



# Wildlife warning reflectors do not mitigate wildlife–vehicle collisions on roads



Anke Bente<sup>a,\*</sup>, Torsten Hothorn<sup>b</sup>, Torsten Vor<sup>a</sup>, Christian Ammer<sup>a</sup>

<sup>a</sup> *Silviculture and Forest Ecology of the Temperate Zones, Forest Sciences, University of Göttingen, Büsgenweg 1, 37077 Göttingen, Germany*

<sup>b</sup> *Epidemiology, Biostatistics and Prevention Institute, University of Zürich, Hirschengraben 84, 8001 Zürich, Switzerland*

## ARTICLE INFO

### Keywords:

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

## 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, 1984 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.

## 1. 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 et al., 1998; Cederlund et al., 1998; Mysterud et al., 2006; Massei et al., 2015). 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

\* Corresponding author.

E-mail address: [abenten@gwdg.de](mailto:abenten@gwdg.de) (A. Bente).

endangered by collisions with vehicles and are widespread in Europe (Cederlund et al., 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., 2018; Schilderwerk 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; Bente 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.

## 2. Materials and methods

### 2.1. 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 1. Data on hunting statistics were provided by local hunting authorities.

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  $2036.43 \text{ m} \pm 280.37 \text{ m}$  long, with a minimum of 960.48 m and a maximum of 2552.78 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.

### 2.2. 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- und Gummiverarbeitung Inc., 2017). 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  $\times$  width  $\times$  depth) of the reflectors were 150 mm  $\times$  87 mm  $\times$  37 mm (“Semicircle reflector”), 260 mm  $\times$  95

**Table 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).

Species	Total annual hunting bag for ungulate species in the study area			
	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

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 microprismatic reflective film (3M Corporation, Minnesota, USA; “*Semicircle reflector*”), blue-transparent plastic with aluminum vapor plating (“*The general*”), a microprismatic 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.

### 2.3. 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  $41.87 \text{ m} \pm 7.52 \text{ m}$ . 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.

### 2.4. 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, 2018). 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  $1.05 \pm 0.31$  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  $H = -\sum_{i=1}^R p_i \cdot \ln p_i$ ; where  $p_i$  is the fraction of individuals belonging to species  $i$  in a sample or population (cf. Spatharis et al., 2011).

### 2.5. 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 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  $\alpha = 2.5\%$ .

The sample size of  $N = 151$  road segments running a total of

**Table 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.

Sequence	Number of road segments (length in km)					Total
	mc	db	db + a	lb	lb + a	
(+, –)	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)

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.

### 3. Results

A total of 1984 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.

#### 3.1. Influence of wildlife warning reflectors on wildlife–vehicle collisions

Neither the year in which the reflectors were present on at a site (Fig. 1) nor the presence of any type of wildlife warning reflector (Fig. 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%. The corresponding non-superiority hypothesis could be rejected

with a one-sided p-value of 0.008; this is in line with the lower bound of the confidence interval for the collision ratio being > 0.9. The standard deviations of the random intercepts for road segment (0.49) and for year within road segment (0.19) indicated the presence of unexplained heterogeneity at the road segment level but relatively small over-dispersion effects. The AIC of 1623.29 of the model without a carry-over effect parameter was smaller than the AIC of a model that adjusted for carry-over (AIC = 1625.27), which suggested that such an effect was absent. After adjustment for the presence of wildlife warning reflectors, 2% more collisions were observed in the second observation year, but this effect was not significant.

#### 3.2. 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), (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. 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 4).

We estimated the AIC and collision ratio for 12 models (Table 5). The model “Total” refers to the model used for the primary confirmatory analysis with an AIC of 1623.29. 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). 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 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 6 gives the results of models with numeric effect modifiers (main and interaction effects). 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., 2015, 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).

