical University Bergakademie Freiberg. 2.

Szél, Á., Röhlich, P., Caffé, A. R., and van Veen, T. (1996). Distribution of cone photoreceptors in the mammalian retina. *Microsc. Res Tech.* 35, 445–462. doi: 10.1002/(SICI)1097-0029(19961215)35:6<445::AID-JEMT4>3.0.CO;2-H

Ujvari, M., Baagøe, H. J., and Madsen, A. B. (1998). Effectiveness of wildlife warning reflectors in reducing deer-vehicle collisions: a behavioral study. *J. Wildl. Manage.* 62, 1094–1099. doi: 10.2307/3802562

Underwood, A. J. (1997). Environmental decision-making and the precautionary principle: what does this principle mean in environmental sampling practice? *Landsc. Urban Plan.* 37, 137–146.

Underwood, A. J., and Chapman, M. G. (2003). Power, precaution, Type II error and sampling design in assessment of environmental impacts. *J. Exp. Mar. Biol. Ecol.* 296, 49–70. doi: 10.1016/S0022-0981(03)00304-6

van den Berk, M. (2017). *Proefprojekt*. Available online at: http://www.itek.co.at/fusszeile/vertriebspartner/proefproject/. (Accessed February 08, 2017).

van der Ree, R., Smith, D. J., and Grilo, C. (2015). *Handbook of Road Ecology*. Oxford, UK: John Wiley & Sons.

van Gelder, J. J. (1973). A quantitative approach to the mortality resulting from traffic in a population of *Bufo bufo* L. *Oecologia* 13, 93–95. doi: 10.1007/BF00379622

van Langevelde, F., and Jaarsma, C. F. (2009). Modeling the effect of traffic calming on local animal population persistence. *Ecol Soc.* 14, 39. doi: 10.5751/ES-03061-140239

VerCauteren, K., and Pipas, M. (2003). A review of color vision in white-tailed deer. *Wildl. Soc. Bull.* 31, 684–691. Available online at: http://www.jstor.org/stable/3784587

Voß, H. (2007). *Unfallhäufungen mit Wildunfällen: Modellversuch im Oberbergischen Kreis*. Berlin: The German Insurers. 36.

Waring, G. H., Griffis, J. L., and Vaughn, M. E. (1991). White-tailed deer roadside behavior, wildlife warning reflectors, and highway mortality. *Appl. Anim. Behav. Sci.* 29, 215–223. doi: 10.1016/0168-1591(91)90249-W

Watson, M., and Klingel, J. (2000). *Assessing Methods for Reducing Deer-Vehicle Accidents*. Available online at: http://www.wildlife.state.nm.us/conservation/habitat-handbook/ (Accessed February 08, 2017).

White, G. C. (1983). *Sample Size Requirements for Reflector Study*. Los Alamos: Los Alamos National Laboratory.

Williamson, L. (1980). Reflectors reduce deer-auto collisions. *Outdoor News Bull.* 34, 2.

Witzel, D. A., Springer, M. D., and Mollenhauer, H. H. (1978). Cone and rod photoreceptors in the white-tailed deer *Odocoileus virginianus*. *Am. J. Vet. Res.* 39, 699–701.

Woodard, T. N., Reed, D. F., and Pojar, T. M. (1973). *Effectiveness of Swareflex Wildlife Warning Reflectors in Reducing Deer-Vehicle Accidents*. Colorado Division of Wildlife. 5.

Woodham, D. (1991). *Evaluation of Swareflex Wildlife Warning Reflectors*. Denver, CO: Colorado Department of Transportation. 6.

Yokoyama, S., and Radlwimmer, F. B. (1998). The "five-sites" rule and the evolution of red and green color vision in mammals. *Mol. Biol. Evol.* 15, 560–567. doi: 10.1093/oxfordjournals.molbev.a025956

Zacks, J. L. (1985). *An Investigation of Swareflex Wildlife Warning Reflectors*. Okemos, MI: U.S. Department of Transportation; Federal Highway Administration and Michigan Department of Transportation. 41.

Zacks, J. L. (1986). *Do White-tailed Deer Avoid Red? An Evaluation of the Premise Underlying the Design of Swareflex Wildlife Reflectors*. Washington, DC: Transportation Research Record 1075; National Research Council. 35–36; 41–43.

Zacks, J. L., and Budde, W. (1983). Behavioral investigations of color vision in the white-tailed deer, *Odocoileus virginianus*. *Invest. Ophthalmol. Visual Sci. Suppl.* 24, 24–183.

Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14. doi: 10.1111/j.2041-210X.2009.00001.x

Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Supplemental materials

Table 2. 2. Literature results on the effectiveness of wildlife warning reflectors (WWR) to reduce wildlife-vehicle collisions (WVC). References were accessible either directly (N = 62) or indirectly (N = 14, i.e. study details were cited by other authors), including information on WWR model, study design and results. Studies containing information on WVC for more than one study design (N = 2) are presented separately (e.g. 55a, 55b). Data provided were standardized to WVC year^{-1} km^{-1} for both, without and with reflectors. Additionally, information on study design (i.e. before-after (BA), control-impact (CI), before-after control-impact (BACI), cover/uncover (C/U), behavior (Beh.), physiology (Physiol.), spectrometry (spec.) and without information on the study design(NA)), duration (months), effective study duration [months] (i.e. period when reflectors were "active"), as well as length of test in distance (ts) and control sites (cs) (m). Authors find either a reduction in WVC after implementation of WWR (-), an increase (+) or no conclusion was provided or found (*).

No.	Author	Title	Year	Reference	WWR model	WVC year^{-1} km^{-1} without reflectors	WVC year^{-1} km^{-1},with reflectors	Study design	study duration [months]	effective study duration [months]	length ts [km]	length cs [km]	Conclusion of authors
1	Alfreider and Mühlegger	Konstruktion einer Wildwarner-Messanlage	2010	indirect	Swareflex			spec.					*
2	Armstrong	An evaluation of the effectiveness of Swareflex deer reflectors	1992	direct	Swareflex	3.90	3.41	C/U	12.50	6.00	4.10	4.10	+
3	Aspinall	Evaluation of wildlife warning reflectors	1994	direct	Swareflex	19.00	20.50	BACI	24.00	12.00	12.00	7.00	+
4	Barlow	Performance evaluation of wildlife reflectors in British Columbia	1997	direct	Strieter Lite			C/U					*

5	Beauchamp	Deer Mirror Evaluation	1970	direct	unknown	5.18	1.04	BA	84.00	24.00	4.83	4.83	*
6	Bertwistle	Review of Strieter-Lite Wild Animal Highway Warning Reflector System	2009	direct	Strieter Lite	46.00	54.00	CI	48.00	48.00	0.50	0.50	+
7	Binetruy and Kenny	Animal Collision Countermeasures on rural Alberta Highways	2005	direct	Strieter Lite			BA					+
8	Boyd	Deer mirrors-do they work?	1966	direct	Van de Ree	2.00	2.50	BACI	48.00	12.00	4.00	NA	*
9	Brieger et al.	Do roe deer react to wildlife warning reflectors? A test combining a controlled experiment with field observations	2017	direct	Beutha			Beh.					+
10	Christensen	Evaluation of Strieter-Lite Wild Animal Highway Warning Reflector System TM on Reducing Vehicle-Animal Collisions	2014	direct	Strieter Lite	7.56	6.67	BA	72.00	24.00	2.25	2.25	*
11	Cottrell	Evaluation of deer warning reflectors in Virginia	2003	direct	Strieter Lite	3.53	2.99	CI	28.00	28.00	13.50	12.00	+
12	Dalton and Stranger	Effectiveness of swareflex reflectors at reducing mule deer-vehicle collisions	1990	direct	Swareflex	12.07	11.20	BA	96.00	24.00	46.80	46.80	+
13	D'Angelo	Evaluation of Wildlife Warning Reflectors for Altering White-Tailed Deer Behavior Along Roadways	2006	direct	Strieter Lite			Beh.					+
14	Ekblom	Undersökning av viltspeglar effekt	1979	direct	Van de Ree	1.43	1.51	CI	32.00	32.00	80.00	80.00	+

15	Fjeld and Antonsen	Viltreflektorers virkning på elgens kryssing av vei	1999	direct	Swareflex			C/U					-
16	Ford and Villa	Reflector Use and the Effect the have on the Number of Mule Deer killed in California Highways. Final Report	1993	direct	Swareflex	7.27	10.08	C/U	15.00	7.50	12.80	12.80	+
17	Garver	Report on 1974-1975 roadside mirror study along Illinois Route 148 in Crab Orchard Refuge	1976	indirect (Waring 1991)	Van de Ree			NA					+
18	Gilbert	Evaluation of deer mirrors for reducing deer-vehicle collisions	1982	direct	Van de Ree	0.52	5.00	CI	34.00	34.00	9.60	0.80	+
19	Gladfelter	Effect of wildlife highway warning reflectors on deer-vehicle accidents	1984	direct	Swareflex, Bosch	1.86	1.39	BACI	48.00	32.00	12.00	6.43	-
20	Gordon	Deer Mirror- a clearer picture	1969	direct	Van de Ree	8.23	4.17	BACI	24.00	12.00	4.00	4.00	+
21	Grenier	A study of the effectiveness of Strieter-Lite® wild animal highway warning reflector systems	2002	direct	Strieter Lite			BA					-
22	Griffis	Effects of Swareflex wildlife highway warning reflectors on behavior and mortality of white-tailed deer	1984	direct	Swareflex	6.88	6.25	Beh.	18.00	16.00	0.80	0.80	+
23	Gulen et al.	Evaluation of Wildlife Reflectors in Reducing Vehicle Deer Collisions on Indiana Interstate 80/90	2006	direct	Strieter Lite			BACI					+

24	Hester	Evaluation of Roadside Reflectors in Preventing Deer-Vehicle Collisions at Bruce Nuclear Power Development	1991	indirect (Armstrong 1992)	Swareflex			NA					+
25	Hildebrand and Hodgson	Effectiveness of Optical Fences in Reducing Vehicle-Deer Collisions in New Brunswick	1995	direct	Swareflex	0.38	0.60	BA	132.00	60.00	5.00	6.40	-
26	Howe	Deer Mirrors Save Deer.....and Cars	1967	indirect (Gilbert 1982)	Van de Ree			BA					-
27	Ingebrigtsen and Ludwig	Effectiveness of Swareflex Wildlife Warning Reflectors in reducing deer-vehicle collisions in Minnesota	1986	direct	Swareflex	23.75	2.03	BA	48.00	24.00	1.60	1.60	-
28	Janssen and Claus	Wildspiegels	1996	indirect	unknown			NA					*
29	Jared	Evaluation of Wild Animal Highway Warning Reflectors	2002	direct	Swareflex	2.50	3.75	BA	84.00	12.00	0.80	0.80	*
30	Johnson	Deer Reflectors Update	1981	indirect (Griffis 1984)	Swareflex	20.00	3.13	BA	24.00	12.00	1.60	1.60	-
31	Johnson et al.	The use of wildlife reflectors as a means of reducing kangaroo road deaths–the Proserpine rock-wallaby experience	1993	direct	Swareflex	56.00	8.00	BA	10.00	5.00	0.50	0.50	*
32	Kämmerle et al.	Temporal patterns in road crossing behaviour	2017	direct	Beutha			Beh.					+
33	Kofler	Aufstellung von Wildwarnreflektoren	1984	direct	Swareflex			NA					*

34	Konings	Een onderzoek naar de werking en effectiviteit van wildspiegels voor dassen	1986	direct	Van de Ree			Beh.					*
35	Ladstätter	Wildwarnreflektoren	1974	direct	Swareflex	5.89	1.19	BA	18.00	12.00	36.00	36.00	-
36	Lehtimaki	Elk mirrors and traffic	1979	direct	unknown			BACI					+
37	Libjå and Gundersen	Viltreflektorers virkning på elgens kryssing av veg	2001	direct	Swareflex			C/U					-
38	Lien	Viltreflektorers virkning på elgens kryssing av vei	2004	direct	Swareflex			C/U					+
39	Lück	Untersuchung an einer Swareflex-Wildwarnreflektoranlage im Reinhardswald	1977	direct	Swareflex	1.69	1.65	BA	72.00	12.00	30.00	30.00	+
40	Mah	Wildlife Warning Reflectors	1989	indirect (Armstrong 1992)	Swareflex			NA					-
41	McLain	The story of the deer mirrors on the parkway	1964	indirect (Gilbert 1982)	Van de Ree	2.33	2.89	BA	60.00	12.00	9.00	9.00	-
42	Müller	Protection des routes contre le gibier	1977	indirect	unknown			NA					*
43	Nettels	Mirrors to reduce deer-auto collisions	1965	direct	Van de Ree	8.33	0.00	BA	24.00	12.00	2.40	2.40	*
44	Norman	Reducing Deer-Vehicle Collisions by the Use of Reflectors	2001	direct	Strieter Lite			Physiol.					+

45	O'Rourke	Report on effectiveness of 'Swareflex wildlife warning reflectors'	1990	indirect (Ramp 2006)	Swareflex			BA					*
46	Olbrich	Untersuchung der Wirksamkeit von Wildwarnreflektoren und der Eignung von Wilddurchlässen	1984	direct	Bosch, WEGU	10.00	5.00	BA	48.00	12.00	1.60	1.60	-
47	Ossinger	Discovery Bay deer reflector study	1992	direct	Swareflex	4.04	3.85	C/U	40.00	20.00	5.20	5.20	+
48	Pafko and Kovach	Experience with deer reflectors	1996	direct	Swareflex, Unknown	16.32	3.03	BA	180.00	72.00	26.16	26.16	-
49	Paxson	Flashing lights seem to save lives of deer	1981	indirect (Griffis 1984)	Swareflex			BA					-
50	Pepper	Road traffic accidents and deer reflectors	1999	indirect (Langbein 2010)	unknown			NA					+
51	Pepper et al.	Deer Reflectors and Road Traffic Accidents through Forestry Commission Forests	1998	indirect	unknown			NA					*
52	Pluntke	Halt bei blau ist schlau	2014	direct	Beutha, Unknown	4.02	6.70	BA	24.00	12.00	11.20	11.20	+
53	Queal	Effectiveness of roadside mirrors in controlling deer-car accidents	1968	direct	Ruppert	1.22	3.33	BACI	72.00	12.00	24.00	14.40	+
54	Ramp and Croft	Do wildlife warning reflectors elicit aversion in captive macropods?	2006	direct	Swareflex, Strieter Lite			Beh.					+

55a	Reeve and Anderson	Ineffectiveness of Swareflex reflectors at reducing deer-vehicle collisions	1993	direct	Swareflex	20.00	39.38	CI	32.00	32.00	3.20	3.20	+
55b	Reeve and Anderson	Ineffectiveness of Swareflex reflectors at reducing deer-vehicle collisions	1993	direct	Swareflex	1.22	3.33	CU	32.00	16.00	3.20	3.20	
56a	Riginos et al.	Effects of Wildlife Warning Reflectors (“Deer Delineators”) on Wildlife-Vehicle Collisions in Central Wyoming	2015	direct	Strieter Lite	15.27	14.34	BA	120.00	54.00	36.81	36.81	
56b	Riginos et al.	Effects of Wildlife Warning Reflectors (“Deer Delineators”) on Wildlife-Vehicle Collisions in Central Wyoming	2015		Strieter Lite	30.00	19.97	CU	7.50	3.75	19.20	19.20	*
57	Rogers and Premo	An Ecological Landscape Study of Deer-Vehicle Collisions in Kent County, Michigan	2004	direct	Strieter Lite	2.42	2.40	BACI	108.00	36.00	9.60	9.60	+
58	Rudelstorfer and Schwab	Optische Einrichtungen im Dienste der Verkehrssicherheit	1975	direct	Swareflex	7.82	1.85	BA	20.00	12.00	29.80	29.80	-
59	Schafer et al.	Effectiveness of wildlife warning reflectors in reducing deer-vehicle accidents in Washington State	1985	direct	Swareflex	14.13	1.63	C/U	21.00	10.50	3.68	3.68	-
60	Scholten et al.	Effectiveness of Swareflex Reflectors	1989	indirect (Strieter flawed reports)	Strieter Lite			NA					+
61	Schwabe et al.	An analysis of deer-vehicle collisions: the case of Ohio	2000	direct	Swareflex	2.21	1.18	BA	108.00	48.00	4.80	4.80	-

62	Sheridan	The effectiveness of Swareflex and Wegu brand wildlife reflectors in deterring *Perameles gunnii* (barred bandicoot) from crossing a section of roadway	1991	direct	Swareflex			Beh.					+
63	Sivic and Sielecki	Wildlife Warning Reflectors	2001	direct	Swareflex, Strieter Lite			spec.					+
64	Sielecki	Wildlife Accident Reporting and Mitigation in British Columbia	2010	direct	Swareflex, Strieter Lite			BA					+
65	Steiner	Wildtierbestände und Verkehr-Reduktion von verkehrsbedingtem Fallwild	2011	direct	Swareflex, WEGU	19.64	12.74	BA	24.00	12.00	16.80	16.80	-
66	Stoyan	Gutachten zur Wirksamkeit des AWIWA-Sytems	2000	direct	AWIWA			BA					-
67	Ujvari et al.	Effectiveness of wildlife warning reflectors in reducing deer-vehicle collisions: a behavioral study	1998	direct	WEGU			Beh.					+
68	van den Berk	Proefprojekt	NA	direct	ITEK	7.63	2.00	BA	60.00	12.00	2.00	2.00	-
69	Voß	Unfallhäufungen mit Wildunfällen	2007	direct	WEGU, AWIWA	7.60	6.80	BA	72.00	12.00	2.50	2.50	*
70	Waring et al.	White-tailed deer roadside behavior, wildlife warning reflectors, and highway mortality	1991	direct	Swareflex	7.50	7.50	BA	14.00	14.00	0.80	0.80	+

71	White	Sample size requirements for reflector study	1983	indirect (Watson and Klingel 2000)	NA			NA					*
72	Williamson	Reflectors reduce deer-auto collisions	1980	indirect (Dalton, Ford, etc.)	unknown			NA					*
73	Woodard et al.	Effectiveness of Swareflex wildlife warning reflectors in reducing deer-vehicle accidents	1973	direct	Swareflex	10.00	13.75	C/U	6.00	3.00	1.60	1.60	+
74	Woodham	Evaluation of Swareflex Wildlife Warning Reflectors	1991	direct	Swareflex			C/U					+
75	Zacks	An investigation of Swareflex wildlife warning reflectors	1985	direct	Swareflex			Beh.					+
76	Zacks	Do White-tailed Deer Avoid Red?	1985	direct	Swareflex			Beh.					+

Chapter 3

Wildlife Warning Reflectors Do not Mitigate Wildlife-Vehicle Collisions on Roads

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Wildlife Warning Reflectors Do not Mitigate Wildlife–Vehicle Collisions on Roads

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Abstract

Wildlife–vehicle collisions cause human fatalities and enormous economic and ecological losses on roads worldwide. A variety of mitigation measures have been developed over the past decades to separate traffic and wildlife, warn humans, or prevent wildlife from entering a road while vehicles are passing by, but only few are economical enough to be applied comprehensively. One such measure, wildlife warning reflectors, has been implemented over the past five decades. However, their efficacy is questioned because of contradictory study results and the variety of applied study designs and reflector models. We used a prospective, randomized non-superiority cross-over study design to test our hypothesis of the inefficacy of modern wildlife warning reflectors. We analyzed wildlife–vehicle collisions on 151 testing sites of approximately 2 km in length each. During the 24-month study period, 1,984 wildlife–vehicle collisions were recorded. Confirmatory primary and exploratory secondary analyses using a log-link Poisson mixed model with normal nested random intercepts of observation year in road segment, involved species, and variables of the road segment and the surrounding environment showed that reflectors did not lower the number of wildlife–vehicle collisions by a relevant amount. In addition, variables of the road segment and the surrounding environment did not indicate differential effects of wildlife warning reflectors. Based on our results, we conclude that wildlife warning reflectors are not an effective tool for mitigating wildlife–vehicle collisions on roads.

Key words

Animal–vehicle collisions, Deer–vehicle collisions, Wildlife mirrors, Roadside reflectors, Deer mirrors

Introduction

Traffic systems worldwide affect nature directly and indirectly. The physical presence of roads directly destroys habitats, increases fragmentation, and interrupts ecological processes (cf. Forman and Alexander, 1998, Mladenoff et al., 1999). Often noticed effects of roads and traffic on the environment are wildlife–vehicle collisions, as wildlife remains are a common sight along roads. These collisions are not distributed randomly but are clustered in time and space (Malo et al., 2004, Gunson et al., 2011). Their temporal patterns are influenced by the time of day and year; they peak during twilight and at night and during mating season and litter dispersion (Peris et al., 2005, Langbein et al., 2011, Lagos et al., 2012, Hothorn et al., 2015). The occurrence of wildlife–vehicle collisions is also affected by the animal species involved and weather conditions (e.g., Bruinderink and Hazebroek, 1996, Compare et al., 2007, Langbein, 2007, Olson et al., 2015). Spatial clusters of these collisions occur where roads intersect habitats and migration routes, but also local factors influence their occurrence (cf. Gunson et al., 2011). For example, local differences in hotspots of wildlife–vehicle collisions depend on the proximity of roads to feeding and resting sites (Primi et al., 2009) or are related to habitat characteristics, traffic volume, and type of road (Clarke et al., 1998, Langbein et al., 2011, Beben, 2012).

The ecological consequences of wildlife–vehicle collisions depend on the animal species involved and their population size and growth rate. For rare species, collisions with vehicles are a serious threat (e.g., Harris and Gallagher, 1989). For example, approximately 50% of the population of the Florida panther (*Puma concolor*) and Florida Key deer (*Odocoileus virginianus clavium*) populations are killed on roads (Harris and Scheck, 1991, Forman and Alexander, 1998, Lopez et al., 2003). Other species are much less affected. In Europe, for example, < 5% of the populations of European hare (*Lepus europaeus*), red foxes (*Vulpes vulpes*), house sparrows (*Passer domesticus*), and crows (*Corvus corone*) are involved in collisions with wildlife (Bennett, 1991, Rodts, 1998, Cederlund, 1998, Mysterud, 2006). Even populations of ungulates, such as roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*), which are the species mainly involved in vehicle collisions in Germany (GDV, 2017), are not at all endangered by collisions with vehicles and are widespread in Europe (Cederlund, 1998). Nevertheless, in 2016, 264,000 collisions with roe deer or wild boar were officially reported in Germany, which resulted in an economic loss of almost 0.7 billion Euro (GDV, 2017). Moreover, it is expected that the number of unreported collisions is three times as high as the number reported (e.g., Huijser and Kociolek, 2008, Hesse and Rea, 2016).