**Table 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
Raccoon	(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		1984

**4. Discussion**

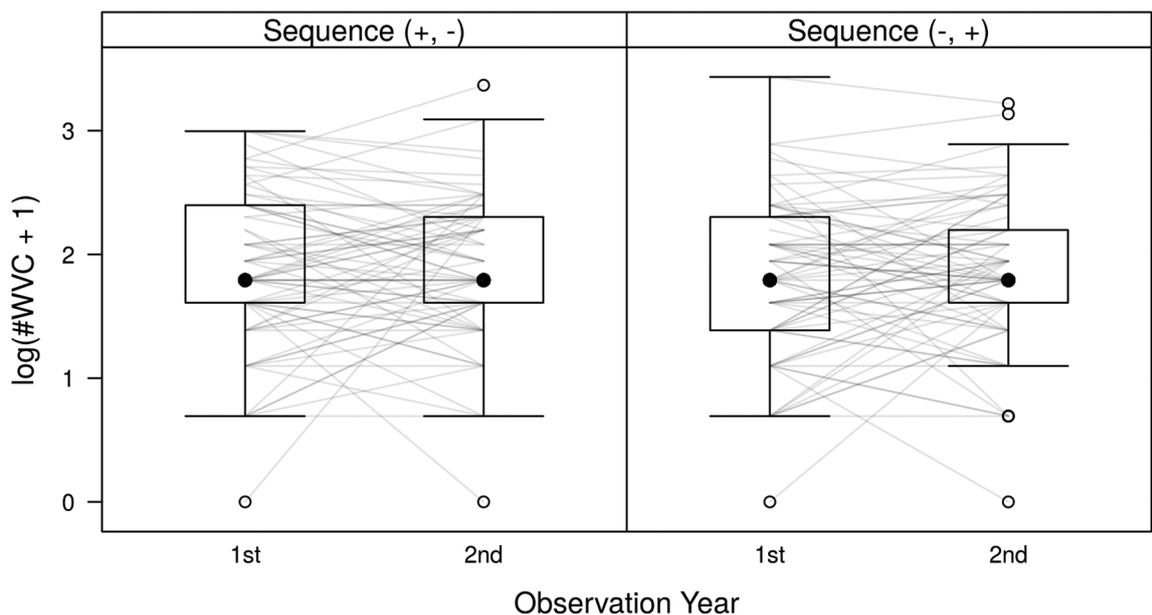
Our cross-over experimental design revealed that modern wildlife warning reflectors did not lead to a relevant reduction in wildlife–vehicle collisions. None of the tested reflectors, including opto-acoustic devices, were able to reduce the number of reported collisions. Moreover, other variables describing 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.

**4.1. 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., 2008). 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., 2008). 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



**Fig. 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.

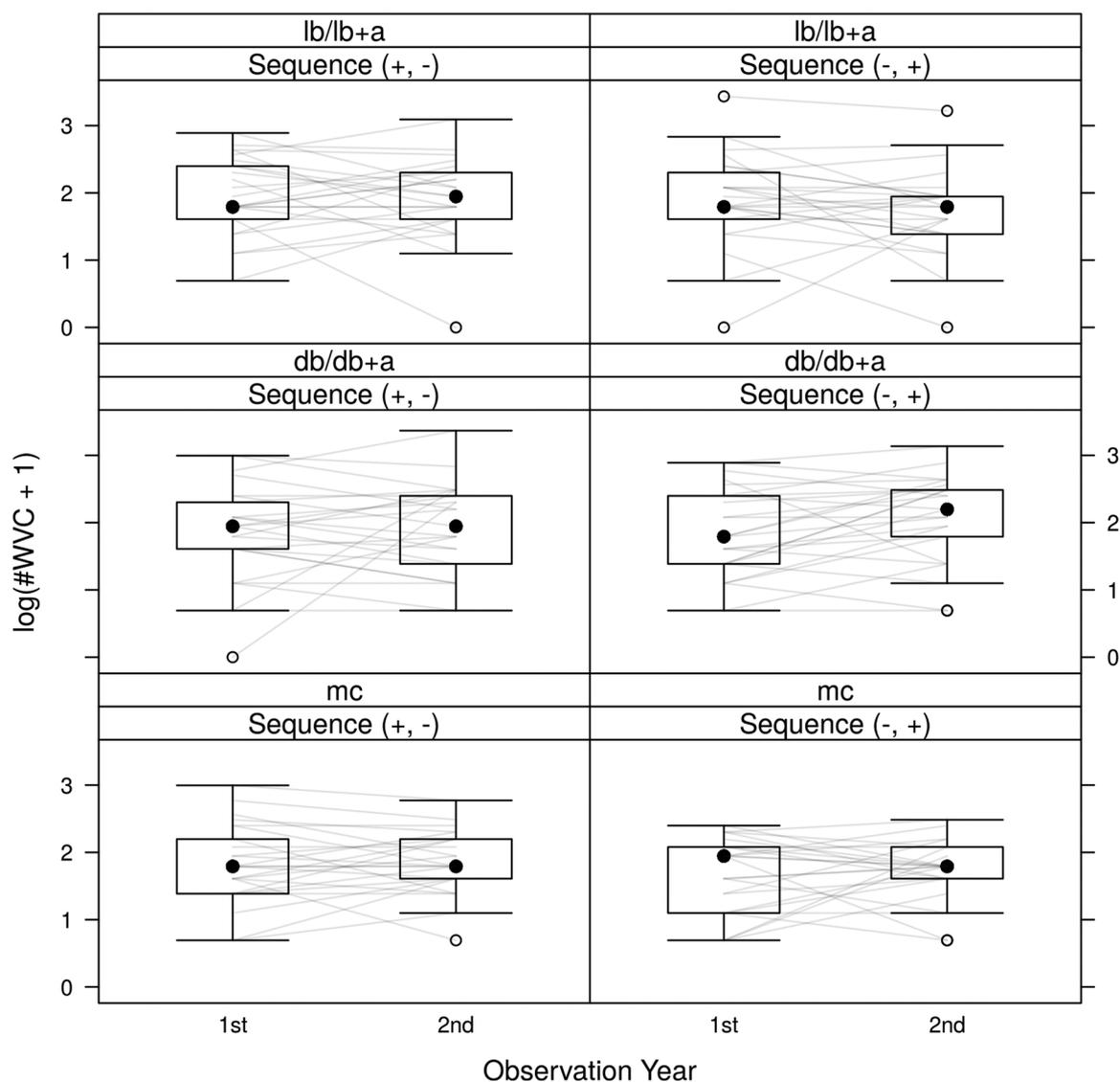


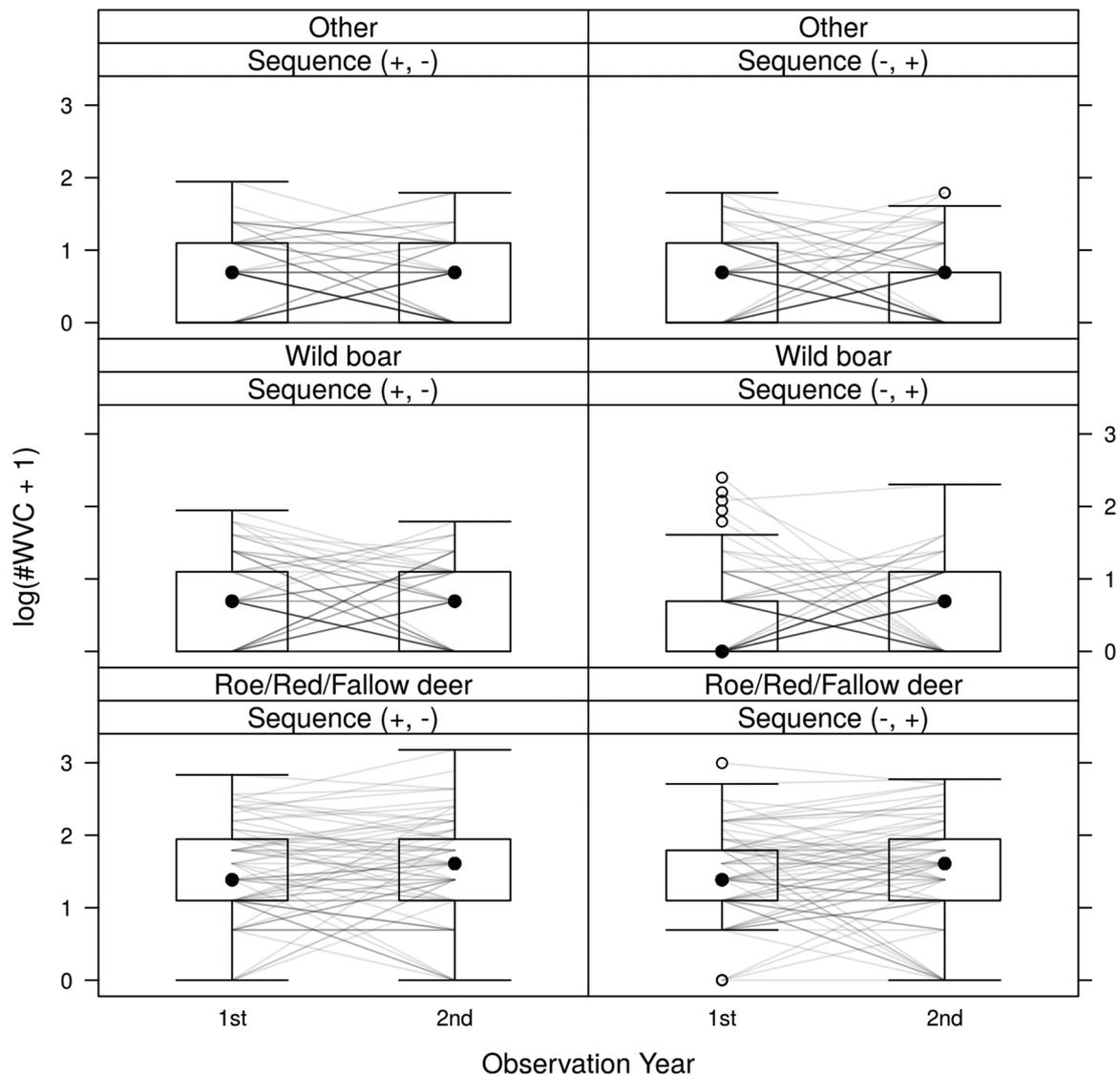
Fig. 2. Number of wildlife–vehicle collisions (WVC, on a log scale) with the two possible active/passive sequences (+, -) and (-, +), stratified by type of reflector. The boxplots represent the marginal distributions of wildlife–vehicle collisions observed over the two years. The joint distribution is 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.

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 et al., 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 et al., 2001; Ahnelt et al., 2006; Schivitz et al., 2008). Ungulates, e.g., roe deer, frequent open areas and agricultural fields at night (Mysterud et al., 1999a,b), 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 et al., 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, b; 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