The construction and maintenance of wildlife–vehicle collisions mitigation measures on roads, e.g., fencing, green bridges, and electric warning signs, are often costly (Kruidering et al., 2005, Huijser et al., 2007). Other, less costly measures, e.g., olfactory repellents, wildlife warning signs, speed limit reductions, and specific training to warn humans, have been shown to be ineffective in the long term, partly owing to habituation (Elmeros et al., 2011, Beben, 2012). To date, only optical scaring devices, i.e., wildlife warning reflectors, might potentially reduce wildlife–vehicle collisions, but their efficacy remains doubtful and contrasting results have been reported (cf. Brieger et al., 2016). The reflectors are supposed to deter wildlife from entering the road by reflecting the headlights of approaching vehicles to the road shoulder or by building up a light fence (e.g., Beilharz Straßenausrüstung Inc., 2017, Beutha Inc., 2017). Such reflectors have been used since the early 1960s and have been modernized continuously. Nowadays, they reflect short wavelengths, as an adaptation to the dichromasy of most mammals (Jacobs et al., 1998, Carroll et al., 2001, Ahnelt et al., 2006, Schiviz et al., 2008).

Most studies that have tested the efficacy of wildlife warning reflectors have applied either a before–after (BA) or a control–impact (CI) study design (Brieger et al., 2016, Benten et al., 2018). Observational and randomized CI study designs are associated with high variability because not only the effect of warning reflectors but also other characteristics of road segment and its environment determine the local risk of wildlife–vehicle collisions. BA designs address this issue by comparing the risk of wildlife–vehicle collisions locally with and without mounted warning reflectors. The temporal and spatial biases inherent in BA designs is addressed in randomized cross-over studies, where a randomization procedure is used to assign a specific experimental sequence (with/without vs. without/with warning reflector) to a specific road segment, thus breaking potential temporal and spatial associations. To the best of our knowledge, this study is the first of this type for the evaluation of warning reflectors. Furthermore, all studies that we are aware of aimed at testing the null hypothesis of an absent effect (no difference between wildlife–vehicle collisions with or without warning reflectors). A failure to reject this null hypothesis does not allow the postulation of an absent effect [“absence of evidence is not evidence of absence’’ (Altman and Bland 1995)]. In light of current evidence against a substantial effect of warning reflectors (Brieger et al., 2016), we designed and analyzed an experiment with the aim of demonstrating the non-superiority of wildlife warning reflectors by testing the null hypothesis of a superior effect.

In the study reported here, we investigated the efficacy of modern blue and multi-colored wildlife warning reflectors to reduce wildlife–vehicle collisions on roads by applying a randomized non-superiority cross-over design (Jones and Kenward, 2014). To our knowledge, this is not only the first study to apply a comparative designed experiment for testing the effect of modern wildlife warning reflectors on wildlife–vehicle collisions and to include temporal and spatial controls, but also by far the most comprehensive investigation, including 294.83 km of road sections. We obtained data on wildlife–vehicle collisions from 151 testing sites on primary, secondary, and tertiary roads where we installed dark-blue reflectors (51 sites), light-blue reflectors (50 sites), or multi-colored reflectors (50 sites). On five sites with dark-blue reflectors and five sites with light-blue reflectors, we also installed opto-acoustic reflectors. We tested our primary hypothesis H1) that modern wildlife warning reflectors do not reduce wildlife–vehicle collisions by a relevant amount, and our two secondary hypotheses that H2a) there is no difference in the inefficacy between the tested reflector models and H2b) other environmental variables do not influence the inefficacy of the reflectors. Tests of the secondary hypotheses were conducted to assess the stability of the primary hypothesis under various reflector models and roadside conditions.

Materials and methods

Study sites and species

The study was conducted between September 2014 and October 2017 within the four counties Göttingen (51°32′N, 9°56′E), Lahn-Dill (50°34′N, 8°30′E), Kassel (51°19′N, 9°29′E), and Höxter (51°46′N, 9°22′E) in central Germany. Silvicultural and agricultural land-use patterns differ slightly between the counties, with 25.5% (Höxter), 32.9% (Göttingen), 39.2% (Kassel), and 48.5% (Lahn-Dill) forest coverage, and 21.9% (Lahn-Dill), 47.5% (Kassel), 54.7% (Göttingen), and 61.9% (Höxter) agricultural land-use (European Environmental Agency, 2013).

Species distributions vary marginally within the study area, with roe deer and wild boar being the most abundant large mammals in all four counties. Detailed information on species distributions in 2016/17 are given in Table 3.1. Data on hunting statistics were provided by local hunting authorities.

Table 3. 1. Species distributions according to hunting bag data of 2016/2017 within the four different counties of the study area (Göttingen, Lahn-Dill, Kassel, and Höxter).

	County			
Species	Göttingen	Lahn-Dill	Kassel	Höxter
Roe deer	3,543	4,677	4,602	4,326
Wild boar	3,178	4,224	2,620	2,811
Red deer	196	410	107	131
Fallow deer	1	1	12	598
Sika deer	0	0	0	63
European mouflon	0	15	0	36

Study sites (N = 151) were selected after ArcGIS (version 10.3, ESRI, 2014) analysis of wildlife–vehicle collisions reported to the police on primary (N = 45), secondary (N = 75), and tertiary (N = 31) roads during the three years before the start of the testing period. We merged points of collisions with an existing road shapefile, which was cut into 500 m sections, and categorized these sections into four risk classes (1-5 collisions, 6-8 collisions, 9-10 collisions, >10 collisions) according to the average number of wildlife–vehicle collisions per year. Study sites were on average 2,036.43 m ± 280.37 m long, with a minimum of 960.48 m and a maximum of 2,552.78 m. We excluded sites that were already equipped with modern, i.e., blue or multi-colored, wildlife warning reflectors, so that the experimental design would not be potentially distorted by possible habituation of wildlife to these reflector models.

Wildlife warning reflectors

We tested dark-blue wildlife warning reflectors from Schilderwerk Beutha Inc. ("*Semicircle reflector*"), light-blue reflectors from Beilharz Inc. ("*The general*"), and recently released multi-colored wildlife warning reflectors ("*Multi-wildlife warner*", Motzener Kunststoff- and Gummiverarbeitung Inc.). In addition, we examined the efficacy of one type of opto-acoustic reflectors from WEGU GFT and Eurohunt Inc. ("*Opto-acoustic wildlife warner*") in combination with dark-blue and light-blue reflectors.

The sizes (height × width × depth) of the reflectors were 150 mm × 87 mm × 37 mm ("*Semicircle reflector*"), 260 mm × 95 mm × 25 mm ("*The general*"), 175 mm × 55 mm × 35 mm ("*Multi-wildlife warner*"), and 182 mm × 86 mm × 70 mm ("*Opto-acoustic wildlife warner*"). The reflectors consisted of micro prismatic reflective film (3M Corporation, Minnesota, USA; "*Semicircle reflector*"), blue-transparent plastic with aluminum vapor plating ("*The general*"), a micro prismatic reflective film (3M) with eight additional multi-colored honeycomb platelets ("*Multi-wildlife warner*"), and transparent mirrors in a 4 mm raster with silver and aluminum vapor plating ("*Opto-acoustic wildlife warner*"). Vehicle headlights reflect either a light fence along the road ("*Semicircle reflector*", "*The general*", "*Multi-wildlife warner*") and/or a fan of light at the road shoulder at an angle between 120° and 135° ("*The general*", "*Multi-wildlife warner*", "*Opto-acoustic wildlife warner*"). The acoustic wildlife warner emits sounds of 83 dB and 4 kHz for 1.5 s when a headlight hits light-sensitive solar panels.

Dark-blue, light-blue, and opto-acoustic reflectors were installed following the manufacturers' instructions at a height of 55–80 cm on the standard reflector posts of the roads. The manufacturer of the multi-colored wildlife warning reflector provided instructions for installing the reflectors at a height of 80–100 cm on posts. We installed these reflectors accordingly only in the first year; thereafter, following objections of the road authorities, the reflectors were set up at the height of the other models. None of the optic reflectors needed to be adjusted to the slope of the surrounding terrain, as specified by the manufacturers. The opto-acoustic wildlife warning reflectors were installed only at roads surrounded by flat terrain, which made adjustment to slopes unnecessary.

Experimental design

Testing sites for light-blue (N = 50), multi-colored (N = 50), and dark-blue (N = 51) reflectors were determined by block randomization and divided into two groups (A and B), compliant with a randomized non-superiority cross-over design (Jones and Kenward, 2014). Testing sites in group A were "active" in the first year (12 months), i.e., equipped with wildlife warning reflectors, and passive in the second year (12 months) as a control, i.e., reflectors were removed (+, -), whereas testing sites in group B were "passive" in the first year as a control and active in the second year (-, +). Each testing site was tested for 24 months between September 2014 and October 2017. In addition, ten sites with dark- or light-blue reflectors were selected randomly. Five of them were each equipped with eight opto-acoustic wildlife warning reflectors for one year. In the next year, opto-acoustic wildlife warning reflectors were installed at the five other sites (N = 3 light blue + acoustic and N = 2 dark blue + acoustic reflectors in the first year and vice versa in the second year). Four opto-acoustic reflectors were set up along each side of a ~ 200 m stretch within each testing site; optic reflectors were installed in between and across from opto-acoustic reflectors.

The distances between the standard reflector posts of the roads varied between 25 m (curve) and 50 m (straight stretch), with a median distance of 41.87 m ± 7.52 m. Wildlife warning reflectors were attached to all standard reflector posts, even to barely accessible sections, to avoid any relocation of wildlife–vehicle collision hotspots. Furthermore, testing sites were controlled frequently to ensure that the installed wildlife warning reflectors were still present, that no wildlife warning reflectors were installed by others at control (passive) sites, and that the wildlife warning reflectors were not concealed by vegetation.

Data collection

Wildlife–vehicle collision data were provided by the police. This information included location of collision (coordinates, road, municipality), time of collision (date and time), state of the road (dry, wet, slippery), light conditions (light, twilight, dark), and species involved. We assumed that the police data did not report all wildlife–vehicle collisions. However, we assumed that this underreporting was evenly distributed in the study area, thus excluding spatial bias (Groves, 2004, Lavrakas, 2008, Snow et al., 2015). To estimate the number of unreported wildlife–vehicle collisions, we sent out questionnaires to 378 hunters for information on location, time of the collisions, and species involved. Only 32 completed questionnaires were returned, which indicates the low number of wildlife–vehicle collisions not reported to the police.

We carried out secondary analyses to test for the influence of variables of the road section and surrounding landscape on the efficacy of the wildlife warning reflectors. We collected data on road characteristics (e.g., sinuosity, speed limit, traffic volume) and surrounding vegetation (ratio of forest to agricultural areas, Shannon diversity index of land-use types). The sinuosity was calculated using ET GeoWizards 11.2 for ArcGIS 10.3 (ET GeoWizards, 2015). It is defined as the ratio of the total length of the road segment and the length of the linear distance between the start and end point of the segment. The value ranges between 1 (straight) to infinity (closed circle) (cf. Mueller, 1968), with a median of 1.05 ± 0.31 at the testing sites. Data on annual average daily traffic volume were provided by the German Federal Highway Research Institute (BASt) and local road authorities; data on primary, secondary, and tertiary roads were collected in 2010. Speed limit data were obtained on site.

To specify the potential influence of the surrounding vegetation on the effect of wildlife warning reflectors on wildlife–vehicle collisions, we collected data on the area of forest, cultivated crops, grasslands, and other agricultural areas (e.g., meadows, nature reserve) within 500 m of the testing sites in ArcGIS using CORINE Land Cover data (European Environmental Agency, 2013) and data of the Integrated Administration and Control System (InVeKos). InVeKos data were provided by the Chamber of Agriculture of the respective federal states. These data have to be updated and controlled annually following the Commission Regulations of the European Union (EC No. 1122/2009, Art. 6; EC No. 73/2009, Art. 17), which provides a high-quality data set for landscape analyses. The diversity of land-use types was estimated using the Shannon diversity index (H), with $H=-\sum_{i=1}^{R} p_i * \ln p_i$; where p_i is the fraction of individuals belonging to species i in a sample or population (cf. Spatharis et al., 2011).

Statistical design and analysis

We used a prospective, randomized non-superiority cross-over study (Jones and Kenward, 2014) to test the hypothesis H1 that wildlife warning reflectors do not reduce wildlife–vehicle collisions by a relevant amount. The primary outcome was defined as the number of wildlife–vehicle collisions reported on a specific road segment over the course of a year. In this type of experiment, each road segment (the independent observational unit) contributed to the observed number of collisions twice; one year with wildlife warning reflectors mounted (active) and one year without any wildlife warning reflectors (passive control). The active/passive sequence (+, - vs. -, +; year 1, year 2) was determined by block randomization to ensure that the same number of road segments were assigned to the two possible sequences.

The treatment parameter for the confirmatory primary analysis was defined as the ratio of the expected number of wildlife–vehicle collisions per one kilometer road length with wildlife warning reflectors present to the expected number of collisions per one kilometer road length with no reflectors ("collision ratio") (Table 3. 2). A relevant reduction in collisions, i.e., > 10% or a collision ratio < 0.9, was defined *a priori* by a non-superiority margin of 90%. The null hypothesis of relevant superiority was to be rejected in favor of our non-superiority hypothesis H1 when the lower bound of a two-sided 95% profile confidence interval for the collision ratio was > 0.9 or, equivalently, when the one-sided null hypothesis "collision ratio" < 0.9 could be rejected at level $\alpha = 2.5\%$.

Table 3. 2. Number of road segments (observational units) for the two possible active/passive sequences (+, -) and (-, +), with corresponding lengths in km for the tested wildlife warning reflectors and combinations thereof. mc, multi-colored reflector; db, dark-blue reflector; lb, light-blue reflector; a, acoustic reflector.

	Type and combinations of reflectors					
Sequence	mc	db	db+a	lb	lb+a	Total
(+, -)	25 (49.67 km)	23 (45.78 km)	2 (3.42 km)	22 (44.04 km)	3 (6.70 km)	75 (149.61 km)
(-, +)	25 (46.10 km)	23 (44.41 km)	3 (5.89 km)	23 (44.63 km)	2 (4.19 km)	76 (145.22 km)
Total	50 (95.77 km)	46 (90.19 km)	5 (9.31 km)	45 (88.67 km)	5 (10.89 km)	151 (294.83 km)

The sample size of $N = 151$ road segments running a total of 294.83 km was planned in simulation experiments with an *a priori* specified power of 80%. The primary confirmatory analysis was performed using a log-link Poisson mixed model with normal nested random intercepts of observation year in road segment (Jones and Kenward, 2014). The random intercepts for each road segment adjust for the cross-over design. Possible over-dispersion was dealt with by the random intercept for each observation year nested in road segments. The model included the logarithm of the road segment lengths in km as an offset, such that the model parameters on the exponential scale can be interpreted as multiplicative changes of the collision ratio. A potential carry-over effect of wildlife warning reflectors was tested by comparing the Akaike information criterion (AIC) of models with and without adjustment for the sequence (+, -). The same Poisson mixed model was also fitted to three secondary outcomes defined as the number of vehicle collisions with roe deer, red deer, fallow deer; with wild boar; and with other animal species. Further secondary analyses were performed with the aim of investigating possible deviations from the overall effect of wildlife warning reflectors that could be explained by variables describing the shape of the road segment or the adjacent environment. The above-introduced Poisson mixed model was used with additional main effects and reflector presence interaction effects to investigate potential modifiers of reflector-presence effects. Simultaneous 95% confidence intervals adjusted for multiplicity (Hothorn et al., 2008, package multcomp, version 1.4-8) were reported for subgroup-specific effects of reflector presence. All analyses were performed using the R system for statistical computing (R Core Team, 2018, version 3.4.3); mixed models were fitted using the add-on package lme4 (Bates et al., 2015, version 1.1-17). Computational details of the analysis are given in the supplementary material.

Results

A total of 1,984 wildlife–vehicle collisions were observed during the course of the study. The conditional distribution of collisions for each animal species, type of wildlife warning reflector, and active/passive sequence is given in Table 3. 3.

Influence of wildlife warning reflectors on wildlife–vehicle collisions

Neither the year in which the reflectors were present on at a site (Fig. 3. 1) nor the presence of any type of wildlife warning reflector (Fig. 3. 2) led to any systematic pattern of lower numbers of wildlife–vehicle collisions. The corresponding Poisson mixed model led to an estimated collision ratio of 1.02 with the corresponding 95% confidence interval (0.92, 1.12). This multiplicative effect of the presence of wildlife warning reflectors compared to the passive control, i.e., to road segments without any wildlife warning reflectors mounted, suggests that the number of collisions increase when wildlife warning reflectors are mounted by an average of 2%. In particular, the lower bound of the confidence interval of 0.92 shows that the relative reduction in the number of collisions caused by wildlife warning reflectors is lower than the *a priori* defined non-superiority margin of 90%.

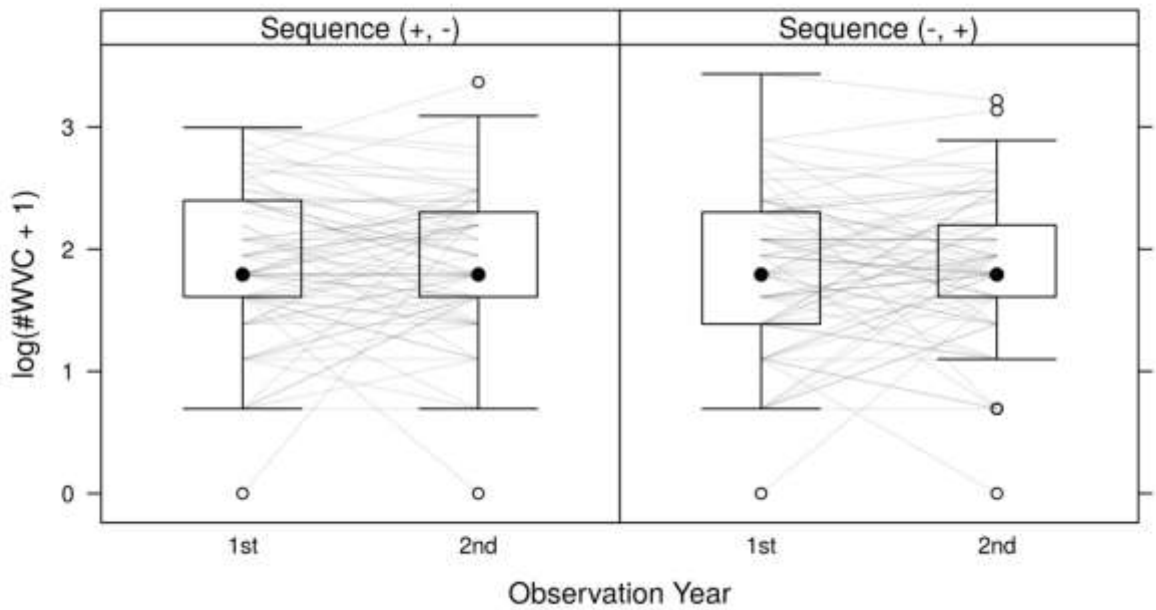

Figure 3. 1. Number of wildlife–vehicle collisions (WVC, on a log scale) with the two possible active/passive sequences (+, -) and (-, +).The boxplots represent the marginal distributions of wildlife–vehicle collisions observed over the two years. The joint distribution is visualized by lines, where each line represents one road segment. In the left panel, a positive slope indicates a lower number of collisions when wildlife warning reflectors are mounted (active) compared to the passive control with no reflectors. In the right panel, a negative slope indicates a lower number of collisions when wildlife warning reflectors are mounted compared to the passive control with no reflectors.

Table 3. 3. Number of wildlife–vehicle collisions for each type of wildlife warning reflector and combinations thereof (mc, multi-colored reflector; db, dark-blue reflector; a, acoustic reflector; lb, light-blue reflector) and each animal species as a quadruple of the two possible active/passive sequences (+, -) and (-, +).

	Number of wildlife–vehicle collisions (+, -),(-, +)						
	Type and combinations of reflectors						
Species	mc	db	db+a	lb	lb+a	Total	Sum
Roe deer	(91, 90),(79, 66)	(102, 128),(113, 142)	(6, 5),(13, 21)	(98, 105),(99, 100)	(15, 18),(4, 5)	(312, 346),(308, 334)	1,300
Red deer	(4, 1),(1, 2)	(0, 0),(3, 1)	(0, 0),(0, 0)	(3, 3),(0, 2)	(1, 2),(0, 0)	(8, 6),(4, 5)	23
Fallow deer	(1, 2),(1, 2)	(0, 0),(0, 0)	(0, 0),(0, 0)	(0, 0),(0, 0)	(0, 0),(0, 0)	(1, 2),(1, 2)	6
Wild boar	(34, 21),(20, 22)	(33, 31),(13, 29)	(1, 0),(6, 4)	(27, 25),(45, 24)	(2, 3),(0, 1)	(97, 80),(84, 80)	341
Badger	(5, 8),(2, 7)	(6, 4),(2, 2)	(0, 0),(0, 0)	(3, 1),(4, 3)	(0, 0),(0, 1)	(14, 13),(8, 13)	48
Red fox	(7, 11),(7, 8)	(6, 3),(6, 7)	(1, 0),(4, 1)	(9, 3),(9, 2)	(0, 1),(0, 1)	(23, 18),(26, 19)	86
Hare/Rabbit	(6, 2),(4, 4)	(2, 3),(3, 3)	(0, 0),(0, 1)	(5, 4),(4, 3)	(0, 1),(0, 1)	(13, 10),(11, 12)	46
Wildcat	(0, 0),(1, 0)	(0, 0),(0, 0)	(0, 0),(0, 0)	(0, 0),(0, 0)	(0, 0),(0, 0)	(0, 0),(1, 0)	1
Racoon	(4, 13),(6, 14)	(2, 4),(0, 2)	(0, 1),(0, 0)	(2, 1),(3, 1)	(0, 0),(0, 0)	(8, 19),(9, 17)	53
Unknown	(4, 2),(4, 4)	(10, 5),(10, 6)	(0, 1),(1, 0)	(10, 2),(12, 3)	(4, 1),(1, 0)	(28, 11),(28, 13)	80
Total	(156, 150),(125, 129)	(161, 178),(150, 192)	(8, 7),(24, 27)	(157, 144),(176, 138)	(22, 26),(5, 9)	(504, 505),(480, 495)	
Sum	560	681	66	615	62		1,984

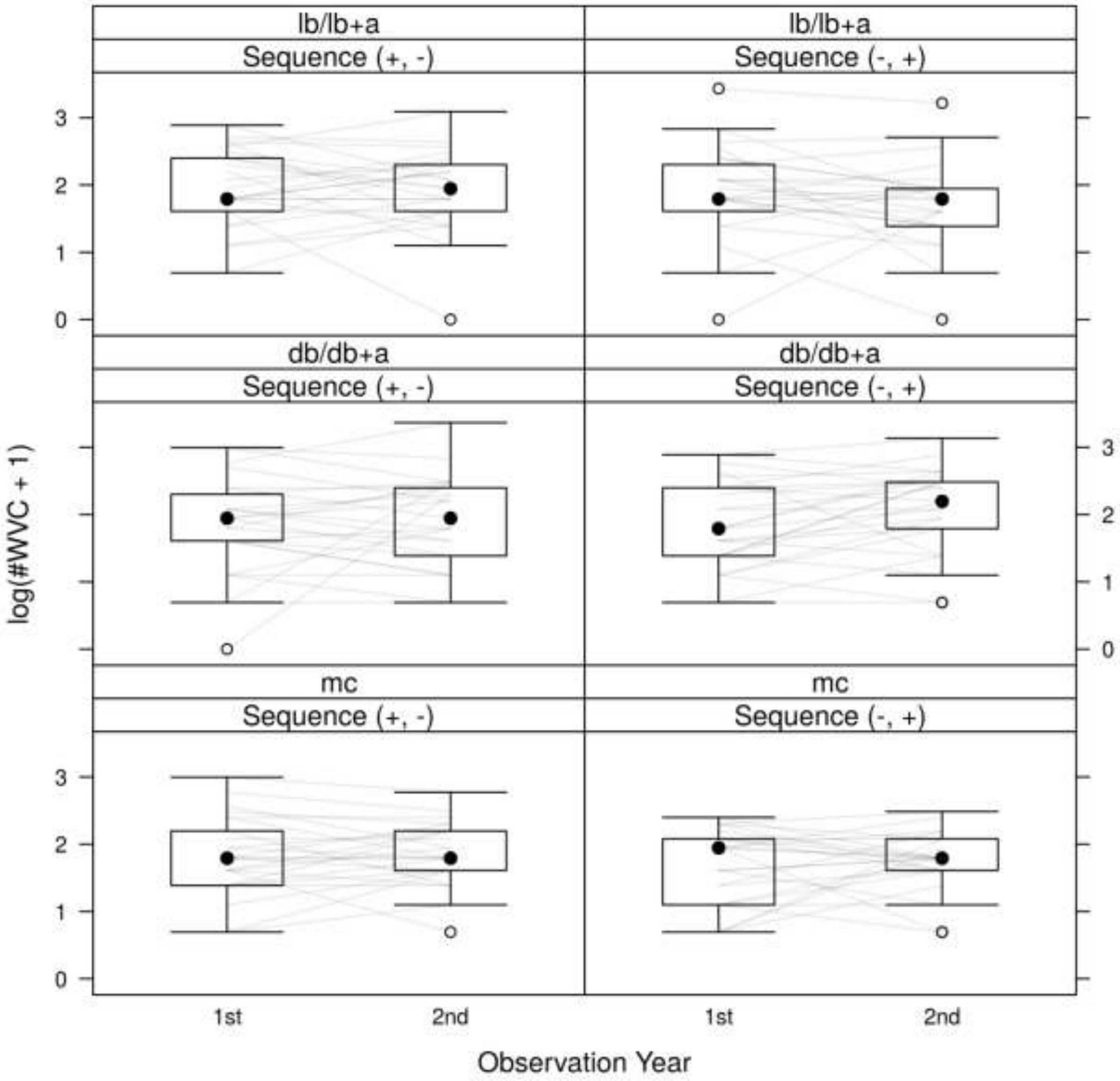

Figure 3. 2. Number of wildlife–vehicle collisions (WVC, on a log scale) with the two possible active/passive sequences (+, -) and (-, +), stratified by type of reflector. The boxplots represent the marginal distributions of wildlife–vehicle collisions observed over the two years. The joint distribution is visualized by lines, where each line represents one road segment. In the left panels, a positive slope indicates a lower number of collisions when wildlife warning reflectors are mounted (active) compared to the passive control with no reflectors. In the right panels, a negative slope indicates a lower number of collisions when wildlife warning reflectors are mounted compared to the passive control with no reflectors.

Influence of road characteristics and environmental variables on the effect of wildlife warning reflectors

We investigated the stability of the above-reported global effect of the presence of reflectors by analyzing models (1) with the number of collisions for different animal species as secondary outcomes (Fig. 3. 3), (2) with subgroups defined by the type of wildlife warning reflector used and the amount of forest or agricultural land adjacent to each road segment, as well as the combination of (1) and (2) (Fig. 3. 4). In addition, we studied (3) the numeric variables sinuosity, annual average daily traffic volume, Shannon diversity, and speed limit as potential effect modifiers (Table 3. 4).

Table 3. 4. Median and range of road segment characteristics.

Characteristic	Median and range
Length (m)	2,036.43 (960.48 to 2,552.78)
Ratio forest/forest	0.04 (-0.02 to 1.00)
Ratio forest/field	0.10 (0.00 to 1.00)
Ratio field/field	0.65 (0.00 to 1.00)
Sinuosity	1.05 (1.00 to 3.80)
Annual average daily traffic volume	3,114.00 (500.00 to 104,444.00)
Shannon index	1.85 (0.26 to 2.58)
Speed limit (km h^{-1})	100.00 (50.00 to 100.00)

We estimated the AIC and collision ratio for 12 models (Table 3. 5). The model “Total” refers to the model used for the primary confirmatory analysis with an AIC of 1,623.29. The same model fitted separately to the three different groups of animal species showed similar effects, and, in particular, the number of wildlife–vehicle collisions was not reduced for any of these three groups of animals. Subgroups of the type of wildlife warning reflector used did not improve the total model or the three models for different animal groups. The corresponding collision ratios were close to 1. Forest and field coverage along the road segment improved the total model and the model for other animal species slightly (measured by AIC).

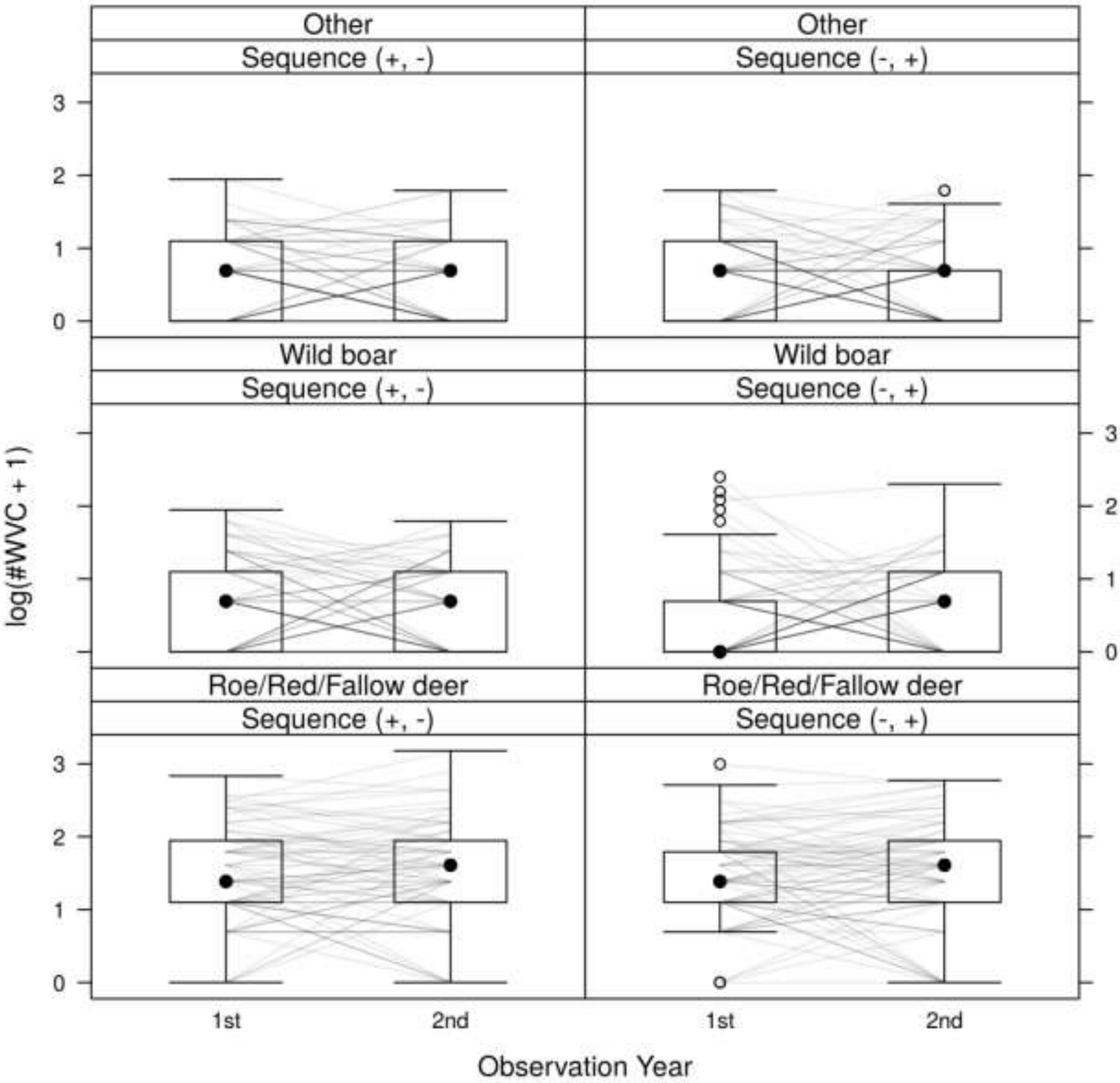

Figure 3. 3. Number of wildlife–vehicle collisions (WVC, on a log scale) with the two possible active/passive sequences (+, -) and (-, +), stratified by animal species. The boxplots represent the marginal distributions of wildlife–vehicle collisions observed over the two years. The joint distribution is visualized by lines, where each line represents one road segment. In the left panels, a positive slope indicates a lower number of collisions when wildlife warning reflectors are mounted (active) compared to the passive control with no reflectors. In the right panels, a negative slope indicates a lower number of collisions when wildlife warning reflectors are mounted compared to the passive control with no reflectors.

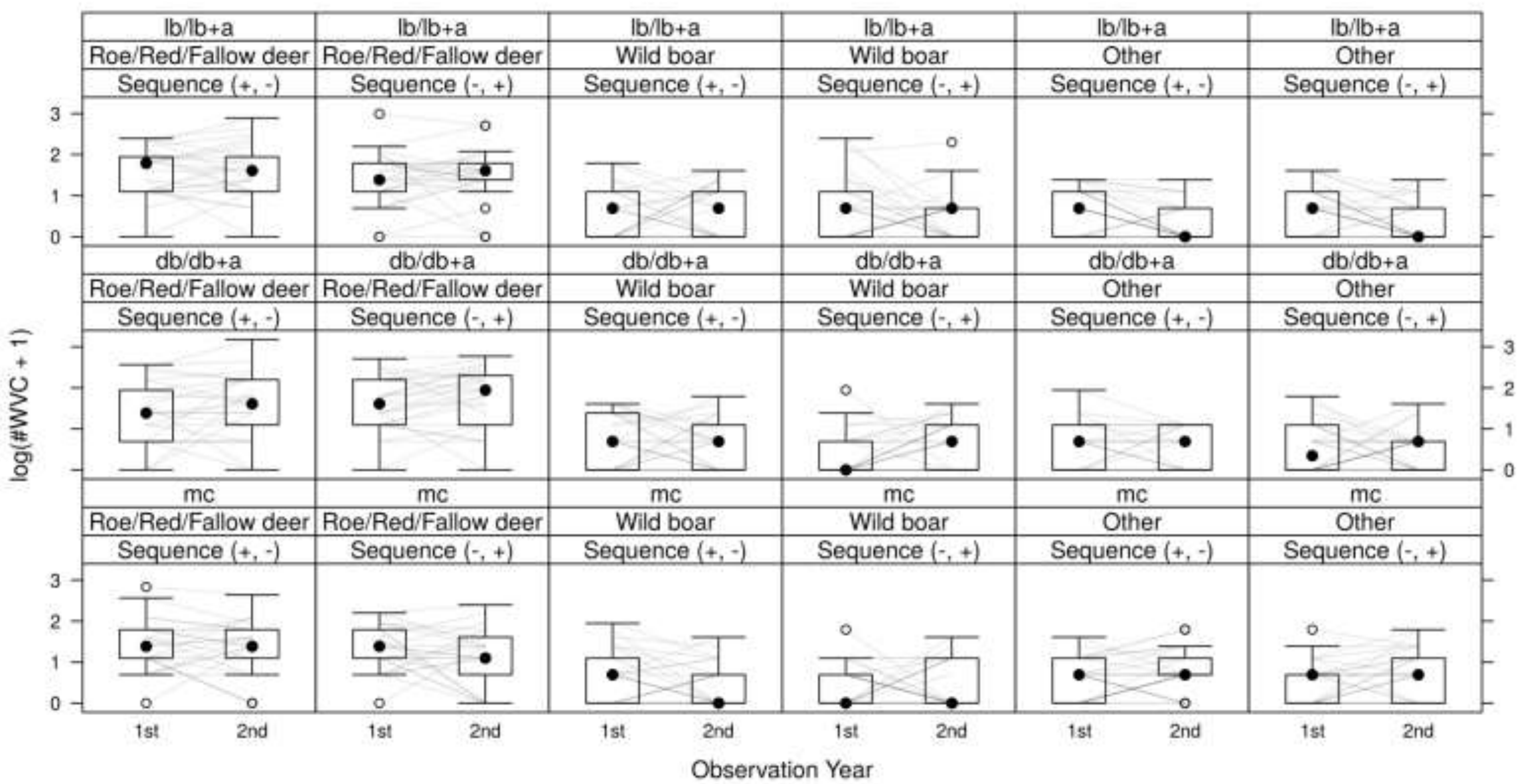

Figure 3. 4. Number of wildlife-vehicle collisions (WVC, on a log scale) with the two possible active/passive sequences (+,-) and (-, +), stratified by animal species and type of reflector. The boxplots represent the marginal distributions of wildlife–vehicle collisions observed over the two years. The joint distribution is visualized by lines, where each line represents one road segment. For sequence (+, -), a positive slope indicates a lower number of collisions when wildlife warning reflectors are mounted (active) compared to the passive control with no reflectors. For sequence (-, +), a negative slope indicates a lower number of collisions when wildlife warning reflectors are mounted compared to the passive control with no reflectors.

Table 3. 5. AIC and collision ratios with 95% confidence intervals for different outcomes(total, roe/red/fallow deer, wild boar, and other animals) and subgroups (total, by type of wildlife warning reflector, and by forest/field cover). mc, multi-colored reflector; db, dark-blue reflector; a, acoustic reflector; lb, light-blue reflector.

Model		Total	Roe/red/fallow deer	Wild boar	Other animals
Total	AIC	1623.29	1459.94	894.8	842.78
	Global collision ratio	1.02 (0.92, 1.12)	1.00 (0.89, 1.12)	1.12 (0.83, 1.53)	1.12 (0.82, 1.32)
Type of reflector	AIC	1626.63	1460.55	897.98	846.72
	Collision ratio (mc)	1.03 (0.83. 1.28)	0.95 (0.73, 1.24)	1.35 (0.71, 2.57)	1.05 (0.69, 1.60)
	Collision ratio (db/db+a)	1.03 (0.71. 1.49)	0.86 (0.55, 1.34)	1.90 (0.77, 4.70)	1.04 (0.51, 2.11)
	Collision ratio (lb/lb+a)	0.89 (0.62, 1.26)	0.90 (0.60, 1.36)	0.69 (0.24, 2.04)	1.02 (0.46, 2.28
Forest/field cover	AIC	1622.59	1460.42	896.24	836.92
	Collision ratio (forest only)	0.72 (0.50, 1.02)	0.84 (0.56, 1.27)	0.45 (0.16, 1.31)	0.74 (0.27, 2.02)
	Collision ratio (mixture)	1.15 (0.95, 1.38)	1.07 (0.86, 1.34)	1.15 (0.66, 2.01)	1.40 (0.92, 2.12)
	Collision ratio (field only)	1.02 (0.74, 1.41)	0.96 (0.67, 1.38)	2.39 (0.84, 6.80)	0.51 (0.20, 1.29)
Sinuosity	AIC	1629.71	1467.29	896.4	847.39
	Collision ratio (almost straight)	1.02 (0.86, 1.21)	0.97 (0.80, 1.18)	1.11 (0.67, 1.85)	1.09 (0.73, 1.63)
	Collision ratio (winding)	1.05 (0.87, 1.27)	1.05 (0.85, 1.29)	1.15 (0.62, 2.12)	1.09 (0.68, 1.75)
	Collision ratio (twisty)	0.90 (0.62, 1.30)	0.91 (0.61, 1.37)	1.08 (0.32, 3.70)	0.66 (0.26, 1.68)

However, the corresponding collision ratios were not consistent with increasing forest coverage, and none of the confidence intervals excluded one, i.e., a non-significant effect. It should also be mentioned that only very few road segments had very high forest coverage (Table 3. 4). Sinuosity (subdivided into three categories) did not improve the model, and the confidence intervals were in line with the overall effect of mounted reflectors. Table 3. 6 gives the results of models with numeric effect modifiers (main and interaction effects).

Table 3. 6. AIC and collision ratios with 95% confidence intervals for models with numeric effect modifiers.

	Sinuosity	Speed	Traffic	Shannon
AIC	1618.46	1626.21	1627.12	1626.95
Collision ratio	1.43 (0.81 to 2.62)	1.02 (0.92 to 1.12)	1.02 (0.92 to 1.13)	1.02 (0.92 to 1.12)
Main effect	0.09	0.88	0.71	0.66
Interaction effect	0.23	0.32	0.74	0.9

Only the model for sinuosity improved upon the model of the primary analysis; however, the adjusted collision ratio did not indicate a positive effect of wildlife warning reflectors. The remaining variables did not seem to improve the model. We finally tried to identify differential effects of reflectors using model-based recursive partitioning for generalized linear mixed models (Fokkema et al., 2017, package glmertree, version 0.1-2), but no explanatory variable improved the model (p-value for the null hypothesis of the primary model being correct: 0.10).

Discussion

Our cross-over experimental design revealed that modern wildlife warning reflectors did not lead to a relevant reduction in wildlife–vehicle collisions. None of the tested reflectors, including opto-acoustic devices, were able to reduce the number of reported collisions. Moreover, other variables describing the surrounding environment (i.e., forest/agricultural land ratio, sinuosity, speed limit, traffic volume, and Shannon diversity index of land use) did not show any differential effect on the overall inefficacy of the reflectors.

Influence of wildlife warning reflectors on wildlife–vehicle collisions

Testing the efficacy of wildlife warning reflectors is as old as the reflectors themselves (e.g. McLain, 1964, Gladfelter, 1984, Waring et al., 1991, Brieger et al., 2017a), but outcomes have always been doubtful. This skepticism might be due to the study designs implemented and small sample data sets collected in earlier studies. Especially studies that applied a before–after design have occasionally reported the efficacy of wildlife warning reflectors (e.g., Schafer et al., 1988, Pafko and Kovach, 1996). However, such a study design lacks independence of different levels of single treatments and true replications (Roedenbeck, 2007, Morrison et al., 2010). Thus, a potential change in the number of collisions after the installation of reflectors can also be assigned to factors other than the reflectors (Morrison et al., 2010). Therefore, when analyzing the efficacy of mitigation measures, it is important to control for potential fluctuations in the number of collisions due to, e.g., environmental changes and natural population fluctuation. Thus, experimental designs that include temporal and spatial controls (e.g., BACI, cross-over) have the highest inferential strength for assessing impacts on the environment (Green, 1979, Underwood and Chapman, 2003, Roedenbeck, 2007).

From an epistemological point of view, the rejection of a superiority null hypothesis (a reduction in the number of collisions by > 10%) in favor of our non-superiority hypothesis H1 (a reduction in the number of collisions by < 10%) in our randomized non-superiority cross-over design provides strong scientific support for the inefficacy of wildlife warning reflectors. In contrast to earlier studies designed and analyzed with the aim of demonstrating a positive effect of such reflectors by testing the null hypothesis of a zero treatment effect (e.g., Waring et al., 1991, D'Angelo et al., 2006, Ramp and Croft, 2006), we were able to report a statistically significant result on a practically relevant hypothesis. Previous studies often failed to reject the null of a zero treatment effect, yet they could not demonstrate the inefficacy (Altman and Bland 1995). The level of evidence of the result reported here is as high as the level of evidence required for approval of a generic drug in equivalence or non-inferiority trials (Jones and Kenward 2014).

Modern reflectors reflect light of short wavelengths that fit the color sensitivity of animals (Carroll, 2001, Ahnelt et al., 2006, Schiviz et al., 2008). Ungulates, e.g., roe deer, frequent open areas and agricultural fields at night (Mysterud et al., 1999a, 1999b), increasing the vulnerability to predators (Hothorn et al., 2015), which results in a higher perception for mesopic and scotopic vision below 540 nm (Szél et al., 1996, VerCauteren and Pipas, 2003, Hanggi and Ingersoll, 2007). In this regard, one could argue that reflector models that reflect light of long wavelengths are inefficient because of the lack of color sensitivity of ungulates. However, recent studies on the efficacy of blue reflectors also did not find any influence of the devices on roe deer behavior—not under controlled experimental conditions or in the field or by observing road crossing behavior (Pluntke, 2014, Brieger et al., 2017a, Brieger et al., 2017b, Kämmerle et al., 2017).

Brieger et al. (2017a) and Kämmerle et al. (2017) observed the behavior of roe deer in studies of the efficacy of blue "*semicircle reflectors*". In a mixture of controlled experiments and field observations, Brieger et al. (2017a) tested whether blue light stimuli of reflectors elicit any threat-related behavior in the absence of vehicles. They also tested the reactions of roe deer towards oncoming vehicles in the absence and presence of reflectors. In both experimental setups, the behavior of the roe deer did not change in any way attributable to the presence of the reflectors. In a study using telemetry, Kämmerle et al. (2017) showed that the timing and frequency of road crossings of free-ranging roe deer did not change in the presence of reflectors. However, the authors did not study whether the number of collisions with vehicles changed, or whether the reflectors influenced roe deer behavior in the period immediately following reflector installation and whether the deer became habituated towards the reflectors over time.

The inverse-square law of light states that light intensity is inversely proportional to the distance between the illuminated surface and the source of light. Hence, spectrometric analyses of wildlife warning reflectors showed that the reflected light intensity is infinitesimal already at short distances from the reflectors and is cross-faded by the headlights of approaching vehicles (Sivic and Sielecki, 2001, Schulze and Polster, 2017). Thus, whether the light reflected from reflectors has sufficient intensity to elicit any reaction from animals, let alone sufficient for decreasing the risk of a collision with vehicles, can be contested. It is therefore surprising that local hunters sometimes report a positive effect of various models of wildlife warning reflectors, including red reflectors, in preventing wildlife–vehicle collisions. Proposed possible explanations for the reduction in collisions include chance, independent changes in the environment, or natural fluctuations in populations (Fryxell et al., 2010) or the influence of the reflectors on the behavior of drivers rather than on the behavior of animals (Zacks, 1985, Rowden et al., 2008). For instance, deer whistles increase the attention of drivers to wildlife next to the road, which in turn decreases collisions with wildlife (Zacks, personal communication, 2015). Moreover, light intensity of the direct reflection back to the driver is larger than to the surroundings of the road (Schulze and Polster 2017). Therefore, reflectors might serve as a warning device that influences driver behavior (Rowden et al., 2008). However, as we did not observe any reduction in wildlife–vehicle collisions, we did not find any evidence that motorists have adapted their driving behavior to the presence of the reflectors and, thus, wildlife-collision areas.