**Fig. 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.

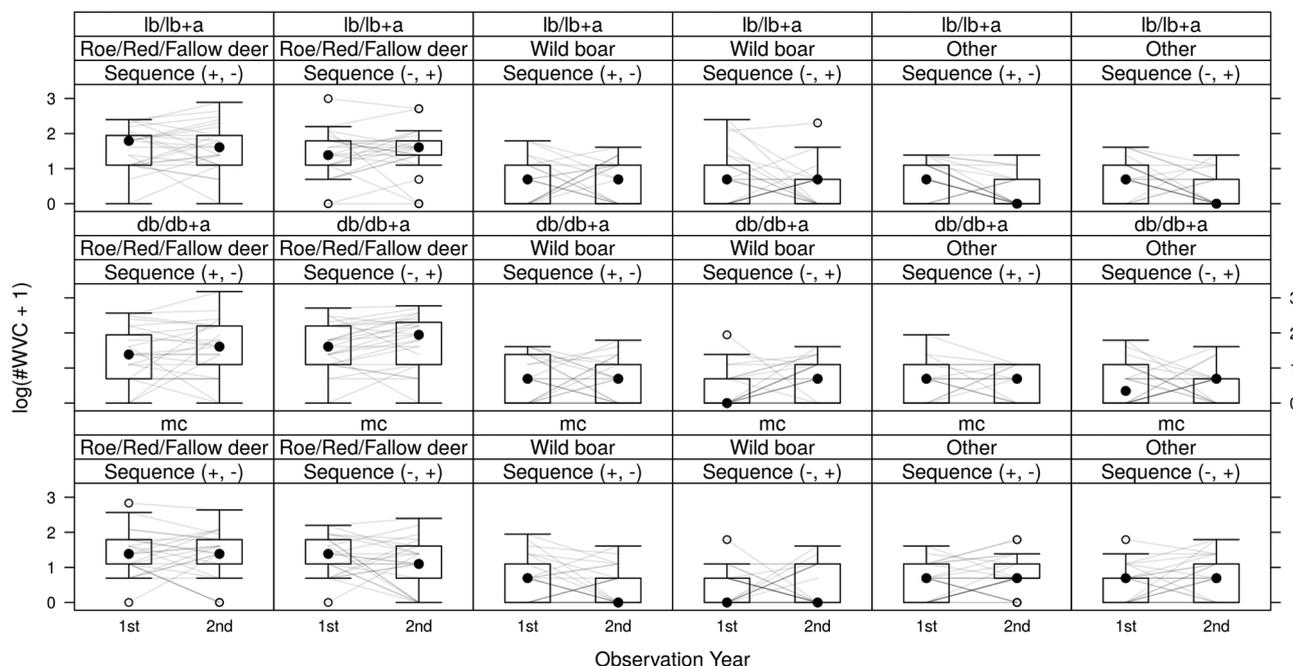
in the period immediately following reflector installation and whether the deer became habituated towards the reflectors over time.

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.

#### 4.2. 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



**Fig. 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 4**  
Median and range of road segment characteristics.

Characteristic	Median and range
Length (m)	2036.43 (960.48 to 2552.78)
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 <sup>-1</sup> )	100.00 (50.00 to 100.00)

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

**Table 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

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).

**Table 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)

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.

## 5. 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.

## Acknowledgements

We thank F. Schulz, S. Betge, E. Geitel, J. Himmel, and their colleagues for their efforts in providing data on wildlife–vehicle collisions. We thank the hunting authorities associated with the study area, represented by M. Schölzel, J. Güthoff, and R. Hankel, for their support and time spent providing access to local hunters. We thank U. Westphal, M. Unger, K. Heine, M. Montero, S. Tielbürger, S. Fuhrmann, T. Lübbe, and K. Höwler for their help in mounting thousands of wildlife warning reflectors. We thank E. Bakaba and J. Ortlepp for fruitful discussions and support in obtaining traffic data. We thank J. Brockhaus for compiling the land-use data in the 500 m buffer zones. Funding was provided by the German Insurance Association (GDV). Moreover, we thank K. A. Brune for improving the text linguistically.

## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.aap.2018.08.003>.