Influence of road characteristics and environmental variables on the effect of wildlife warning reflectors

We did not find any influence of environmental variables (i.e., ratio of forest to open land, sinuosity, speed limit, traffic volume, and Shannon diversity index of land use) on the inefficacy of wildlife warning reflectors. However, most of these variables seem to have an increased or decreased effect on wildlife–vehicle collision hotspots in general (cf. Gunson et al., 2011). For instance, studies on the effect of road-side topography indicate that narrower road shoulders lead to higher numbers of wildlife–vehicle collisions (Ramp et al., 2006). Higher speed limits (Seiler, 2005) and higher curvature (sinuosity) (Grilo et al., 2009, Ramp et al., 2005) also lead to higher numbers of collisions with wildlife. Studies on the influence of the surrounding landscape showed different effects. For example, a close proximity to or a higher proportion of forest stands (e.g., Malo et al., 2004, Seiler, 2005, Gunson et al., 2009) and a higher Shannon diversity index (Nielsen et al., 2003, Malo et al., 2004) lead to more collisions, and more obstructions lead to fewer collisions with wildlife (Hubbard et al., 2000, Malo et al., 2004, Seiler, 2005, Gunson et al., 2009).

We did not find a relationship between the annual average daily traffic volume and the inefficacy of wildlife warning reflectors on wildlife–vehicle collisions. Morelle et al. (2013) observed that more than half of the collisions with wildlife in Wallonia, Belgium, occurred on national roads and highways, even though these roads account for only 14.6% of the road network. Such a clustering of collisions has also been reported for roe deer in Denmark (Madsen et al., 1998) and roe deer and wild boar in Spain (Diaz-Varela et al., 2011). Van Langevelde and Jaarsma (2004) identified traffic volume as one of the most influential parameters leading to an increase in collisions with wildlife, as has also been observed for collisions with moose in Sweden (Seiler, 2005). Seiler (2005) identified a positive relationship between annual average daily traffic volume, mean speed limit, and occurrence of wildlife–vehicle collisions.

Our data did not indicate any correlation between agricultural and forestry land-use diversity and wildlife warning reflectors. In other studies, this variable was found to both increase (Seiler 2005) and decrease (Hubbard et al., 2000) the number of wildlife–vehicle collisions (cf. Gunson et al., 2011). These studies focused on explaining variables of wildlife–vehicle collision hotspots, whereas our testing sites were much longer than hotspots per se; thus, such variables might be masked by variables that affect the entire length of the site. Moreover, for hotspot analyses, a much higher sample size that covers the many potentially influencing factors might be needed.

Conclusions

In our randomized non-superiority cross-over study, we demonstrated the inefficacy of wildlife warning reflectors in reducing the number of wildlife–vehicle collisions on roads by a relevant amount. None of the tested reflector models was able to reduce the number of collisions during the experiment. Our findings are in accordance with behavioral studies that show that wildlife warning reflectors do not elicit any reaction in deer that would prevent collisions with vehicles (Brieger et al., 2017a, Kämmerle et al., 2017). Our results are also in line with the results of spectrometric studies that indicate that light reflected from wildlife warning reflectors is not sufficiently intense to elicit any reaction in animals that would decrease the risk of collisions with vehicles (Sivic and Sielecki, 2001, Schulze and Polster, 2017). We assume that studies that have shown that wildlife warning reflectors lower the number of wildlife–vehicle collisions either lack spatial and temporal controls to evaluate environmental changes and natural fluctuation in populations or have an insufficient amount of independent replications. Possible reductions in the number of collisions after implementation of reflectors might be attributed to changes in human behavior rather than to changes in animal behavior. Moreover, we could not find any influence of environmental variables on the efficacy of the reflectors. Considering our results and the results of other studies, we do not recommend the use of wildlife warning reflectors as a tool for mitigating wildlife–vehicle collisions on roads.

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References

Ahnelt, P. K., Schubert, C., Kuebber-Heiss, A., Schiviz, A., & Anger, E. (2006). Independent variation of retinal S and M cone photoreceptor topographies: a survey of four families of mammals. Visual Neurosci. 23, 429-435.

Altman, D. G., & Bland, J. M. (1995). Statistics notes: Absence of evidence is not evidence of absence. BMJ, 311(7003), 485.

Bates D, Mächler M, Bolker B, & Walker S. (2015). “Fitting Linear Mixed-Effects Models Using lme4.” J Stat Softw. 67, 1–48. doi:10.18637/jss.v067.i01.

Beben, D. (2012). Crossings for animals–an effective method of wild fauna conservation. J Environ Eng Landsc. 20, 86–96.

Beilharz Straßenausrüstung. (2017). "Der General" - Wildwarnreflektor. https://www.beilharz.eu/de/wildwarnreflektor.html. Accessed December 6 2017.

Bennett. A. F. (1991). Roads, roadsides and wildlife conservation: a review In: Nature Conservation 2: the role of corridors (ed. by D.A. Saunders and R.J. Hobbs), pp. 99-118. Surrey Neatty & Sons Pty Limited, Western Australia.

Brieger, F., Hagen, R., Kröschel, M., Hartig, F., Petersen, I., Ortmann, S., & Suchant, R. (2017b). Do roe deer react to wildlife warning reflectors? A test combining a controlled experiment with field observations. Eur J Wildlife Res. 63, 10.1007/s10344-017-1130-5.

Brieger, F., Hagen, R., Vetter, D., Dormann, C. F., & Storch, I. (2016). Effectiveness of light-reflecting devices: A systematic reanalysis of animal-vehicle collision data. Accident Anal Prev. 97, 242–260.

Brieger, F., Kämmerle, J.-L., Martschuk, N., Ortmann, S., & Hagen, R. (2017a). No evidence for a 'warning effect'of blue light in roe deer. Wildlife Biol. 17. 10.2981/wlb.00331.

Bruinderink, G., Hazebroek, E. (1996). Ungulate traffic collisions in Europe. Conserv Biol. 10, 1059–1067.

Buckland, S. T., Rexstad, E. A., Marques, T. A., & Oedekoven, C. S. (2015). Distance Sampling: Methods and Applications, Methods in Statistical Ecology. Springer International Publishing, Cham. doi:10.1007/978-3-319-19219-2.

Carroll, J., Murphy, C. J., Neitz, M., Hoeve, J. N. ver, & Neitz, J. (2001). Photopigment basis for dichromatic color vision in the horse. J Vision. 1, 2.

Cederlund, G., Bergqvist, J., Kjellander, P., Gill, R., Gaillard, J. M., Boisaubert, B., Ballon, P., & Duncan, P. (1998). Managing roe deer and their impact on the environment: Maximising the net benefits to society. In: The European roe deer: the biology of success (eds. R. Andersen, P. Duncan, JDC. Linnell), pp. 189-219. Scandinavian University Press. Oslo, Norway.

Clarke, G. P., White, P. C. L., & Harris, S. (1998). Effects of roads on badger *Meles meles* populations in south-west England. Biol Conserv. 86, 117–124.

Compare, D. L., Sturaro, E., Cocca, G., & Ramanzin, M. (2007). An analysis of roe deer (*Capreolus capreolus*) traffic collisions in the Belluno province, eastern Italian Alps. Ital J Anim Sci. 6, 848–850.

Diaz-Varela, E. R., Vazquez-Gonzalez, I., Marey-Pérez, M. F., & Álvarez-López, C. J. (2011). Assessing methods of mitigating wildlife–vehicle collisions by accident characterization and spatial analysis. Transport Res D-Tr E. 16, 281–287.

Elmeros, M., Winbladh, J. K., Andersen, P. N., Madsen, A. B., & Christensen, J. T. (2011). Effectiveness of odour repellents on red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*): A field test. Eur J Wildlife Res. 57, 1223–1226.

ET GeoWizards. Version 11.2. Available from: http://www.ian-ko.com/ET_GeoWizards/gw_main.htm. Accessed January 17 2018.

European Environmental Agency. (2013). CORINE Land Cover (CLC) 2006.

ESRI. ArcGIS Desktop. (2014). Release 10.3 Environmental Systems Research Institute. Redlands, CA.

Fokkema, M.; Smits, N.; Zeileis, A.; Hothorn, T.; Kelderman, H. (2017): Detecting treatment-subgroup interactions in clustered data with generalized linear mixed-effects model trees. In Behavior Research Methods. DOI: 10.3758/s13428-017-0971-x.

Forman, R.T.T., & Alexander, L.E. (1998). Roads and their major ecological effects. Annu Rev Ecol Syst. 29, 207–231.

Fryxell, J. M., Packer, C., McCann, K., Solberg, E. J., & Sæther, B.-E. (2010). Resource management cycles and the sustainability of harvested wildlife populations. Science. 328, 903–906.

GDV. (2017). Täglich kracht es 720Mal. http://www.gdv.de/2017/11/versicherer-registrieren-taeglich-ueber-720-wildunfaelle/. Accessed December 12 2017.

Gladfelter, L. (1984). Effect of wildlife highway warning reflectors on deer-vehicle accidents. Iowa Highway Research Board Project HR-210. Iowa Department of Transportation, Ames, Iowa, USA. 16 pp.

Green, R. H. (1979). Sampling design and statistical methods for environmental biologists. John Wiley & Sons. 272 pp.

Grilo, C., Bissonette, J. A., & Santos-Reis, M. (2009). Spatial–temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. Biol Conservation. 142, 301–313.

Groves, R.M., 2004. Survey errors and survey costs. New York. John Wiley & Sons. 590 pp.

Gunson, K. E., Clevenger, A. P., Ford, A. T., Bissonette, J. A., Hardy, A. (2009). A comparison of data sets varying in spatial accuracy used to predict the occurrence of wildlife-vehicle collisions. Environ Manage. 44, 268–277.

Gunson, K. E., Mountrakis, G., & Quackenbush, L.J. (2011). Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. J Environ Manage. 92, 1074–1082.

Hanggi, E. B., Ingersoll, J. F., & Waggoner, T. L. (2007). Color vision in horses (*Equus caballus*): Deficiencies identified using a pseudoisochromatic plate test. J Comp Psychol. 121, 65.

Harris, L. D., & Gallagher, P. B. (1989). New initiatives for wildlife conservation: The need for movement corridors. In: Preserving communities and corridors. Defenders of Wildlife (ed. G. Mackintosh), pp. 11-34. Washington, D. C, USA:

Harris, L. D., & Scheck, J. (1991). From implications to applications: The dispersal corridor principle applied to the conservation of biological diversity. In: Nature conservation the role of corridors (eds. D. A. Saunder and R. J. Hobbs), pp. 189-220. Surrey Beatty and Sons, Chipping Norton, Australia.

Hesse, G., & Rea, R. V. (2016). Quantifying wildlife vehicle collision underreporting on northern British Columbia highways (2004-2013): Unpublished report prepared for the BC Ministry of Transportation and Infrastructure. 53 pp.

Hothorn, T., Bretz, F., & Westfall, P. (2008). Simultaneous inference in general parametric models. Biometrical J. 50, 346-363.

Hothorn, T., Brandl, R., & Müller, J. (2012). Large-scale model-based assessment of deer-vehicle collision risk. PLoS one. 7, e29510.

Hothorn, T., Müller, J., Held, L., Möst, L., & Mysterud, A. (2015). Temporal patterns of deer–vehicle collisions consistent with deer activity pattern and density increase but not general accident risk. Accident Anal Prev. 81, 143–152.

Hubbard, M. W., Danielson, B. J., & Schmitz, R. A. (2000). Factors influencing the location of deer-vehicle accidents in Iowa. J Wildlife Manage. 64, 707–713.

Huijser, M. P., Kociolek, A., McGowen, P., Hardy, A., Clevenger, A. P., Ament, R. (2007). Wildlife-vehicle collision and crossing mitigation measures: A toolbox for the Montana Department of Transportation. Bozeman: Western Transportation Institute. 123 pp.

Huijser, M. P., Kociolek, A. V. (2008). Wildlife-vehicle collision and crossing mitigation measures: A literature review for Blaine County, Idaho. Western Transportation Institute, Montana State University, Bozeman. 106 pp.

Jacobs, G. H., Deegan, J. F., Neitz, J. A. Y. (1998). Photopigment basis for dichromatic color vision in cows, goats, and sheep. Visual Neurosci. 15, 581–584.

Jones, B., & Kenward, M. G. (2014). Design and analysis of cross-over trials. CRC Press. 438 pp.

Kämmerle, J.-L., Brieger, F., Kröschel, M., Hagen, R., Storch, I., & Suchant, R. (2017). Temporal patterns in road crossing behaviour in roe deer (*Capreolus capreolus*) at sites with wildlife warning reflectors. PLoS One. 12, e0184761. https://doi.org/10.1371/journal.pone.0184761.

Kruidering, A. M., Veenbaas, G., Kleijberg, R., Koot, G., Rosloot, Y., & van Jaarsveld, E. (2005). Leidraad faunavoorzieningen bij wegen. Rijkswaterstaat, Dienst Weg-en Waterbouwkunde, Delft, the Netherlands. 122 pp.

Lagos, L., Picos, J., & Valero, E. (2012). Temporal pattern of wild ungulate-related traffic accidents in northwest Spain. Euro J Wildlife Res. 58, 661–668.

Lalo, J. (1987). The problem of road-kill. Am Forests. 93, 50-52.

Langbein, J. (2007). National deer-vehicle collisions project: England 2003–2005. Final report to the Highways Agency. The Deer Initiative, Wrexham, UK. 94 pp.

Langbein, J., Putman, R., & Pokorny, B. (2011). Traffic collisions involving deer and other ungulates in Europe and available measures for mitigation. In: Ungulate management in Europe: problems and practices (eds. R. Putman, M. Apollonio, R. Andersen), pp 215–259. Cambridge University Press, Cambridge, USA.

Lavrakas, P. J. (2008). Sampling bias. In:, Encyclopedia of survey research methods (ed. P.J. Lavrakas), 56-61 pp. Sage Publications. California, USA.

Lopez, R. R., Vieira, M. E., Silvy, N. J., Frank, P. A., Whisenant, S. W., & Jones, D. A. (2003). Survival, mortality, and life expectancy of Florida Key deer. J Wildlife Manage. 67, 34-45.

Madsen, A. B., Fyhn, H. W., & Prang, A. (1998). Traffic killed animals in landscape ecological planning and research. Trafikdræbte dyr i landskabsøkologisk planlægning og forskning. Danmarks Miljøundersøgelser. Faglig Rap. DMU 22. 43 pp.

Malo, J. E., Suarez, F., & Diez, A. (2004). Can we mitigate animal–vehicle accidents using predictive models? JouJAppl Ecol. 41, 701–710.

Massei, G., Kindberg, J., Licoppe, A., Gačić, D., Šprem, N., Kamler, J., Baubet, E., Hohmann, U., Monaco, A., & Ozoliņš, J. (2015). Wild boar populations up, numbers of hunters down? A review of trends and implications for Europe. Pest Manag Sci. 71, 492–500.

McLain, P.D. (1964). The story of the deer mirrors on the parkway. New Jersey Outdoors. 15, 13–18.

Mladenoff, D. J., Sickley, T. A., & Wydeven, A. P. (1999). Predicting gray wolf landscape recolonization: Logistic regression models vs. new field data. Ecol Appl. 9, 37–44.

Morelle, K., Lehaire, F., & Lejeune, P. (2013). Spatio-temporal patterns of wildlife-vehicle collisions in a region with a high-density road network. Nat Conserv. 5, 53-73.

Morrison, M. L., Block, W. M., Strickland, M. D., Collier, B. A., & Peterson, M. J. (2010). Wildlife study design. Springer Science & Business Media. New York, USA. 386 pp.

Motzener Kunststoff- und Gummiverarbeitung Inc. (2017). Multiwildschutzwarner. https://www.wildwechsel-unfall-vermeiden.de/index.html. Accessed December 6 2017.

Mueller, J. E. (1968). An introduction to the hydraulic and topographic sinuosity indexes 1. Ann Assoc Am Geogr. 58, 371–385.

Mysterud, A., Larsen, P. K., Ims, R. A., & Østbye, E. (1999). Habitat selection by roe deer and sheep: Does habitat ranking reflect resource availability? Can J Zool. 77, 776–783.

Mysterud, A., Lian, L.-B., & Hjermann, D. Ø. (1999). Scale-dependent trade-offs in foraging by European roe deer (*Capreolus capreolus*) during winter. Can J Zool. 77, 1486–1493.

Mysterud, A., Tryjanowski, P., & Panek, M. (2006). Selectivity of harvesting differs between local and foreign roe deer hunters: Trophy stalkers have the first shot at the right place. Biol Letters. 2, 632–635.

Nielsen, C. K., Anderson, R. G.,& Grund, M. D. (2003). Landscape influences on deer-vehicle accident areas in an urban environment. J Wildlife Manage. 67, 46–51.

Olson, D. D., Bissonette, J. A., Cramer, P. C., Bunnell, K. D., Coster, D. C., & Jackson, P. J. (2015). How does variation in winter weather affect deer—vehicle collision rates? Wildlife Biol. 21, 80–87.

Pafko, F., & Kovach, B. (1996). Experience with deer reflectors. Trends in addressing transportation-related wildlife mortality. Minnesota Department of Transportation, Office of Environmental Services, Minnesota, USA. 10 pp.

Peris, S., Baquedano, R., Sánchez, A., & Pescador, M. (2005). Mortalidad del jabalí (*Sus scrofa*) en carreteras de la provincia de Salamanca (NO de España): ¿Influencia de su comportamiento social? Galemys. 17, 13–23.

Pluntke, D. (2014). Halt bei Blau ist Schlau: Auswertung der Wildunfallzahlen im Landkreis Oldenburg sowie Rückschlüsse auf die Wirksamkeit blauer Wildwarnreflektoren als Präventionsmaßnahme. Bachelor thesis, University of Hannover. 41 pp.

Primi, R., Pelorosso, R., Nicolina Ripa, M., & Amici, A. (2009). A statistical GIS-based analysis of wild boar (*Sus scrofa*) traffic collisions in a Mediterranean area. Ital J Anim Sci. 8, 649–651.

R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. (2018). URL https://www.R-project.org/.

Ramezani, H., & Holm, S. (2011). Sample based estimation of landscape metrics; accuracy of line intersect sampling for estimating edge density and Shannon's diversity index. Environ Ecol Stat. 18, 109–130.

Ramp, D., Caldwell, J., Edwards, K.A., Warton, D., & Croft, D.B. (2005). Modelling of wildlife fatality hotspots along the snowy mountain highway in New South Wales, Australia. Biol Conserv. 126, 474–490.

Ramp, D., Wilson, V. K., & Croft, D. B. (2006). Assessing the impacts of roads in peri-urban reserves: Road-based fatalities and road usage by wildlife in the Royal National Park, New South Wales, Australia. Biol Conserv. 129, 348–359.

Rodts, J., Holsbeek, L., Muyldermans, S., & België, V. (1998). Dieren onder onze wielen: Fauna en wegverkeer. Vubpress. Brussel. 190 pp.

Roedenbeck, I.A.E. (2007). Landscape-scale effects of roads on wildlife. PhD thesis. University of Giessen. 157 pp.

Rowden, P., Steinhardt, D., & Sheehan, M. (2008). Road crashes involving animals in Australia. Accident Anal Prev. 40, 1865-1871.

Schafer, J. A., Carr, W. P., & Penland, S. (1988). Effectiveness of wildlife warning reflectors in reducing deer-vehicle accidents in Washington State. J Safety Res. 19, 99–100.

Schilderwerk Beutha. (2017). Der Wildwarnreflektor. http://www.halbkreisreflektor.de/. Accessed December 6 2017.

Schiviz, A. N., Ruf, T., Kuebber-Heiss, A., Schubert, C., & Ahnelt, P. K. (2008). Retinal cone topography of artiodactyl mammals: Influence of body height and habitat. J Comp Neurol. 507, 1336–1350.

Schulze, C., & Polster, J.U. (2017). Wirkungsweise von Wildwarnern. Heft 1127/2017. In: Forschung Straßenbau und Straßenverkehrstechnik. Hrsg: Bundesministerium für Verkehr und digitale Infrastruktur. 96 pp.

Seiler, A. (2005). Predicting locations of moose–vehicle collisions in Sweden. J Appl Ecol. 42, 371–382.

Sivic, A., & Sielecki, L. (2001). Wildlife Warning Reflectors Spectrometric Evaluation. Ministry of Transportation, British Columbia, Canada. 9 pp.

Snow, N. P., Porter, W. F., Williams, D. M. (2015). Underreporting of wildlife-vehicle collisions does not hinder predictive models for large ungulates. Biol Conserv. 181, 44–53.

Spatharis, S., Roelke, D. L., Dimitrakopoulos, P. G., & Kokkoris, G. D. (2011). Analyzing the (mis) behavior of Shannon index in eutrophication studies using field and simulated phytoplankton assemblages. Ecol Indic. 11, 697-703.

Szél, Á., Röhlich, P., Caffé, A.R., & van Veen, T. (1996). Distribution of cone photoreceptors in the mammalian retina. Micros Res Techniq. 35, 445–462.

Underwood, A. J. (1997). Environmental decision-making and the precautionary principle: What does this principle mean in environmental sampling practice? Landscape Urban Plan. 37, 137–146.

Underwood, A. J., & Chapman, M. G. (2003). Power, precaution, Type II error and sampling design in assessment of environmental impacts. J Exp Mar Biol Ecol. 296, 49–70.

van Langevelde, F., & Jaarsma, C F. (2004). Using traffic flow theory to model traffic mortality in mammals. Landscape Ecol. 19, 895-907.

VerCauteren, K. C., & Pipas, M. J. (2003). A review of color vision in white-tailed deer. Wildlife Soc B. 31, 684–691.

Waring, G. H., Griffis, J. L., & Vaughn, M. E. (1991). White-tailed deer roadside behavior, wildlife warning reflectors, and highway mortality. Appl Anim Behav Sci. 29, 215–223.

Zacks, J. L. (1985). An investigation of Swareflex wildlife warning reflectors. Report No. HRP 0010 (7). United States Department of Transportation Federal Highway Administration. Washington, D.C. 14 pp.

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Chapter 4

Wildlife Warning Reflectors Do not Alter the Behavior of Ungulates and Motorists even in the Short Term to Reduce the Risk of Wildlife-Vehicle Collisions

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(in review)

[1] Anke Benten was responsible for data collection, analyses, results and writing the manuscript. Niko Balkenhol, Torsten Vor and Christian Ammer supervised the data analyses and the manuscript.

Wildlife Warning Reflectors Do not Alter the Behavior of Ungulates and Motorists even in the Short Term to Reduce the Risk of Wildlife-Vehicle Collisions

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Abstract

Collisions of vehicles with wildlife pose a serious risk to humans and animals, causing high economical and ecological damage each year. From various mitigation measures developed over the years only few measures are economical sound to be implemented. Among these, wildlife warning reflectors enjoy great popularity, although recent studies have shown that they have no long-term impact on wildlife-vehicle collisions or on the behavior of animals along roads. However, beliefs on their effect on animals and motorists, at least temporary, persist among manufacturers and hunters. In our study, we analyzed the reaction of ungulates towards oncoming vehicles and motorists towards wildlife near roads before and after installation of modern multi-colored wildlife warning reflectors. We also tested for a potential habituation effect. In total, we recorded 13 study sites during a 12 month study period with thermal network cameras before and after wildlife warning reflector installation and controls for seasonal variation in animal behavior. We used linear mixed-effects models (LMM) and generalized linear mixed-effects models (GLMM) to evaluate the effect of the reflectors on road crossing events, reaction of animals to vehicles (positive vs. negative; *no reaction* < *alarm* < *locomotion* < *flight*), flight events, flight initiation distance and motorist behavior. We did not find any habituation effect, as wildlife warning reflectors did not influence the behavioral response of animals to oncoming vehicles, except for the transition phase from *alarm* to *locomotion* when ungulates were more likely to move with reflectors present. But this effect only lasted 16.5 days and did not influence the risk of a collision with vehicles. In addition, reflectors did not alter the driving behavior of motorists. We conclude that wildlife warning reflectors are not effective for reducing vehicle collisions with wildlife.

Key words

Animal-vehicle collisions, Deer-vehicle collisions, Wildlife Mirrors, Roadside reflectors, Deer mirrors

Introduction

Threat assessment and predator recognition are crucial for the survival of animals. While prey species developed sophisticated strategies to avoid natural predators, including visual, auditory or olfactory cues or a combination of these modalities (Caro, 2005), man-made sources of mortality, e.g. vehicle traffic, do not resemble theses predators and are often described as an evolutionary novel sort of 'predator' (Lima et al., 2014). However, the ability of animals to identify causes of mortality, known or novel, will likely trigger some kind of anti-predator behavior (Lima et al., 2014), including predator-elicited alarm calls, seeking out refuges, vigilance, moving away from a source of danger (Blumstein et al., 2001), and is thought to correlate positively with the associated seriousness of danger (Blackwell et al., 2014).

One of the most directly human caused sources of mortality for wildlife species are collisions with vehicles. These wildlife-vehicle collisions have become a serious threat towards humans and animals, with an economic loss in the billions. More specifically, more than 264,000 collisions have been reported every year in Germany. These collisions were mainly caused by ungulates (Seiler, 2004, Colino-Rabanal, 2011, Hothorn et al., 2015, GDV, 2017), each estimated between 7,000 € (roe deer (*Capreolus capreolus*)) up to 50,000 € (wild boar (*Sus scrofa);* Olsson and Widén, 2007, Thurfjell et al., 2015). Temporal patterns, such as time of the day, animals' and species' activity phases or moon phases influence the collision risk with wildlife (e.g. Peris et al., 2005, Langbein et al., 2011, Hothorn et al., 2015). The spatio-temporal distribution depends on other local factors, as well, such as land-use patterns or forest coverage (e.g. Malo et al., 2004, Seiler, 2005, Gunson et al., 2009). Other factors, such as speed limit, also have an effect on collisions, increasing the mortality of various species from 10 to 75% by an increase of 30 km/h (Farmer and Brooks, 2012).

In Europe, ungulate-vehicle collisions follow a north-south gradient, with moose and roe deer being mostly involved in collisions in Sweden (Seiler, 2004), while wild boars are mainly involved in collisions in Spain (Colino-Rabanal, 2011). In Germany, reported wildlife-vehicle collisions especially comprise roe deer and wild boar (GDV, 2017). Roe deer form small groups in winter and are rather solitary for the rest of the year (Vincent et al., 1995, Mysterud, 1999). They frequent open areas and shift between forests and agricultural fields during night for feeding and shelter (Danilkin and Hewison, 1996, Mysterud et al., 1999). Hence, road crossing occurs especially during the dark hours (Hothorn et al., 2015). Wild boars live in groups of females and juveniles, while adult males are solitary (Briedermann, 2009). Collisions with this species are often related to forest cover and maize fields (Colino-Rabanal et al., 2012).

Identifying adequate, cost effective mitigation measures are of great interest for both, economists and animal ecologists. Certainly, most measures are concomitant with high costs and maintenance (Kruidering et al., 2005, Huijser et al., 2007), ineffective due to habituation of humans (Beben, 2012) or fail to alter wildlife road crossing behavior, such as odor repellents (Elmeros et al., 2011). Besides olfactory scaring devices, optic devices such as wildlife warning reflectors are widespread on the market. These reflectors are attached to guidance posts, supposedly reflecting the headlight of a vehicle to the road shoulder in order to deter wildlife from entering the road while a vehicle is passing (Motzener Wildschutzwarner, 2018). While the efficacy of these reflectors has been contradictorily discussed ever since their first release (cf. Brieger et al., 2016, Benten et al., 2018), their alleged effect is carried on anecdotally via manufacturers and hunters. However, recent studies demonstrated that the reflectors have no impact on wildlife-vehicle collisions (Brieger et al., 2017, Benten et al., in review.), but it has been reported that they may influence deer behavior for a short time (Waring et al., 1991, Ujvári et al., 1998). Thus, if ungulates alter their behavior in the presence of the reflectors in the short term, thereby reducing the risk of colliding with a vehicle, the reflectors might be effective in reducing wildlife-vehicle collisions during high peak collision seasons. However, well designed studies on this subject are missing. Here, we tested if wildlife warning reflectors changed the reaction of animals to oncoming vehicles or of motorists to animals near the road, supporting a reduction in wildlife-vehicle collisions. According to the manufacturer's information about the effect of the reflectors, animals stop moving and remain while vehicles drive by, we expected that ungulates reduce road crossings (H1a), increase responses that would reduce the risk of a collision with vehicles, i.e. positive, compared to negative reactions when vehicles are approaching (H1b), decrease flight events (H1c), decrease flight initiation distance (H1d) and shift their behavioral response to alarm (H1d) if reflectors are present. We further expected that motorists more often slow down or stop due to increased attention to wildlife near roads with reflectors present (H2).

Materials and methods

Study area

The study was conducted between 2015-08-18 18:00 and 2016-09-15 06:30 within the Weser-Leine Uplands in Central Germany (52°0’ N, 9°0’ E) on a total area measuring about 2,300 km^2. Study locations (*N* = 13, Fig. 4.1) were located in Göttingen (*N* = 10; 51°32’ N, 9°56’ E), Kassel (*N* = 2; 51°19’ N, 9°29’ E) and Höxter (*N* = 1; 51°46’ N, 9°22’ E). Forest coverage ranges from 25.5% (Höxter), 32.9% (Göttingen) up to 39.2% (Kassel). Agricultural land covers between 47.5% (Kassel), 54.7% (Göttingen) and 61.9% (Höxter) of the total area. Study sites were selected by the occurrence of wildlife-vehicle collisions reported to the local police authorities as an indicator for high occurrence of wildlife near roads on one primary, six secondary and six tertiary roads. Speed limit was 100 km/h except for one tertiary road with 70 km/h. Roads with forest on one side and agricultural land-use on the other side were prioritized, as ungulates tend to shift between forest and open field and to allow animal observations in various distances to the road. Trees outside the forest or forest patches were used to mount thermal network cameras in about 3 m height for video observations.

Wildlife entering the area observed was recorded using a thermal network camera (Axis Q1931-E, Axis Communications AB, Inc., Lund, Sweden) with a 35 mm focal lens and a viewing angle of 10.7°. With this, objects of 1.8 m x 0.5 m (e.g. humans) can be detected at a distance of more than 1000 m, recognized at a distance of 260 m and identified at 130 m (Axis Communications AB Inc., 2017). This camera lens allowed lateral coverage of the surrounding up to 75 m at a distance of about 400 m, depending on study site conditions (i.e. slope). Cameras were equipped with a network connector (Power over Ethernet Adapter PoE T81B22 30W, Axis Communications AB, Inc.) with energy supply provided by a car battery (Banner Running Bull Autobatterie 12V 70Ah, Banner Inc., Linz, Austria), allowing evening and nocturnal recording durations of approximately 7 days. Data recorded was stored inside the camera on a 64 GB SDXC Extreme Mini memory card (SanDisk Corp., Milpitas, USA). The SD cards and car batteries were changed every week.

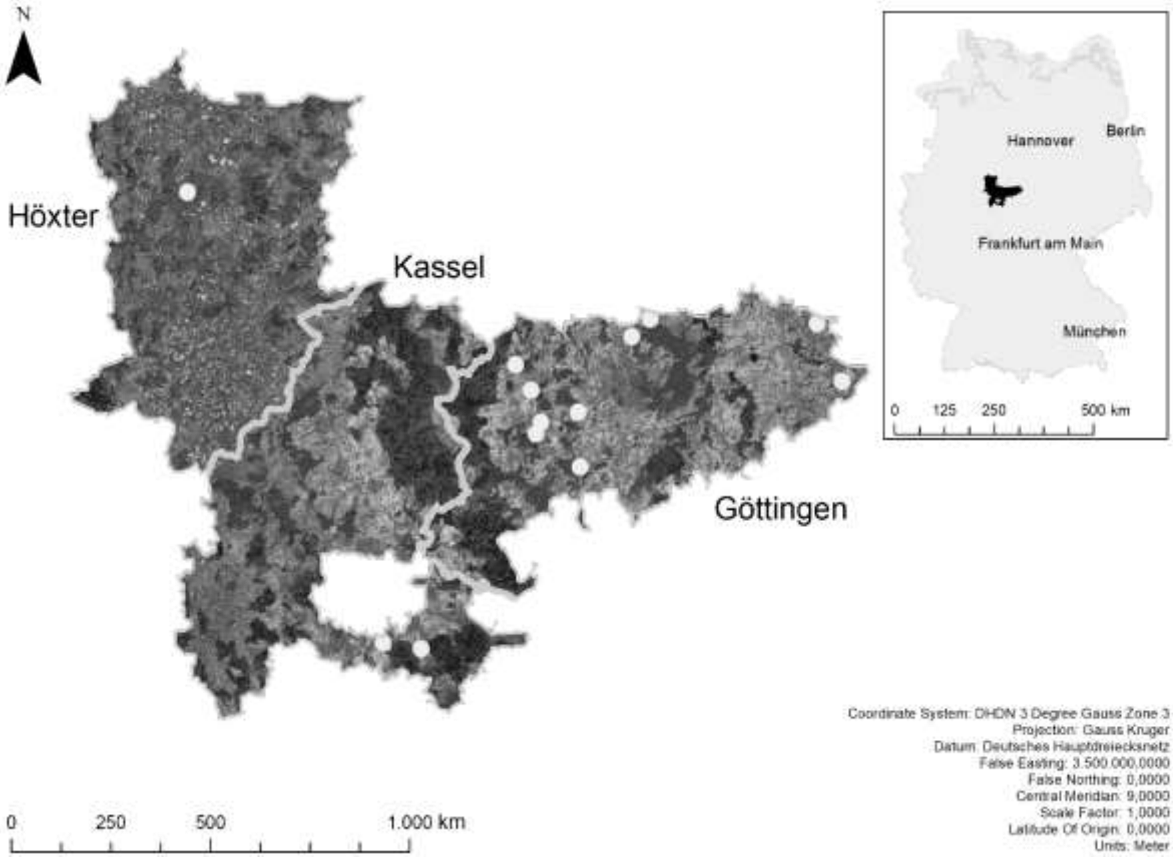

Figure 4. 1. Map of the study area (2,300 km^2) including the counties Göttingen (N = 10 study locations), Kassel (N = 2 study locations) and Höxter (N = 1 study location). Study locations were recorded without wildlife warning reflectors ('control') for four weeks and hereafter with wildlife warning reflectors ('test') for another four weeks using a thermal network camera (image © 2018 Axis Communications AB). Basemap: Aerial Imagery Basemap.

Main species involved in wildlife-vehicle collisions in this area are roe deer, followed by wild boar. Their occurrence varies slightly within the study area, detailed information on annual harvest is given in Table 4. 1. Data on hunting statistics were provided by local hunting authorities.

Reflectors used in this study were “*multi-wildlife warner*” by Motzener Kunststoff- and Gummiverarbeitung Inc. Reflectors are 175 mm x 55 mm x 35 mm in size and have a micro prismatic reflective film by 3M (Minnesota, USA) with additional eight multi-colored platelets with a honeycomb structure. Reflectors were mounted on guidance posts alongside roads. The reflectors were installed in accord with the manufacturer’s instructions at the 25 cm wide black strip of the reflector posts at a height of 55 cm - 80 cm and were not needed to be adjusted to the slope of the surrounding landscape. The distance between these posts varied between 25 m (curve) and 50 m (straight stretch) with a median distance of 41.87 m ± 7.52 m.

Table 4. 1. Species distribution within the three studied counties Göttingen, Kassel and Höxter indicated by the annual harvest in 2016/17. Roe deer (*Capreolus capreolus*) and wild boar (*Sus scrofa*) are most abundant, while red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) occur only occasionally within the study area.

	counties		
species	Göttingen	Kassel	Höxter
roe deer	3,543	4,602	4,326
wild boar	3,178	2,620	2,811
red deer	196	107	131
fallow deer	1	12	598

Study design

Two study sites were equipped simultaneously with one thermal network camera each. The first study site (A) was filmed without the reflectors for four weeks from 30 min before dusk to 30 min after dawn. Hereafter, wildlife warning reflectors were installed along posts at the road stretch within camera sight. A second study site (B) was equipped with another thermal network camera, recording the study site B without reflectors for the first four weeks. When camera A was relocated to a new study site (C) after a total of eight weeks, reflectors were installed at study site B, which has been observed without reflectors for four weeks by then. This alternating switch of study sites and reflector attachments was kept up for 12 months, allowing us to compare the behavior of wildlife before and after implementation of the reflectors as well as study sites with and without reflectors simultaneously to control for a temporal bias, e.g. behavioral variations during to rutting season. As study sites had to be visited weekly for changing batteries and memory cards, we also controlled that the reflectors were complete and not covered by the roadside vegetation or road dirt.

Data analysis

In this study we collected about 10.000 hours of video material. At first, recordings were revised for events including wildlife and vehicles. Video sequences were excised from 20 sec before vehicles appeared with animals being around until the encounter has passed to observe neutral behavior and a change in behavioral patterns of observed animals. At a main speed limit of 100 km/h, the approaching vehicles distance is > 550 m at 20 sec before reaching the animals position. Blackwell (et al., 2014) assumed that approaching vehicles are not perceived as a threat until the animal-vehicle distance is < 470 m, presumably the zone of awareness for white-tailed deer (*Odocoileus virginianus*; Stankowich and Coss, 2005). Pre-analyzing the first 100 events this time frame has been shown to be sufficient to observe both, neutral behavior and the reaction to oncoming vehicles. We included information on species, number of animals (single or group), sex when possible, weather conditions, distance to the road and road crossing events. We categorized the distances of the animals to the road into five categories: 1) on the road, 2) within 1 m to the road, 3) between 1.1 and 5 m to the road, 4) between 5.1 and 10 m to the road and 5) more than 10 m to the road, while a vehicle was passing by. For flight initiation distances we estimated distances between the animals and vehicles when animals started leaving the roadside area. This distance is used as a measure of fear and correlates positively with the associated seriousness of danger (e.g. Blackwell et al., 2014). Moreover, to prevent an observer bias, video sequences were analyzed double-blind for the reaction of wildlife to oncoming vehicles, i.e. without information on when reflectors were installed. Events (*N* = 1,070) including more than one animal were analyzed for each animal present individually (*N* = 1,673 individual responses). We categorized the overall reaction of animals to oncoming vehicles in regard to Valitzky (et al., 2007) into the groups *negative*, i.e. the risk of a collision increases, and *positive*, i.e. the risk of a collision does not increase, but refrained from using the category *neutral* as the reaction either increased or not increased the risk of a collision.

Moreover, we analyzed the behavior of animals in accord to Ujvári (et al., 1998) for deer responding to oncoming vehicles into four categories (*flight*, *alarm*, *movement of head, no visible reaction*), but modified the category *movement of head* to *locomotion.* Detailed information on behavioral categories is given in Table 4. 2. These categories have been ranked *no visible reaction* < *alarm* < *locomotion* < *flight*. Besides the reaction of animals, also the reaction of drivers was ranked and included in further analyses (i.e. *no visible reaction* < *slowing down* < *full break*). *Full break* means that the vehicle comes to a stop, while *slowing down* is defined as a reduction in speed, increasing the average time for passing two guidance posts. Hereafter we included information on times without reflectors (control) and with reflectors (test), as well as on the duration of the treatment (i.e. duration of control = days since camera installation, duration of test = days since reflector installation). Furthermore, we included information on whether reflectors could have influenced the behavior of animals for each event. We defined that the reflectors would not have been able to act if the animals had left the road area before the car was in sight, if the animal is already on the road or between the guidance posts and the road, and if the animal is already far away before the car comes in sight, heading away from the road.

Statistics

Statistical analyses were performed using the R system for statistical computing (R Core Team, 2018, version 3.4.3). Mixed models were fitted using the add-on packages *lme4* for

GLMM (Bates et al., 2015, version 1.1-17). For analyses of animal behavior we filtered video analyses according to the actual events in which the reflectors could have acted from the animal's point of view (N = 1,093 individual responses), but included all events for the analyses of the motorist's behavior (N = 1,070 events).

Table 4. 2. Behavioral categories based on the studies by Valitzky et al. (2007; positive, negative) and Ujvári et al. (1998; flight, alarm, no reaction visible), including a new category locomotion. The distance of 150 m was chosen due to the stopping and breaking distances of vehicles at 100 km/h ([1]).

behavior	description
positive	animal remains in a certain distance to the road, leaves the road area without crossing the road, leaving the road area with road crossing > 150m in front of the car
negative	animal remains on the road, animal crosses the road < 150 m in front of the car
flight	sudden and rapid movement away from the reflectors by walking, trotting or galloping
alarm	sudden raise of the head, stays with its neck straight, possibly with tense muscles and movement of the ears
locomotion	animal moves calmly away from the reflectors without sudden or rapid movement
no reaction visible	no reaction visible, animal shows no alteration in behavior

[1] https://www.bussgeldkatalog.org/anhalteweg/

We applied a generalized linear mixed-effects model (GLMM) for analyzing animals' road crossing behavior while a vehicle was approaching (H1a; *no crossing* vs. *responding crossing*), binary analyses of negative (H1b; 0 = increase in collision risk) and positive (1 = no increase in collision risk) reaction of ungulates to approaching vehicles, and a potential reduction in flight events with reflectors present (H1c). These models included the explanatory variables *treatment* (control vs. test), *duration of treatment, species* (roe deer, fallow deer, wild boar, deer (i.e. more detailed identification not possible)), *unit* (individual, group ≥ 2), and *distance to road* (0 m, 1 m, 1-5 m, 5 - 10m, > 10m). We included testing sites and event ID as random effects:

```
response.variable ~ treatment*treatment_days + species
      + unit + distance_road + (1|Site) + (1|Event)
```

To test for a reduction in flight initiation distances (H1d), we performed a linear mixed-effects model (LMM) using the same explanatory variables. To model a potential change in the reaction of animals towards oncoming vehicles, relating to the duration since wildlife warning reflectors have been installed (H1e), we modified generalized linear mixed-effects models to perform a rank-ordered logit model with the order: *no visible reaction* < *alarm* < *locomotion* < *flight.* We included the same explanatory variables as in the previous models. Finally, to determine whether the reaction of motorists relates to the presence of the reflectors, we also used a rank-ordered logit model (order: *no visible reaction* < *slowing down* < *full break)*, comparing deer and wild boars.

Results

Overall, we analyzed 1,070 events including 1,673 individual animals. We identified three different ungulate species (roe deer: N = 843 individuals, fallow deer: N = 268 individuals, wild boar: N = 362 individuals). In 200 cases deer species could not further be specified. In this study, we did not include other animal species than ungulates. Group sizes varied from each other, with slight differences within deer species and large difference between deer species and wild boar (mean ± SD for roe deer: 1.95 ± 1.18; fallow deer: 2.62 ± 1.45; deer: 2.02 ± 1.10; wild boar: 7.28 ± 4.12).

We found that wildlife warning reflectors could have altered the behavior of an animal in 1,093 out of 1,673 individual responses (i.e. 65.33%). We examined whether the presence of wildlife warning reflectors influenced the road crossing behavior of the animals at side. We found that the presence of reflectors and therefore the duration since installation did not affect the road crossings of ungulates while vehicles are approaching (H1a; GLMM: $p = 0.948$ for the treatment control vs. test, and $p = 0.617$ for the duration of treatment). We found no change in positive or negative reactions towards oncoming vehicles when reflectors were installed (H1b; GLMM: $p = 0.419$ for the treatment control vs. test, and $p = 0.343$ for the duration of treatment; Table 4. 3). However, positive reactions correlated positively with the distance to the road (GLMM: $p = 0.002$). This also accounts for flight events (H1c; Table 4. 3), which decreased with increased distance to the road (GLMM: $p < 0.001$). Moreover, wild boars were more likely to flee compared to the other ungulate species (GLMM: $p = 0.003$). Nevertheless, the presence of wildlife warning reflectors did not influence the flight events (GLMM: $p = 0.397$ for the treatment vs. control, and $p = 0.920$ for the duration of treatment) nor the flight initiation distance (H1d; LMM: $p = 0.813$ for the treatment control vs. test, and $p = 0.648$ for the duration of treatment). Additionally, none of the other explanatory variables affected the flight events or flight initiation distance.

We tested whether the reaction of animals (H1e; *no visible reaction* < *alarm* < *locomotion* < *flight*) related to the presence of the reflectors (Table 4. 4). We found no change in the reaction categories of *no visible reaction* and *alarm* when reflectors were attached (GLMM rank-ordered logit model: $p = 0.882$ for the treatment control vs. test, and $p = 0.876$ for the duration of treatment).

Table 4. 3. Response of ungulates to approaching vehicles for negative vs. positive behavioral categories (H1b; negative: the risk of a collision increases, and positive: the risk of a collision does not increase), modified after Valitzky et al., 2007 (left), and for flight events (H1c; right), giving the estimates, standard errors (SE), z values (z) and p values (p).

	positive vs. negative reaction (H1b)				flight events (H1c)			
	estimate	SE	z	p	estimate	SE	z	p
Intercept	4.816	1.558	3.090	0.002 **	-11.921	2.597	-4.590	< 0.001 ***
Treatment_test	-1.336	1.656	-0.807	0.419	1.345	1.591	0.846	0.397
Duration_Treatment	-0.049	0.052	-0.948	0.343	0.006	0.064	0.100	0.920
Species_fallow deer	0.468	1.412	0.332	0.739	-1.336	2.352	-0.568	0.569
Species_roe deer	-0.049	1.139	-0.043	0.096	4.077	2.209	1.846	0.064
Species_wild boar	-1.062	1.443	-0.736	0.461	7.609	2.612	2.913	0.003**
Unit	1.088	0.814	1.337	3.076	-1.072	0.794	-1.350	0.177
Distance_road	0.876	0.285	3.076	0.002 **	0.911	0.135	6.736	< 0.001 ***
Treatmenttest:Duration	0.136	0.094	1.440	0.149	0.021	0.090	0.239	0.811

Treatment_test (i.e. wildlife warning reflectors installed) compared to Treatment_control (i.e. without wildlife warning reflectors). Duration_Treatment for the days of the treatment (for control = days since camera installation, for test = days since reflector installation). Species_fallow deer/ Species_roe deer and Species_wild boar compared to Species_deer (i.e. a more precise determination of the deer species was not possible). Unit compared individual (1 animal) with group (≥ 2 individuals). Distance_road (0 m, 1 m, 1.1 - 5 m, 5.1 – 10 m, > 10 m). Treatment_test: Duration temporal influence of the presence of the reflectors (relates to Treatment_test).

Table 4. 4. Response of ungulates to approaching vehicles for determining the influence of wildlife warning reflectors on the behavioral categories no visible reaction < alarm < locomotion < flight, modified after Ujvári et al., 1998 (H1e), comparing the categories no visible reaction < alarm (left), alarm < locomotion (middle), and locomotion < flight (right), giving the estimates, standard errors (SE), z values (z) and p values (p).

	ungulates' reaction to oncoming vehicles *no visible reaction < alarm < locomotion < flight*											
	no visible reaction < alarm				*alarm < locomotion*				*locomotion < flight*			
	estimate	SE	z	p	estimate	SE	z	p	estimate	SE	z	p
Intercept	12.524	9.318	1.343	0.178	36.425	14.891	2.445	0.014 *	-27.130	13.196	-2.055	0.039 *
Treatment_test	-0.636	4.286	-0.148	0.882	19.746	7.028	2.809	0.004 **	-0.312	11.540	-0.027	0.978
Duration_Treatment	-0.027	0.179	-0.155	0.876	0.568	0.279	2.037	0.041 *	-0.006	0.417	-0.016	0.986
Species_fallow deer	330.207	< 0.001	< 0.001	0.999	-18.076	13.241	-1.365	0.172	16.504	12.409	1.329	0.183
Species_roe deer	-2.635	9.143	-0.288	0.773	-24.163	13.366	-1.807	0.070	16.534	9.385	1.761	0.078
Species_wild boar	-6.186	9.078	-0.681	0.495	-7.756	17.442	-0.444	0.656	15.842	12.911	1.226	0.291
Unit	-0.122	2.300	-0.053	0.957	3.762	3.708	1.014	0.310	-0.435	5.890	-0.073	0.941
Distance_road	-0.150	0.219	-0.687	0.491	-1.960	0.512	-3.828	< 0.001 ***	0.037	0.663	0.055	0.955
Treatmenttest:Duration	0.037	0.245	0.152	0.878	-1.203	0.420	-2.860	0.004 **	0.073	0.618	0.119	0.904

Treatment_test (i.e. wildlife warning reflectors installed) compares to Treatment_control (i.e. without wildlife warning reflectors). Duration_Treatment for the days of the treatment (for control = days since camera installation, for test = days since reflector installation). Species_fallow deer/ Species_roe deer and Species_wild boar compared to Species_deer (i.e. a more precise determination of the deer species was not possible). Unit compared individual (1 animal) with group (≥ 2 individuals). Distance_road (0 m, 1 m, 1.1 – 5 m, 5.1 – 10 m, > 10 m). Treatment_test: Duration temporal influence of the presence of the reflectors (relates to Treatment_test).

We found that animals were more likely to shift from *alarm* to *locomotion* when reflectors were present (GLMM rank-ordered logit model: $p = 0.004$ for the treatment control vs. test, and $p = 0.041$ for the duration of treatment). However, this effect decreased with time (estimates for the treatment: 19.746; and for the treatment relating to the duration since installation: -1.203) and disappeared after 16.5 days. Additionally, the distance to the road significantly influenced whether an animal started to move and increased with less distance (GLMM rank-ordered logit model: $p < 0.001$). The subsequent transition from locomotion to flight was not significantly affected by any of the explanatory variables (*locomotion* < *flight*).

Finally, we were interested whether the reflectors influence the driving behavior of motorists (H2; *no visible reaction* < *slowing down* < *full break*). We found no evidence that wildlife warning reflectors altered the driving behavior of motorists (GLMM rank-ordered logit model: *no visible reaction* < *slowing down* $p = 0.988$ for the treatment control vs. test and $p = 0.814$ for the duration of treatment; *slowing down* < *full brake* $p = 0.279$ for the treatment control vs. test, and $p = 0.512$ for the duration of treatment). Moreover, none of the other explanatory variables significantly influenced the behavior of motorists.

Discussion

We studied the behavioral response of ungulates to oncoming vehicles in relation to wildlife warning reflectors and days since installation to evaluate if the reflectors are an effective tool to alter the behavior of animals and motorists in the short-term, in order to reduce wildlife-vehicle collisions. We could not find any significant effect of the reflectors on road crossing events, positive or negative reactions to oncoming vehicles, flight events or flight initiation distance. Negative reactions and flight events correlated significantly with the distance to the road. Moreover, wild boars were more likely to initiate flight when vehicles were approaching compared to other ungulate species and ungulates were more likely to elicit dynamic responses to oncoming vehicles with reflectors present, which also correlates with the distance to the road. However, this did not influence the risk of wildlife-vehicle collisions. Animals were more likely to move when reflectors were present and with decreased distance to the road. However, the reflectors did not influence, whether the animals moved in a relaxed (*locomotion*) or in a stressed (*flight*) manner. This effect decreased over time and disappeared after 16.5 days. Moreover, we did not find any significant shift in driving behavior of motorists, reducing the risk of wildlife-vehicle collisions.

The efficacy of wildlife warning reflectors has been a topic of interest and contradictions ever since their first release (e.g. McLain, 1964, Waring et al., 1991, Benten et al., 2018). As the reflectors are comparably cost-effective in contrast to most other mitigation measures that aim to reduce the number of wildlife-vehicle collisions, manufacturers and few studies advertise them as the method of choice to prevent accidents with wildlife (Gladfelter, 1984, Grenier, 2002, Motzener Wildschutzwarner, 2018). While recently published meta-analyses on the efficacy of the reflectors, analyzing wildlife accident data in literature (Brieger et al., 2016, Benten et al., 2018), as well as a comprehensive study on the inefficacy of modern wildlife warning reflectors (Benten et al., in review) give reason to rule out any effect of the reflectors on reducing wildlife-vehicle collisions, the rumor of a short-term influence of the reflectors on the behavior of animals in the vicinity of roads is still circulating.

Most behavioral studies on the reaction of animals to oncoming vehicles with wildlife warning reflectors present could not find any change in behavioral response of the animals in the long-term (Griffis, 1984, Zacks, 1986, Sheridan et al., 1991, D’Angelo et al., 2006, Ramp and Croft, 2006, Brieger et al., 2017). Only Ujvári et al. (1998) considered a potential effect of habituation and analyzed a change in reaction over time. The authors found that the reflectors altered the behavior of fallow deer for as long as 17 days, before the animals habituated. Interestingly, the only effect of the reflectors on animal behavior we found, to shift from *alarm* to *locomotion*, also vanished after 16.5 days. However, this observation is in contrast to the manufacturers' statements that the reflectors cause the animals to increase their vigilance and poise their position (Motzener Wildschutzwarner, 2018). Moreover, this effect correlates positively with the proximity to the road. The closer the animals were to the road, the more likely it was that they showed evasive behavior (*alarm* > *locomotion*; flight events) and the more likely was a negative reaction, increasing the risk of a collision. Hence, if the reflectors lead to an increased locomotion at short distances to the road with simultaneous increase in collision risk, animals are more likely to be involved in negative animal-vehicle interactions. This was also described by D'Angelo et al. (2006), evaluating white-tailed deer (*Odocoileus virginianus*) behavior in regard to various wildlife-warning reflector models. In this study, deer were more likely to react negatively, i.e. increasing the likelihood of causing a deer-vehicle collision, when reflectors were attached (D'Angelo et al., 2006). In contrast, Riginos et al. (2018) found that deer road-crossing behavior was less risky with reflector treatment compared to no reflectors. The authors also found that deer road-crossing behavior was least risky when guidance posts were covered with white canvas bags, but reflectors were more effective than 'nothing'. Considering the effect of white canvas bags over reflectors, white canvas bags may stand out more clearly from the surrounding landscape than reflectors. These 'novel objects' may alter the behavior of animals in the beginning, but habituation is to be expected (cf. Forkman et al., 2007).

Besides the 'novel object' theory, a lack of reaction to wildlife warning reflectors might be explained by the choice of color rather than the potential of reflecting devices *per se*. Whereas humans are trichromatic, perceiving light in the blue, green and red spectrum (Elliot et al., 2007), most mammals are dichromatic (e.g. Carroll et al., 2001, Ahnelt et al., 2006, Schiviz et al., 2008). Hitherto, only one study evaluated the influence of blue wildlife warning reflectors on the reaction of roe deer to oncoming vehicles so far (Brieger et al., 2017). However, these authors could not find any shift in behavioral response of roe deer to oncoming vehicles with modern, blue reflectors present. D'Angelo et al. (2006) argued that the visual system of nocturnal animals, concomitant with a higher density of rods and a better perceptibility of light below 540 nm (Szél et al., 1996, VerCauteren and Pipas, 2003, Hanggi and Ingersoll, 2007). Thus, a visual adaptation to rapid increases in light intensity, i.e. vehicle headlights, is considerably slower. Moreover, spectrometric analyses of wildlife warning reflectors indicated that the light intensity of the reflections to the roadside area is already very small at short distances and cross-faded by the vehicle headlights (Sivic and Sielecki, 2001, Schulze and Polster, 2017).

As the light intensity of the direct reflection back to the driver is far larger than to the road shoulder (Schulze and Polster, 2017) the reflectors could rather influence the behavior of vehicle drivers than of animals. While an effect of deer-whistles on motorists' attention to animals near roads, who were knowingly involved in the study, has been reported, resulting in a decrease of collisions with wildlife (Zacks, pers. comm., 2015), our results did not indicate any effect of the reflectors on drivers. Motorists were either not aware of the presence of the reflectors or did not take the reflectors into further consideration. Admittedly, the evaluation of the reaction of motorists to the presence of wildlife warning reflectors could need more psychological consideration. If the reflectors caused any effect on vehicle drivers that had reduced the numbers of collisions with wildlife, this would have been reflected in the studies on wildlife-vehicle accident analyses. However, since none of these studies found a reduction in collisions numbers (Brieger et al., 2016, Benten et al., 2018, Benten et al., in review), it is unlikely that the reflectors influence drivers, leading to a reduction of wildlife-vehicle collisions.

In addition, our data show that wild boars tend to fly earlier than other ungulate species. While the social organization of wild boars is centered around female groups (Mauget, 1980), and females give birth to large litters (Kaminski et al., 2005), herds of wild boar usually consist of a few adult females and many offspring. Moreover, group sizes of wild boars involved in vehicle interactions differ substantially from deer group sizes, although we could not find any difference in the reaction for single individuals and more than one individual. LaGory (1987) reported that group size may positively affect flight response, although this has only been examined for deer, so far. Consequently, the more frequent flight events of wild boars probably result in the social structure of the herds and their group size.

Conclusions

This study has shown that ungulates did not alter their response to oncoming vehicles far enough to reduce the risk of a collision with vehicles when wildlife warning reflectors are present, independent of the days since installation. Ungulates were more likely to temporarily transit from *alarm* to *locomotion* when reflectors were present. However, this effect only lasted for 16.5 days and did not influence the risk of a collision with vehicles. Animals, especially wild boar, were more likely to initiate flight and to transit *alarm* to *locomotion* when their distance to the road decreased, independent of the presence of reflectors. Our findings are in accordance with other studies showing that the reflectors do not alter animal behavior or elicit any reaction that would prevent the risk of collision for long (e.g. D'Angelo et al., 2006, Ramp and Croft, 2006, Brieger et al., 2017). Additionally, with respect to the spectrometric characteristics of the devices (Sivic and Sielecki, 2001, Schulze and Polster, 2017), any change in behavioral response with reflectors present might be rather related to the 'novel object' theory than to the physical properties of reflectors (cf. Forkman et al., 2007). However, while reflections back to the driver are far larger than to the road shoulder (Schulze and Polster, 2017), we did not find any significant change in driving behavior of motorists, either. We assume that occasional reductions of wildlife-vehicle collisions after reflector installation are more related to chance or to naturally oscillating fluctuations in population density (Fryxell et al., 1991), thus, independent of the reflectors. Considering our results and the findings of other studies, we do not recommend wildlife warning reflectors as a tool for mitigating wildlife-vehicle collisions on roads.

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References

Ahnelt, P., K., Schubert, C., Kuebber-Heiss, A., Schiviz, A., & Anger, E. (2006). Independent variation of retinal S and M cone photoreceptor topographies: a survey of four families of mammals. Visual Neurosci. 23, 429-435.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). “Linear Mixed-Effects Models Using lme4.” J Stat Softw. 67, 1–48. doi:10.18637/jss.v067.i01.

Beben, D., (2012). Crossings for animals–an effective method of wild fauna conservation. J Environ Eng Landsc. 20, 86–96.

Benten, A., Hothorn, T., Vor, T., & Ammer, C. (in review). Wildlife Warning Reflectors do not Mitigate Wildlife-Vehicle Collisions on Roads. Accident Anal Prev.

Benten, A., Annighöfer, P., & Vor, T. (2018). Wildlife Warning Reflectors’ Potential to Mitigate Wildlife-Vehicle Collisions–A Review on the Evaluation Methods. Front Ecol Evol. 6, 37.

Blackwell, B. F., Seamans, T. W., & DeVault, T. L. (2014) White-Tailed Deer Response to Vehicle Approach: Evidence of Unclear and Present Danger. Plos One. 9: e109988. doi:10.1371/journal.pone.010998.

Blumstein, D. T., Daniel, J. C., & Bryant, A. A. (2001). Anti-predator behavior of Vancouver Island marmots: Using congeners to evaluate abilities of a critically endangered mammal. Ethology. 107, 1-14.

Briedermann, L. (1990). Schwarzwild. VEB Deutscher Landwirtschaftsverlag. 524 pp.

Brieger, F., Hagen, R., Vetter, D. Dormann, C. F., & Storch, I. (2016). Effectiveness of light-reflecting devices: A systematic reanalysis of animal-vehicle collision data. Accident Anal Prev. 97, 242–260. doi: 10.1016/j.aap.2016.08.030.

Brieger, F., Hagen, R., Kröschel, M., Hartig, F., Petersen, I., Ortmann, & S., Suchant, R. (2017). Do roe deer react to wildlife warning reflectors? A test combining a controlled experiment with field observations. Eur J Wildlife Res. 63, 10.1007/s10344-017-1130-5.

Bruinderink, G., & Hazebroek, E. (1996). Ungulate traffic collisions in Europe. Conserv Biol. 10, 1059–1067.

Caro, T. (2005). Antipredator defenses in birds and mammals. University of Chicago Press. 592 pp.

Carroll, J., Murphy, C. J., Neitz, M., Hoeve, J. N. & Neitz, J. (2001). Photopigment basis for dichromatic color vision in the horse. J Vision. 1, 80-7.

Colino-Rabanal, V. J. (2011). Contribuciones al análisis de mortalidad de vertebrados en carreteras.(Doctoral dissertation). University of Salamanca. 503 pp.

Colino–Rabanal, V. J., Bosch, J., Muñoz, M. J., & Peris, S. J. (2012). Influence of new irrigated croplands on wild boar (*Sus scrofa*) road kills in NW Spain. Anim Biodiv Conserv. 35, 247-252.

D'Angelo, G., D'Angelo, J. G., Gallagher, G. R., Osborn, D. A., Miller, & Warren, R. J. (2006). Evaluation of Wildlife Warning Reflectors for Altering White-Tailed Deer Behavior along Roadways. Wildlife Soc B. 34, 1175–1183.

Danilkin, A. A., & Hewison, A. M. (1996). Behavioural ecology of Siberian and European roe deer. Chapman & Hall. 278 pp.

Elliot, A. J., Maier, M. A., Moller, A. C., Friedman, R., & Meinhardt, J. (2007). Color and psychological functioning: the effect of red on performance attainment. J Exp Psychol Gen. 136, 154-68.

Elmeros, M., Winbladh, J.K., Andersen, P.N., Madsen, A.B., & Christensen, J.T. (2011). Effectiveness of odour repellents on red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*): A field test. Euro J Wildlife Res. 57, 1223–1226.

Farmer, R. G., & Brooks, R. J. (2012). Integrated risk factors for vertebrate roadkill in southern Ontario. J Wildlife Manage. 76(6), 1215-1224.

Forkman, B., Boissy, A., Meunier-Salaün, M. C., Canali, E., & Jones, R. B. (2007). A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. Physiol Behav. 92, 340-374.

Fryxell, J. M., Hussell, D. J. T., Lambert, A. B., & Smith, P. C. (1991). Time lags and population fluctuations in white-tailed deer. J Wildlife Manage. 3, 377–385.

Fryxell, J. M., Packer, C., McCann, K., Solberg, E. J., & Sæther, B.-E. (2010). Resource management cycles and the sustainability of harvested wildlife populations. Science. 328, 903–906. doi: 10.1126/science.1185802.

GDV. (2017). http://www.gdv.de/2016/11/wildunfaelle-erreichen-hoechststand-alle-zwei-minuten-kracht-es/. Accessed February 8 2017.

Gladfelter, L. (1984). Effect of wildlife highway warning reflectors on deer-vehicle accidents. Project HR-210. Boone, Io: Iowa Highway Research Board. 11 pp.

Grenier, R. H. (2002). A study of the effectiveness of Strieter-Lite® wild animal highway warning reflector systems. Commissioned report for Strieter Corporation. 19 pp.

Griffis, J. L. (1984). Effects of Swareflex wildlife highway warning reflectors on behavior and mortality of white-tailed deer. Master thesis. Southern Illinois University at Carbondale, USA. 71 pp.

Gunson, K. E., Mountrakis, G., & Quackenbush, L. J. (2011). Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. J Environ Manage. 92, 1074–1082.

Hanggi, E. B., Ingersoll, J. F., & Waggoner, T. L. (2007). Color vision in horses (*Equus caballus*): Deficiencies identified using a pseudoisochromatic plate test. J Comp Psychol. 121, 65-72.

Hothorn, T., Müller, J., Held, L., Möst, L., & Mysterud, A. (2015). Temporal patterns of deer–vehicle collisions consistent with deer activity pattern and density increase but not general accident risk. Accident Anal Prev. 81, 143–152.

Huijser, M. P., Kociolek, A., McGowen, P. T., Hardy, A., Clevenger, A. P., & Ament, R. J. (2007). Wildlife-vehicle collisions and crossing mitigation measures: a toolbox for the Montana Department of Transportation. Helena, MT: Montana Department of Transportation. 123 pp.

Kaminski, G., Brandt, S., Baubet, E., & Baudoin, C. (2005). Life-history patterns in female wild boars (*Sus scrofa*): mother–daughter postweaning associations. Can J Zool. 83, 474-480.

Kruidering AM., Veenbaas, G., Kleijberg, R., Koot, G., Rosloot, Y., & van Jaarsveld, E. (2005). Leidraad faunavoorzieningen bij wegen. Delft, Nl: Rijkswaterstaat. 122 pp.

LaGory, K. E. (1987). The influence of habitat and group characteristics on the alarm and flight response of white-tailed deer. Anim Behav. 35, 20-25.

Lalo, J., (1987). The problem of road-kill. Am Forests. 93, 50-52.

Langbein, J., Putman, R., Pokorny, B., Apollonio, M., & Andersen, R. (2011). Traffic collisions involving deer and other ungulates in Europe and available measures for mitigation. 215-259 pp. In: Ungulate management in Europe: problems and practices, eds. R. Putman, M. Apollonio, R. Andersen (Cambridge University Press).

Lima, S. L., Blackwell, B. F., DeVault, T. L., & Fernández-Juricic, E. (2015). Animal reactions to oncoming vehicles: a conceptual review. Biol Rev. 90, 60-76.

Malo, J. E., Suarez, F., & Diez, A. (2004). Can we mitigate animal-vehicle accidents using predictive models? J Appl Ecol. 41, 701–710.

Mauget, R. (1980). Régulations écologiques, comportementales et physiologiques (fonction de reproduction): de l'adaptation du sanglier, *Sus scrofa* L., au milieu. (Doctoral dissertation). Université de Tours. 299 pp.

McLain, P.D. (1964). The story of the deer mirrors on the parkway. New Jers Outdoors. 15, 13–18.

Motzener Wilschutzwarner (2018). https://en.wildwechsel-unfall-vermeiden.de/index.html. Accessed June 20 2018.

Mysterud, A., Larsen, P. K., Ims, R. A., & Østbye, E. (1999). Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Can J Zool. 77, 776–783.

Olsson, M., & Widén, P. (2007). (Wild boar and roads) Vildsvin och Vägar. Trafikverket.https://www.trafikverket.se.

Peris, S., Baquedano, R., Sánchez, A., & Pescador, M. (2005). Mortalidad del jabalí (*Sus scrofa*) en carreteras de la provincia de Salamanca (NO de España): ¿Influencia de su comportamiento social? Galemys. 17, 13–23.

R Core Team. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, 2018. URL https://www.R-project.org/.

Ramp, D., & Croft, D. B. (2006). Do wildlife warning reflectors elicit aversion in captive macropods? Wildl Res. 33, 583–590.

Riginos, C. , Graham, M. W., Davis, M. J., Johnson, A. B., May, A. B., Ryer, K. J. & Hall, L. E. (2018), Wildlife warning reflectors and white canvas reduce deer–vehicle collisions and risky road-crossing behavior. Wildl. Soc. Bull. doi:10.1002/wsb.862.

Schiviz, A.N., Ruf, T., Kuebber-Heiss, A., Schubert, C., & Ahnelt, P.K. (2008). Retinal cone topography of artiodactyl mammals: Influence of body height and habitat. J Comp Neurol. 507, 1336–1350.

Schulze, C., Polster, J.U (2017). Wirkungsweise von Wildwarnern, in: Forschung, Straßenbau und Straßenverkehrstechnik, 1127/2017. 96 pp.

Seiler, A. (2004). Trends and spatial patterns in ungulate-vehicle collisions in Sweden. Wildlife Biol., 10, 301-313.

Seiler, A. (2005). Predicting locations of moose–vehicle collisions in Sweden. J Appl Ecol. 42, 371–382.

Sheridan, G. J. (1991). The effectiveness of Swareflex and Wegu brand wildlife reflectors in deterring *Perameles gunnii* (barred bandicoot) from crossing a section of roadway. Ballarat, AUS: Ballarat University College. 23 pp.

Sivic, A., & Sielecki, L. E. (2001). Wildlife Warning Reflectors: Spectrometric Evaluation. Victoria, BC: Ministry of Transportation and Highways. 24 pp.

Szél, Á., Röhlich, P., Caffé, A. R., & van Veen, T. (1996). Distribution of cone photoreceptors in the mammalian retina. Microsc. Res Techniq. 35, 445–462.

Thurfjell, H., Spong, G., Olsson, M., & Ericsson, G. (2015). Avoidance of high traffic levels results in lower risk of wild boar-vehicle accidents. Landscape Urban Plan. 133, 98-104.

Ujvári, M., Baagøe, H. J., & Madsen, A. B. (1998). Effectiveness of wildlife warning reflectors in reducing deer-vehicle collisions: a behavioral study. J Wildlife Manage. 62, 1094–1099.

Valitzski, S. A., D'Angelo, G. J., Gallagher, G. R., Osborn, D. A., Miller, K. V., & Warren, R. J. (2009). Deer responses to sounds from a vehicle-mounted sound-production system. J Wildlife Manage. 73, 1072-1076.

VerCauteren, K. C., & Pipas, M. J. (2003). A review of color vision in white-tailed deer. Wildlife Soc B. 31, 684–691.

Vincent, J. P., Bideau, E., Hewison, A. J. M., & Angibault, J. M. (1995). The influence of increasing density on body weight, kid production, home range and winter grouping in roe deer (*Capreolus capreolus*). J Zool. 236, 371-382.

Waring, G. H., Griffis, J. L., & Vaughn, M. E. (1991). White-tailed deer roadside behavior, wildlife warning reflectors, and highway mortality. Appl Anim Behav. Sci. 29, 215–223. doi: 10.1016/0168-1591(91)90249-W.

Zacks, J. L. (1986). Do White-tailed Deer Avoid Red? An Evaluation of the Premise Underlying the Design of Swareflex Wildlife Reflectors. Washington, D.C.: Transportation Research Record 1075. National Research Council. 43 pp.

Chapter 5

Synopsis

Considering the general objectives of this dissertation: (i) evaluating the contradictions in literature and identifying influencing variables on previous study results, (ii) determining the efficacy of reflectors to mitigate collisions with wildlife, (iii) comparing the reaction of wildlife to oncoming vehicles and the driving behavior of motorists in response to the presence of wildlife warning reflectors, and (iv) assessing a potential habituation effect, this chapter aims to summarize and to discuss the results of the included studies, while also assessing the achievement of the main objectives.

5.1 Factors influencing the results of studies evaluating the efficacy of wildlife warning reflectors

As mentioned above (Chapter 1.4), a variety of studies on the efficacy of wildlife warning reflectors has already been conducted. However, as study results deviate markedly from each other it is important to evaluate both: potential reasons for contrasting study results in literature (Chapter 2) as well as the efficacy of modern wildlife warning reflectors when applying a comprehensive study design (Chapter 3 and 4).

Due to the comprehensive meta-analysis we were able to identify main factors influencing previous study results. The discrepancy of findings in the literature can be partly related to shortcomings in the planning and execution of various studies applied. Several studies have tested a considerably small sample size only. Moreover, statistical applications were often found to be insufficient to enable clear testing of hypotheses. However, both aspects are essential to perform an analysis able to provide sufficient evidence. Considering the importance of different covariates, the color and the model type of the tested reflectors surprisingly showed no significant influence for the efficacy. The regression analysis by applying a Boosted regression tree model (BRT) identified (i) the study design applied, (ii) the lengths of effective study duration and, (iii) the length of tested road sections as variables of highest importance to explain the variance between observed results. The impact of a single treatment in a paired study design can usually be tested by analyzing a population before and after a treatment or two very similar populations or locations simultaneously (Morrison et al., 2010). However, other potential factors influencing a change after implementation, so-called confounding variables, might cause a lack of independence that would accrue from different levels of single treatments and true replications (Morrison et al., 2010). Therefore, the interpretation of experiments applying such study designs can be quite difficult, if heterogeneity results in the confounding of experimental errors (Underwood, 1997, Morrison et al., 2010). Although the applied statistics might be correct and the null hypotheses can be rejected, other influencing factors may predominate over the effect of the treatment, resulting in a bias and a misinterpretation of results (Underwood, 1997, Morrison et al., 2010). Particularly, studies comparing the number of collisions with wildlife before and after (BA) the implementation of wildlife warning reflectors, as well as comparing testing sites with control sites (CI) have to be treated with caution, due to discontinuity in time or space. With respect to these shortcomings, before-after control-impact (BACI) and cross-over designs provide a remedy, as they have the highest inferential strength for assessing impacts on the environment (Green, 1979, Underwood and Chapman, 2003, Roedenbeck, 2007).

In addition to the study designs applied, the BRT model revealed that especially studies with short study durations (< 12 months) and short testing site lengths (< 5 km) found effects of wildlife warning reflectors in reducing the number of collisions. Considering such short study durations, it must be assumed that seasonal variations in wildlife-vehicle collisions as well as animal behavior (e.g. rutting season, fawning) cannot have been taken into account. Activity patterns of ungulates vary over the year, with peaks during rut and in the darker seasons (Allen and McCullough, 1976, Hothorn et al., 2015). Thus, studies including all activity periods or at least comparing the same activity period are more likely to include those variables that may influence the reaction of ungulates towards approaching vehicles. The impact of short testing site lengths might relate to a shift in collision hotspots due to human disturbances or by chance, considering the naturally oscillating fluctuations in population density related to hunting effort and food supply (Fryxell et al., 1991). In summary, the analysis of literature revealed several co-varying factors which affected the results of reflector studies. Accordingly, contradictions in the efficacy of the devices are not surprising given the abundance of research methods applied so far. With these results (Chapter 2), we can confirm our first two hypotheses: 1a) existing study results can be explained by the specifics of study designs, and 1b) a meta-analysis of previous studies identifies minimal requirements for a successful study design.

5.2 Visual and acoustic sensitivity of ungulates and spectrometric characteristics of the reflectors

The boosted regression tree model showed that neither reflector type nor reflector color explained the variance in the model. In order to assess whether the reflectors are able to reduce wildlife-vehicle collisions, it is important to know the effects of the devices and to take the visual and acoustic properties of animals into account. In fact, most studies on reflector efficacy have examined red or white wildlife warning reflectors only (cf. Benten et al., 2018). However, color vision differs strongly between non-human mammalian species and humans due to the dichromasy of most non-human mammals. As most ruminant ungulates frequent open areas and agricultural fields during night (Mysterud et al., 1999), a higher perception for mesopic and scotopic visions below 540 nm (Szél et al., 1996, VerCauteren and Pipas, 2003, Hanggi and Ingersoll, 2007) relates to the adaptation of increased vulnerability to predators (cf. Hothorn et al., 2015). Additionally, visual systems of nocturnal animals are concomitant with a higher density of rods and adapt considerably slower to rapid changes in light intensity, such as vehicles' headlights than diurnal species (D'Angelo et al., 2006). Thus, ungulates have one photo-pigment associated with a cone mechanism for short wavelengths with a peak between 450 nm and 460 nm (S-cone), and a second photo-pigment associated with a cone mechanism for middle wavelengths with a peak of 537 nm (M/L-cone; Carroll et al., 2001). In a multiple choice discrimination test, Japanese wild boar (*Sus scrofa leucomystax*) discriminated between bluish colors but failed to differentiate between colors approaching green or yellow (Eguchi et al., 1997). Accordingly, wild boar also lack color sensitivity for light of long wavelengths, thus red light with a wavelength of 650 nm exceeds the visible range of ungulates (Jacobs et al., 1994, Yokoyama and Radlwimmer, 1998, Pürstl, 2006).

Although modern wildlife-warning reflectors are already tuned to the shortwave color spectrum, we did not find any influence of the reflectors on mitigating wildlife-vehicle collisions on roads. This might be explained by the spectrometric properties of the reflective devices, since the light intensity of the reflections to the road shoulder is already very low at close distances near the devices and overlaid by the headlights of approaching vehicles, which applies especially to colored wildlife warning reflectors (Sivic and Sielecki, 2001, Schulze and Polster, 2017). Hence, it must be queried whether the light reflected has a sufficient intensity to elicit any reaction from animals which may cause to decrease the risk for collisions with vehicles.

Moreover, combining optical and acoustic stimuli, opto-acoustic reflectors emit high-frequency sounds for 1.5 s with 83 dB at 0.1 m and 4 kHz when light hits light-sensitive solar panels. D’Angelo et al. (2007) identified the hearing range of white-tailed deer (*Odocoileus virginianus*) between 0.25 - 30 kHz and a mean frequency-specific hearing threshold of minimum 41.9 dB for 4 - 8 kHz. During the installation of the reflectors it could already be established that these devices did not only emit high-frequency sounds when car headlights hit the solar panels, but also sun rays at a certain angle or slight shaking. This noise emission independent of vehicles cannot achieve a stronger impulse for driving vehicles, since animals fail to relate the acoustic signals to the approaching vehicles. In fact, vehicles passing by at a distance of 10 m already generate a sound pressure level of 75 dB at a frequency of 0.7-1.3 kHz (Regulation (EU) No. 540/2014). In open land, with no reflecting or absorbing obstacles, sound transmission decreases by 3 dB per doubled distance from the source of sound with $L_2 = L_1 - |20 * \log(\frac{r_1}{r_2})|$, where L_1 is the sound level at reference distance r_1 (usually 1 m) and L_2 the sound level at reference distance r_2. Forest cover or other barriers, however, can further reduce the sound pressure level of approaching vehicles by 3-5 dB, depending on meteorological conditions (Barrier et al., 2000). D'Angelo et al. (2007) argued that, given the hearing of white-tailed deer at 30 kHz, ultrasonic devices would need to emit sounds between 45 – 60 dB to be reliably perceived by deer. According to the manufacturer's instructions, the opto-acoustic reflectors should emit 83 dB at close distance (0.1 m) which expects sound intensity to be 43 dB at 10 m and 29 dB at 50 m distance. Whether this is sufficient to prevent wildlife from moving towards an approaching vehicle with a minimum of 75 db at 10 m and 61 dB at 50 m distance remains questionable. Therefore, the inefficacy of the reflectors, both the optic and the opto-acoustic, is not surprising, considering the visual and auditory properties of animals and the spectrometric and acoustic qualities of the reflectors. With these findings (Chapter 3), we can confirm our third and fourth hypotheses: 2a) modern wildlife warning reflectors do not reduce wildlife–vehicle collisions by a relevant amount and 2b) other environmental variables do not influence the inefficacy of the reflectors, since the properties of the reflectors themselves already exclude an efficacy.

5.3 Hypotheses on psychological theories related to wildlife warning reflectors

Taken these described physiological and physical principles into account (Chapter 5.2), wildlife warning reflectors could have at most an effect on vehicle drivers. Due to their reflective properties, the light intensity during direct reflection back to the driver is by far larger than for the reflection towards the road shoulder (Schulze and Polster, 2017). However, we did not find any change in motorist behavior with reflectors present (Chapter 4). While other studies reported a reduction of collisions after implementing different devices, such as deer whistles (Zacks, pers. comm., 2015), this finding can more likely be attributed to the

'*Hawthorne effect*' (Wickström and Bendix, 2000) than to an efficacy of the devices. This effect describes a phenomenon in psychological research, referring to behavioral changes of the human subjects due to increased attention and awareness to and by observers or positive response to the stimulus introduced. This is independent to the actual influence of the object of study (Wickström and Bendix, 2000). Actually, humans may easily habituate to stimuli along roads, such as road signs (Huijser et al., 2007) and a habituation to the presence of wildlife warning reflectors can be assumed due to their omnipresence in the traffic landscape as well. However, the evaluation of motorists' reaction to reflectors could be further analyzed by considering thorough psychological studies. Nevertheless, since the presence of wildlife warning reflectors did not alter the frequencies of wildlife-vehicle collisions, an effect on the behavior of vehicle drivers appears to be rather unlikely.

Moreover, we did not find any behavioral change of ungulates with reflectors present, neither on the short nor on the longer term, that would lower the risk of a collision with vehicles. This result is consistent with most other studies on the behavior of animals with reflectors present (e.g. D'Angelo et al., 2006, Brieger et al., 2017). There is only one study available that points to a potential initial effect of the reflectors on fallow deer which diminished over time (Ujvári et al., 1998). However, considering the physical properties of red reflector devices used in this study, an initial effect can be rather explained with the '*novel object*' theory than with the operative effect of the reflectors themselves. As wild animals would avoid or fear novel stimuli in their familiar environment (Barnett, 1958, Cowan, 1976, 1977, Harris and Knowlton, 2001), a repellent or restrained reaction of animals to such novel objects is to be expected, but is independent of the reflective properties of the devices. In this regard, Riginos et al. (2018) found that wildlife warning reflectors were more effective than black canvas bags for manipulating the deer–road-crossing behavior and reducing carcass rates. However, white canvas bags were still found to be more effective than wildlife warning reflectors. Since white canvas bags stand out more from the surrounding landscape than the reflectors, animals might perceive them more easily than the reflectors. However, since we did not find any behavioral change of animals with reflectors present that would lower the risk of collisions, ungulates may either already be habituated to the devices or do not longer notice such comparably small novel objects in our complex, ever more densely populated environment. Furthermore, behavioral reactions may relate to other, confounding factors that occurred unconsciously, but were not further considered, like a high degree of human disturbances caused by weekly to biweekly covering and uncovering of reflectors and guidance posts by Riginos and colleagues. Considering our results (Chapter 4) we can reject our hypotheses on animal and human reaction to wildlife warning reflectors: ungulates did not: 3a) decrease road-crossing events, 3b), increase positive compared to negative reactions when vehicles approach, 3c) decrease flight events, 3d) decrease flight initiation distances, and they did also not 3e) shift their behavioral response to alarm. Additionally, 3f) motorists did not slow down or stop more often with reflectors present.

According to the general requirement of wildlife-vehicle collision prevention, it appears to be of secondary interest whether reflectors affect the behavior of animals or humans because of their physical characteristics or their novelty. However, regarding the constant collision numbers (Chapter 3) in comparison to observations with and without reflectors present (Chapter 4), an efficacy of these devices can be ruled out on the basis of the thesis at hand. Nevertheless, the assumption of reflectors' efficacy is widely accepted and appears to be highly persistent. This might be partly caused by prejudices and well-established opinions by authors and hunters. Konings (1986) evaluated the efficacy of Van de Ree warning reflectors on collisions induced by the European badger. While no effect of the reflectors on road side behavior of badgers was found, local road managers were positive about the functionality of the devices, despite the lack of evidence. Anecdotal reports on the effect of wildlife warning reflectors, either on animal behavior or on the number of wildlife-vehicle collisions (e.g. Gladfelter, 1984, Olbrich, 1984, Koninigs, 1986, Hildebrand and

Hodgson, 1995, Pafko and Kovach, 1996, Grenier, 2002), are widespread, even if scientific proof is missing (cf. Brieger et al., 2016, Benten et al., 2018).

According to a recent study by Trothe et al. (2017), articles in non-scientific journals primarily addressing hunters - the main customers of wildlife-warning reflectors in Germany - promote the efficacy of wildlife warning reflectors (e.g. Preuin, 2018, Viehmann, 2018). Taking the preconditions for studies on implementation effects into account (Chapter 5.1), the evaluation of reflector efficacy lacks standards of scientific requirements. Although the results of this study should be impugned, it finds broad acceptance along the providers of wildlife warning reflectors. This persistence of opinion, the so-called '*belief perseverance'*, has been a subject of interest in psychology, stating that participants tend to retain their first opinion even if they were confronted with a lie or with conflicting scientific data (e.g. Anderson 2007, Greitemeyer 2014). This phenomenon can be referred to the debate on wildlife-warning reflectors efficacy. For example, Gladfelter (1984) and Hildebrand and Hodgson (1995) concluded that the reflectors were effective in reducing collision numbers, although their data provided show the opposite (Chapter 2). It is more likely that occasional 'reductions' relate to natural fluctuations in population densities, as described above (Chapter 5.1).

5.4 Animals reaction to oncoming vehicles

As discussed in the previous chapters, we were able to confirm our hypotheses on the inefficacy of wildlife warning reflectors (Chapter 3) and reject all of our hypotheses addressing a potential behavioral response of animals and motorists with reflectors present that might lower the risk of a collision with one another (Chapter 4). To find a reliable, applicable and practical solution for preventing collisions with wildlife, it is fundamentally important to understand the behavior and threat assessment of animals to oncoming vehicles in general. While humans may habituate to various stimuli rather quick due to a fast-moving environment, wild animals must keep their attention to certain sources of danger ubiquitous.

Since predator recognition and threat assessment are crucial for the survival of animals, developing sophisticated strategies for avoiding natural predation as well as other sources of mortality is of great importance for individuals. This assessment includes a variety of modalities, such as visual, auditory and olfactory cues, or a combination of them (Caro, 2005).

Since man-made causes of mortality don't resemble known predators, and wildlife-vehicle collision numbers are high, it is often argued that vehicle traffic might be an evolutionary novel threat for terrestrial animals and a strategy for avoidance has not been developed yet (cf. Lima et al., 2014). However, the ability of an animal to identify causes of danger and mortality will likely trigger some kind of anti-predator behavior (Lima et al., 2014), including increased vigilance or moving away from the source of danger (Blumstein et al., 2001). Other studies concluded that human activities when unpredictable and infrequent increase the levels of flight distances, which decreases with predictable disturbances, such as vehicle traffic (Miller et al., 2009). Alternatively, prey species may use the proximity to humans, including road traffic, to avoid predation (Frid and Dill, 2002, Berger, 2007), reducing their vigilance near roads and increase foraging behavior (Brown et al., 2012, Shannon et al., 2014). This '*risk allocation hypothesis*' suggests that animals spend less energy and time on anti-predator behavior when sources of danger occur for long periods and frequently, such as vehicle traffic, compared to intervals that are short and irregular to avoid disadvantages in lost foraging (Lima and Bednekoff, 1999, Brown et al., 2012). Hence, evaluating 'positive' and 'negative' reactions of ungulates towards approaching vehicles showed that animals avoid collisions with vehicles in most situations by reacting appropriately to the oncoming source of danger. When analyzing 1,673 individuals involved in animal-vehicle events, only 3 individuals were actually hit by a vehicle in the frame of this project. Thus, high numbers of collisions with wildlife might rather be related to frequent road-crossing events and high numbers of wildlife density than to poor risk assessment of the animals themselves.

5.5 Critical review of the methods applied

For evaluating the efficacy of wildlife warning reflectors, various methods have been applied in this thesis. We provided an extensive overview over literature and meta-analyzed data addressed in previous studies (Chapter 2). However, while we were able to obtain a large part of the original studies, we had to be satisfied with the secondary source for few other publications, although this did not affect the analysis of the data addressed.

Furthermore, for the testing of modern wildlife warning reflectors (Chapter 3) we selected 151 testing sites á 2 km with the highest numbers of wildlife-vehicle collisions reported by the police in four different counties. However, due to the large spreading of wildlife warning reflectors, it was not always possible to take sections with the actual highest occurrence of wildlife-vehicle collisions into account, as modern reflectors had already been installed frequently. The inclusion of an even larger study area with more counties involved would probably have improved the access to a higher number of wildlife-vehicle collision hotspots without modern reflectors attached. However, this would have been difficult to implement because of logistical and personnel reasons. Managing four counties including police, hunting and road authorities has already been very extensive. However, the presence of already existing modern reflectors within collision hotspots further points for the inefficacy of these devices.

Additionally, data quality on wildlife-vehicle collisions has been demonstrated to influence the outcome of study results on the efficacy of wildlife warning reflectors, as demonstrated in Chapter 2. While we decided to consider data provided by local police departments (Chapter 3), we also tried to collect data by local hunting tenants that were not reported by the police in order to get a most detailed overview of actual wildlife-vehicle collisions. However, the feedback by hunters was very low, which indicates that unreported collisions were very few. Therefore, we did not pursue this issue any further. In this regard, our attempt to collect data on hunting efforts, hunting devices and other factors influenced by local hunters has experienced the same low feedback. Addressing hunting-related factors would have been highly valuable in order to evaluate anecdotal reports on the efficacy of the reflectors (Chapter 5.3) with an adaptation in hunting strategies. Some local hunting tenants reported their positive experiences with blue wildlife warning reflectors on reducing collisions with wildlife. However, when we enquired further information on spatial conditions or comprehensive measures of collision prevention, clear-cuttings, increased hunting effort or similar management issues alongside roads became apparent to have occurred simultaneously. These measures are more likely to have influenced wildlife abundancies, behavior and finally wildlife-vehicle collisions. Hence, the reported ‘success’ cannot be distinctly ascribed to the use of reflector devices.

Furthermore, analyses of the behavior of wildlife provided further insights into the reaction of ungulates towards oncoming vehicles (Chapter 4). However, an additional installation of microphones would probably have provided a clearer picture of when an approaching vehicle was actually perceptible for the animals, i.e. audible, at the respective section, including all environmental and landscape-related factors that influence the transition of sound. However, since collision numbers did not change at all, this part of research would be more relevant for a general study on the reaction of wildlife to oncoming vehicles. Finally, a quantification of the velocity of vehicles observed was not feasible with respect to the technical possibilities. This information would probably have provided a clearer picture on the reaction of motorists during a wildlife-vehicle event.

5.6 Conclusions

Measures to mitigate collisions with wildlife are often accompanied by high costs in construction and maintenance (Falk et al., 1978, Putman, 1997, Clevenger et al., 2001, Mastro et al., 2008, Chapter 1.3) or have not been proven without doubt, e.g. olfactory deterrents (Elmeros et al., 2011, Bíl et al., 2018). So far, wildlife warning reflectors have been a subject of discussion because of contradictory results in studies on their efficacy. The thesis at hand was finally able to show that wildlife warning reflectors are not suitable for preventing collisions with wildlife. We could confirm our first two hypotheses (Chapter 2) stating that 1a) existing study results can be explained by the specifics of study designs and, 1b) a meta-analysis of previous studies identified minimal requirements for a successful study design. Moreover, we could confirm out third and fourth hypotheses on the inefficacy of the reflectors (Chapter 3), stating that 2a) modern wildlife warning reflectors do not reduce wildlife–vehicle collisions by a relevant amount and, 2b), other environmental variables do not influence the inefficacy of the reflectors. Since some studies and hunters reported a temporary effect of the reflectors on animals, and potentially also motorists, we evaluated the reaction of ungulates and drivers with and without reflectors to one another. We were able to reject all hypotheses on a potential influence of the reflectors on ungulates or motorists that would reduce the risk of wildlife-vehicle collisions (Chapter 4), i.e. that 3a) ungulates did not change road-crossing events, 3b) ungulates did not change positive compared to negative reactions when vehicles approach, 3c) ungulates did not change the frequency of flight events, 3d) ungulates did not change flight initiation distances, and 3e) ungulates did not shift their behavioral response to be more alarmed. Finally, in accordance with hypothesis 3f), motorists did not slow down or stop more often when reflectors were present. Considering studies on the visual abilities of non-human mammals as well as the reflective properties of the reflectors, a potential efficacy of the reflectors is questionable anyway. Based on our results, we conclude that wildlife warning reflectors are not effective for mitigating wildlife-vehicle collisions on roads.

5.7 Outlook for future work on wildlife-vehicle collision prevention

Risk assessment for collisions with ungulates show that a variety of road-related, species-specific and landscape-specific factors influence the occurrence of wildlife-vehicle collisions (Chapter 1.2, reviewed in Gunson et al., 2011). While road-related characteristics, such as the number of lanes or road width increase the occurrence of collisions with wildlife, their adaptations favoring a reduction in collision numbers would only be possible during the process of road planning and renovation (Hubbard et al., 2000, Grilo et al., 2009). Additionally, a reduction of vehicle traffic, speed limit or wildlife density is unlikely due to the need for transportation and cultural constrains (Chapter 1.3). Moreover, targeted technologies to detect wildlife in the vicinity of the road, as given by the use of thermal camera imaging in vehicles (Adams, 2017), will likely take several decades until the majority of vehicles on roads are equipped with these techniques. Therefore, one future goal should be the identification of other more precise landscape and land-use related factors for wildlife management and wildlife-traffic conflict prevention.

According to the foraging habits of ungulates (Chapter 1.6), collision hotspots involving these species were found to occur more often on roads surrounded by shrub cover and deciduous forest, but also forest habitats and a combination of wooded areas and open land increase the probability of collisions (Malo et al., 2004, Gunson et al., 2009, Gunson et al., 2011, Zuberogoitia et al., 2014, Seidel et al., 2018). Reducing the attractiveness of the roadside vegetation has already been suggested to decrease the foraging of animals near roads and to reduce deer-related collisions (Feldhamer et al., 1986, Rea, 2003, reviewed in Gunson et al., 2011). Forests, forest patches, or trees outside forests are long–lasting, while management actions take a long time to recover and cannot be implemented in the short term (Bashore et al., 1985, Hubbard et al., 2000, Thompson et al., 2003, Malo et al., 2004, Chazdon, 2008, Seidel et al., 2018). Since these landscape elements are important for both humans and wildlife, for noise insulation, shelter and foraging for animals, clear-cuttings might be an option, but should be treated with caution. Therefore, it is promising to put the focus on short-termed and more flexible types of roadside vegetation, such as arable land with different cultivated crop species.

While Hubbard et al. (2000) and Seiler (2005) found that the proportion of crop fields and agriculture decreases the probability of collisions with white-tailed deer or moose (*Alces alces*), Zuberogoitia et al. (2014) showed that roadside shrub cover increases the risk of collisions with wild boar. Wild boars frequent open areas, such as agricultural fields and grassland, to search e.g. for invertebrates and roots, while they prefer to rest in forest or shrub areas (Thurfjell, 2011, Colino-Rabanal et al., 2012, Zuberogoitia et al., 2014). The same is true for deer which switch back and forth between shelter and food sources (Torres et al., 2011). Zuberogoitia et al. (2014) suggested that "road side vegetation management can provide a short to medium-term option to manage risk and guide animals to safe crossing areas". Although agricultural land-use dominates landscapes in many parts of the world (Holzkämper and Seppelt, 2007), the influence of different cultivated crop species on the occurrence of wildlife-vehicle collisions has scarcely been studied. This probably points to the difficulty of obtaining comprehensive spatial data on the cultivation of crops. So far, only Colino-Rabanal et al. (2012) analyzed the relation between common maize (*Zea mays*) and wild boar-vehicle collisions and suggested a compensation system to farmers "for not planting maize near the road, rather than to cover the economic damage derived from wild-boar-vehicle collisions". As comprehensive spatial data have recently become available and accessible because of the Common Agricultural Policy regulation of the EU, future research should provide a more detailed picture on the influence of certain crop species on the occurrence of collision hotspots in space and time considering various wildlife species in order to mitigate wildlife-vehicle collisions.

5.8 References

Adams, E. (2017). Volvo's Cars Now Spot Moose and Hit the Brakes for You. Wired. https://www.wired.com/2017/01/volvos-cars-now-spot-moose-hit-brakes/. Accessed June 6 2018.

Allen, R. E., & McCullough, D. R. (1976). Deer-car accidents in southern Michigan. J Wildl Manage. 40, 317–325.

Anderson, C. A. (2007). Belief perseverance. In: Encyclopedia of social psychology (eds. R. F. Baumeister, and K. D. Vohs), pp. 109–110. Thousand Oaks, CA: Sage, USA.

Barriere, N., Gabillet, Y., Blais, J., Defrance, J., Ducruet, P., & Gaudaire, F. (2000). Experimental study of road traffic noise control by a pine forest. In: Internoise 2000. Proceedings of the 29th International Congress on Noise Control Engineering (ed. D. Cassereau,), pp. 1459-1463. Transport Research Laboratory, Nice, France.

Bashore, T. L., Tzilkowski, W. M. & Bellis, E. D. (1985). Analysis of Deer-Vehicle Collision Sites in Pennsylvania. J Wildlife Manage. 49, 769-774.

Benten, A., Annighöfer, P., & Vor, T. (2018). Wildlife Warning Reflectors' Potential to Mitigate Wildlife-Vehicle Collisions–A Review on the Evaluation Methods. Front Ecol Evol. 6, 37.

Benten, A., Hothorn, T., Vor, T., & Ammer, C. (in review). Wildlife Warning Reflectors do not Mitigate Wildlife-Vehicle Collisions on Roads. Accident Anal Prev.

Berger, J. (2007). Fear, human shields and the redistribution of prey and predators in protected areas. Biol Lett. 3, 620-623.

Bíl, M., Andrášik, R., Bartonička, T., Křivánková, Z., & Sedoník, J. (2018). An evaluation of odor repellent effectiveness in prevention of wildlife-vehicle collisions. J Environ Manage. 205, 209-214.

Blumstein, D. T., Daniel, J. C., & Bryant, A. A. (2001). Anti-predator behavior of Vancouver Island marmots: Using congeners to evaluate abilities of a critically endangered mammal. Ethology. 107, 1-14.

Brieger, F., Hagen, R., Kröschel, M., Hartig, F., Petersen, I., Ortmann, S., & Suchant, R. (2017). Do roe deer react to wildlife warning reflectors? A test combining a controlled experiment with field observations. Eur J Wildlife Res. 63, 10.1007/s10344-017-1130-5.

Brown, C. L., Hardy, A. R., Barber, J. R., Fristrup, K. M., Crooks, K. R., & Angeloni, L. M. (2012). The effect of human activities and their associated noise on ungulate behavior. PloS one. 7, e40505.

Caro, T. (2005). Antipredator defenses in birds and mammals. University of Chicago Press, USA. 592 pp.

Carroll, J., Murphy, C. J., Neitz, M., Hoeve, J. N. & Neitz, J. (2001). Photopigment basis for dichromatic color vision in the horse. J Vision. 1, 80-7.

Chazdon, R. L. (2008). Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science. 320, 1458-1460.

Clevenger, A. P., Chruszcz, B., & Gunson, K. E. (2001). Highway mitigation fencing reduces wildlife-vehicle collisions. Wildlife Soc B .29, 646–653.

Colino-Rabanal, V. J., Bosch, J., Munoz, M. J. & Peris, S. J. (2012). Influence of new irrigated croplands on wild boar (*Sus scrofa*) road kills in NW Spain. Anim Biodiv Conserv. 35, 247-252.

Cowan, P.E. (1976). The new object reaction of *Rattus rattus* L.: the relative importance of various cues. Behav. Biol. 16, 31–44.

Cowan, P.E. (1977). Neophobia and neophilia: new-object and newplace reactions of three *Rattus* species. J. Comp. Physiol. Psychol. 91: 63–71.

D'Angelo, G., D'Angelo, J. G., Gallagher, G. R., Osborn, D. A., Miller, & Warren, R. J. (2006). Evaluation of Wildlife Warning Reflectors for Altering White-Tailed Deer Behavior along Roadways. Wildlife Soc B. 34, 1175–1183.

D'Angelo, G., Chiccis, A., Osborn, D. A., Gallagher, G. R., & Warren, R. J., Miller, K. V. (2007). Hearing Range of White-Tailed Deer as Determined by Auditory Brainstem Response. J Wildlife Manage. 71, 1238–1242.

D'Angelo, G., and van der Ree, R. (2015). Use of Reflectors and Auditory Deterrents to Prevent Wildlife-Vehicle Collisions. In: Handbook of Road Ecology (eds. R. van der Ree, D. J. Smith, and C. Grilo), pp. 213-218. John Wiley & Sons, Ltd., Chichester, UK.

Eguchi, Y., Tanida, H., Tanaka, T., & Yoshimoto, T. (1997). Color discrimination in wild boars. J Ethol. 15, 1-7.

Elmeros, M., Winbladh, J.K., Andersen, P.N., Madsen, A.B., & Christensen, J.T. (2011). Effectiveness of odour repellents on red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*): A field test. Euro J Wildlife Res. 57, 1223–1226.

Falk, N. W., Graves, H. B., & Bellis, E. D. (1978). Highway right-of-way fences as deer deterrents. J Wildlife Manage. 3, 646–650.

Farmer, R. G., & Brooks, R. J. (2012). Integrated risk factors for vertebrate roadkill in southern Ontario. J Wildlife Manage. 76, 1215-1224.

Feldhamer, G. A., Gates, J. E., Harman, D. M., Loranger, A. J., & Dixon, K. R. (1986). Effects of interstate highway fencing on white-tailed deer activity. J Wildlife Manage. 50, 497-503.

Forkman, B., Boissy, A., Meunier-Salaün, M. C., Canali, E., & Jones, R. B. (2007). A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. Physiol Behav. 92, 340-374.

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. Conserv Ecol. 6, 11.

Fryxell, J. M., Hussell, D. J. T., Lambert, A. B., & Smith, P. C. (1991). Time lags and population fluctuations in white-tailed deer. J Wildlife Manage. 3, 377–385.

Gladfelter, L. (1984). Effect of wildlife highway warning reflectors on deer-vehicle accidents. Project HR-210. Iowa Highway Research Board. Boone, Iowa, USA. 11 pp.

Green, R. H. (1979). Sampling design and statistical methods for environmental biologists. John Wiley & Sons, New Jersey, USA. 272 pp.

Greitemeyer, T. (2014). Article retracted, but the message lives on. Psychon B Rev. 21, 557-561.

Grenier, R. H. (2002). A study of the effectiveness of Strieter-Lite® wild animal highway warning reflector systems. Commissioned report for Strieter Corporation, USA. 19 pp.

Grilo, C., Bissonette, J. A., & Santos-Reis, M. (2009). Spatial–temporal patterns in Mediterranean carnivore road casualties: Consequences for mitigation. Biol Conserv. 142, 301–313.

Gunson, K. E., Clevenger, A. P., Ford, A. T., Bissonette, J. A., & Hardy, A. (2009). A comparison of data sets varying in spatial accuracy used to predict the occurrence of wildlife-vehicle collisions. Environ Manage. 44, 268–277.

Gunson, K. E., Mountrakis, G., Quackenbush, L.J. (2011). Spatial wildlife-vehicle collision models: A review of current work and its application to transportation mitigation projects. J Environ Manage. 92, 1074–1082.

Hanggi, E. B., Ingersoll, J. F., Waggoner, T. L. (2007). Color vision in horses (*Equus caballus*): Deficiencies identified using a pseudoisochromatic plate test. J Comp Psychol. 121, 65.

Harris, L.D., & Scheck, J. (1991). From implications to applications: The dispersal corridor principle applied to the conservation of biological diversity. In: Nature conservation the role of corridors (eds. D. A. Saunder and R. J. Hobbs), pp. 189-220. Surrey Beatty and Sons, Chipping Norton, Australia.

Hildebrand, E., & Hodgson, K. (1995). Effectiveness of Optical Fences in Reducing Vehicle-Deer Collisions in New Brunswick. 131-144 pp. In: Proceedings of the Canadian Multidisciplinary Road Safety Conference IX, Quebec, Canada.

Holzkämper, A., & Seppelt, R. (2007). Evaluating cost-effectiveness of conservation management actions in an agricultural landscape on a regional scale. Biol Conserv. 136, 117-127.

Hothorn, T., Müller, J., Held, L., Möst, L., & Mysterud, A. (2015). Temporal patterns of deer–vehicle collisions consistent with deer activity pattern and density increase but not general accident risk. Accident Anal Prev. 81, 143–152.

Hubbard, M. W., Danielson, B. J., & Schmitz, R. A. (2000). Factors Influencing the Location of Deer-Vehicle Accidents in Iowa. J Wildlife Manage. 64, 707.

Huijser, M. P., Kociolek, A., McGowen, P., Hardy, A., Clevenger, A.P., & Ament, R. (2007). Wildlife-vehicle collision and crossing mitigation measures: A toolbox for the Montana Department of Transportation. Bozeman: Western Transportation Institute, Montana, USA. 123 pp.

Jacobs, G. H., Deegan II, J. F., Neitz, J., Murphy, B. P., Miller, K. V., & Marchinton, R. L. (1994). Electrophysiological measurements of spectral mechanisms in the retinas of two cervids: white-tailed deer (*Odocoileus virginianus*) and fallow deer *(Dama dama*). J Comp Physiol. 174, 551–557.

Kämmerle, J.-L., Brieger, F., Kröschel, M., Hagen, R., Storch, I., & Suchant, R. (2017). Temporal patterns in road crossing behaviour in roe deer (*Capreolus capreolus*) at sites with wildlife warning reflectors. PLoS one. 12, e0184761.

Konings, P. (1986). Een onderzoek naar de werking en effectiviteit van wildspiegels voor dassen. Studentenverslag Rijksinstituut voor Naturbeheer. Arnhem, Netherlands. 21 pp.

Lima, S. L., & Bednekoff, P. A. (1999). Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. Am Nat. 153, 649-659.

Lima, S. L., Blackwell, B. F., DeVault, T. L., & Fernández-Juricic, E. (2014). Animal reactions to oncoming vehicles: a conceptual review. Biol Rev. 90, 60-76.

Malo, J. E., Suarez, F., & Diez, A. (2004). Can we mitigate animal-vehicle accidents using predictive models? J Appl Ecol. 41, 701–710.

Miller, K. V. (2007). Hearing range of white-tailed deer as determined by auditory brainstem response. J Wildlife Manage. 71, 1238-1242.

Morrison, M. L., Block, W. M., Strickland, M. D., Collier, B. A., & Peterson, M.J. (2010). Wildlife study design. Springer Science & Business Media. New York, USA. 386 pp.

Mysterud, A., Larsen, P. K., Ims, R. A., & Østbye, E. (1999). Habitat selection by roe deer and sheep: does habitat ranking reflect resource availability? Can J Zool. 77, 776–783.

Olbrich, P. (1984). Untersuchung der Wirksamkeit von Wildwarnreflektoren und der Eignung von Wilddurchlässen. Z Jagdwiss. 30, 101–116.

Pafko, F., & Kovach, B. (1996). Experience with deer reflectors. Trends in addressing transportation-related wildlife mortality. Minnesota Department of Transportation, Office of Environmental Services, Minnesota, USA. 10 pp.

Preuin, H. (2018). Wie können Wildunfälle verhindert werden? Neue Osnabrücker Zeitung. https://www.noz.de/lokales/osnabrueck/artikel/1029884/wie-koennen-wildunfaelle-verhindert-werden#comments-jump-to. Accessed June 26 2018.

Pürstl, A. (2006). Tierärztliches Gutachten zum Farbsehvermögen von Rot- und Rehwild. Vienna: Tierambulanz Türkenschanzplatz. (unpubl.). 7 pp.

Putman, R. J. (1997). Deer and Road Traffic Accidents: Options for Management. J Environ Manage. 51, 43–57.

Riginos, C., Graham, M. W., Davis, M. J., Johnson, A. B., May, A. B., Ryer, K. J. & Hall, L. E. (2018). Wildlife warning reflectors and white canvas reduce deer–vehicle collisions and risky road-crossing behavior. Wildl. Soc. 42, 119-130.

Roedenbeck, I. A. E. (2007). Landscape-scale effects of roads on wildlife. PhD thesis. University of Giessen, Germany. 157 pp.

Rowden, P., Steinhardt, D., & Sheehan, M. (2008). Road crashes involving animals in Australia. Accident Anal Prev. 40, 1865–1871.

Schulze, C., & Polster, J. U. (2017). Wirkungsweise von Wildwarnern, in: Forschung, Straßenbau und Straßenverkehrstechnik, 1127/2017. 96 pp.

Seidel, D., Hähn, N., Annighöfer, P., Benten, A., Vor, T., & Ammer, C. (2018). Assessment of roe deer (*Capreolus capreolus* L.)–vehicle accident hotspots with respect to the location of ‘trees outside forest'along roadsides. Appl Geogr. 93, 76-80.

Seiler, A. (2005). Predicting locations of moose–vehicle collisions in Sweden. J Appl Ecol. 42, 371–382.

Shannon, G., Cordes, L. S., Hardy, A. R., Angeloni, L. M., & Crooks, K. R. (2014). Behavioral responses associated with a human-mediated predator shelter. PLoS one. 9, e94630.

Sivic, A., & Sielecki, L. E. (2001). Wildlife Warning Reflectors: Spectrometric Evaluation. Ministry of Transportation and Highways. Victoria, BC, Canada. 24 pp.

Szél, Á., Röhlich, P., Caffé, A. R., & van Veen, T. (1996). Distribution of cone photoreceptors in the mammalian retina. Micros Res Techniq. 35, 445–462.

Thompson, I. D., Baker, J. A., & Ter-Mikaelian, M. (2003). A review of the long-term effects of post-harvest silviculture on vertebrate wildlife, and predictive models, with an emphasis on boreal forests in Ontario, Canada. Forest Ecol Manage. 177, 441-469.

Thurfjell, H., Spong, G., Olsson, M., & Ericsson, G. (2015). Avoidance of high traffic levels results in lower risk of wild boar-vehicle accidents. Landscape Urban Plan. 133, 98-104.

Torres, R. T., Carvalho, J. C., Panzacchi, M., Linnell, J. D. C., & Fonseca, C. (2011). Comparative use of forest habitats by roe deer and moose in a human-modified landscape in southeastern Norway during winter. Ecol Res. 26, 781-789.

Trothe, C., Meißner, M., & Herzog, S. (2017). Wildunfälle verhindern – Was hilft wirklich? Präventionsmaßnahmen auf dem Prüfstand. Institute for Wildlife Biology Göttingen, Dresden e.V., Final Report. Göttingen, Germany. 153 pp.

Ujvári, M., Baagøe, H. J., & Madsen, A. B. (1998). Effectiveness of wildlife warning reflectors in reducing deer-vehicle collisions: a behavioral study. J Wildlife Manage. 62, 1094–1099.

Underwood, A. J., & Chapman, M. G. (2003). Power, precaution, Type II error and sampling design in assessment of environmental impacts. J Exp Mar Biol Ecol. 296, 49–70.

VerCauteren, K. C., & Pipas, M. J. (2003). A review of color vision in white-tailed deer. Wildlife Soc B. 31, 684–691.

Viehmann, S. (2018). Sicherheit auf der Landstraße: Dazu dienen die blauen Reflektoren an Leitpfosten. Focus. https://www.focus.de/auto/praxistipps/video/sicherheit-auf-der-landstrasse-haetten-sie-es-gewusst-dazu-dienen-die-blauen-reflektoren-an-leitpfosten_id_6108088.html. Accessed July 5 2018.

Wickström, G., & Bendix, T. (2000). The" Hawthorne effect"—what did the original Hawthorne studies actually show? Scand J Work Env Hea. 26, 363-367.

Yokoyama, S., & Radlwimmer, F. B. (1998). The "five-sites" rule and the evolution of red and green color vision in mammals. Mol Biol Evol. 15, 560–567.

Zuberogoitia, I., del Real, J., Torres, J. J., Rodriguez, L., Alonso, M., & Zabala, J. (2014). Ungulate Vehicle Collisions in a Peri-Urban Environment: Consequences of Transportation Infrastructures Planned Assuming the Absence of Ungulates. PloS one. 9, p. e107713.

List of publications

Journal articles

Benten, A., Annighöfer, P., & Vor, T. (2018). Wildlife Warning Reflectors' Potential to Mitigate Wildlife-Vehicle Collisions–A Review on the Evaluation Methods. Frontiers in Ecology and Evolution, 6, 37.

Seidel, D., Hähn, N., Annighöfer, P., **Benten, A.,** Vor, T., & Ammer, C. (2018). Assessment of roe deer (*Capreolus capreolus* L.)–vehicle accident hotspots with respect to the location of 'trees outside forest'along roadsides. Applied Geography, 93, 76-80.

Benten, A., Hothorn, T., Vor, T., & Ammer, C. (2018). Wildlife Warning Reflectors Do not Mitigate Wildlife-Vehicle Collisions on Roads. Accident Analysis & Prevention, 120: 64-73.

Submitted/unpublished manuscripts

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Tinnesand, H. V., Cross, B. C., **Benten, A.**, Zerdrosser, A., & Rosell F. N. (submitted). Distant neighbors: friends or foes? Wild Eurasian beavers show context dependent responses to simulated intruders. Animal Behaviour.

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Curriculum vitae

Curriculum vitae Anke Benten

Personal Information

Date of birth	09.09.1985
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Work Experiences

since 05/2014	Scientific research assistant: Silviculture and Forest Ecology of the Temperate Zones, Forest Sciences, University of Göttingen, Germany (Prof. Dr. Christian Ammer).
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04/2012 – 08/2013	Scientific research assistant and master student: Telemark University College, Bø, Norway (Prof. Dr. Frank Rosell).
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Education

05/2014 - 09/2018	**PhD program:** Forest Sciences and Forest Ecology.
10/2010 – 03/2013	**Master program:** Behavioral-, Neuro- and Cognition Biology, University of Vienna, including Wildlife Ecology and Management at the University of Natural Resources and Life Sciences (BOKU).
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Appendix

Declaration of originality and confirmation of conformance

I, Anke Benten, hereby declare that I am the sole author of this dissertation entitled 'Evaluation of the Efficacy of Wildlife Warning Reflectors to Mitigate Wildlife-Vehicle Collisions on Roads'. All references and data sources that were used in the dissertation have been appropriately acknowledged.

I furthermore declare that this work has not been submitted elsewhere in any form as part of another dissertation procedure.

Moreover, I confirm that the contents of the digital version are identical with the written scientific treatise.

(Place and date) (Signature)