## References

- Ahnelt, P.K., Schubert, C., Kuebber-Heise, 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. <https://doi.org/10.18637/jss.v067.i01>.
- Beben, D., 2012. Crossings for animals—an effective method of wild fauna conservation. *J. Environ. Eng. Landsc. Manag.* 20, 86–96.
- Beilharz Straßenausrüstung Inc, 2018. Der General<sup>®</sup> - Wildwarnreflektor (Accessed 6 December 2017). <https://www.beilharz.eu/de/wildwarnreflektor.html>.
- Bente, 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.
- Bennett, A.F., 1991. Roads, roadsides and wildlife conservation: a review. In: Saunders, D.A., Hobbs, R.J. (Eds.), *Nature Conservation 2: The Role of Corridors*. Surrey Neatty & Sons Pty Limited, Western Australia, pp. 99–118.
- 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. *Accid. 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. *Wildl. Biol.* 17. <https://doi.org/10.2981/wlb.00331>.
- 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. Wildl. Res.* 63. <https://doi.org/10.1007/s10344-017-1130-5>.
- Bruinderink, G., Hazebroek, E., 1996. Ungulate traffic collisions in Europe. *Conserv. Biol.* 10, 1059–1067.
- Carroll, J., Murphy, C.J., Neitz, M., Hovee, 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., Boisauert, B., Ballon, P., Duncan, P., 1998. Managing roe deer and their impact on the environment: maximising the net benefits to society. In: Andersen, R., Duncan, P., Linnell, J.D.C. (Eds.), *The European roe deer: the Biology of Success*. Scandinavian University Press, Oslo, Norway, pp. 189–219.
- 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.
- 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.
- 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. *Transp. Res. D-Transp. Environ.* 16, 281–287.
- Elmeros, M., Winblad, J.K., Andersen, P.N., Madsen, A.B., Christensen, J.T., 2011. Effectiveness of odour repellents on roe deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*): a field test. *Eur. J. Wildl. Res.* 57, 1223–1226.
- ESRI ArcGIS Desktop, 2014. Release 10.3 Environmental Systems Research Institute. Redlands, CA.
- ET Geowizards, 2018. Available from: Version 11.2 (Accessed 17 January 2018). [http://www.ian-ko.com/ET\\_GeoWizards/gw\\_main.htm](http://www.ian-ko.com/ET_GeoWizards/gw_main.htm).
- European Environmental Agency, 2013. CORINE Land Cover (CLC) 2006.
- Fokkema, M., Smits, N., Zeileis, A., Hothorn, T., Kelderman, H., 2015. Detecting treatment-subgroup interactions in clustered data with generalized linear mixed-effects model trees. Working Paper 2015–10, Working Papers in Economics and Statistics, Research Platform Empirical and Experimental Economics. University at Innsbruck URL. <http://EconPapers.RePEc.org/RePEc:inn:wpaper:2015-10>.
- 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 (Accessed 6 December 2017). <http://www.gdv.de/2017/11/versicherer-registrieren-taeglich-ueber-720-wildunfaelle/>.
- 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.
- 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.
- Groves, R.M., 2004. *Survey Errors and Survey Costs*. John Wiley & Sons, New York.
- 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: Mackintosh, G. (Ed.), *Preserving Communities and Corridors*. Defenders of Wildlife, 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: Saunderson, D.A., Hobbs, R.J. (Eds.), *Nature Conservation the Role of Corridors*. Surrey Beatty and Sons, Chipping Norton, Australia, pp. 189–220.
- 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. *Biom. J.* 50, 346–363.
- 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. *Accid. 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. Wildl. Manage.* 64, 707–713.
- 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.
- 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. Western Transportation Institute, Bozeman 123 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.
- 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. *Eur. J. Wildl. Res.* 58, 661–668.
- 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: Putman, R., Apollonio, M., Andersen, R. (Eds.), *Ungulate Management in Europe: Problems and Practices*. Cambridge University Press, Cambridge, USA pp 215–259.
- Lavrakas, P.J., 2008. Sampling bias. In: Lavrakas, P.J. (Ed.), *Encyclopedia of Survey Research Methods*. Sage Publications, California, USA, pp. 56–61.
- 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. Wildl. 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? *J. Appl. 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., 2008. *Wildlife Study Design*. Springer Science & Business Media, New York, USA.
- Motzener Kunststoff- und Gummiverarbeitung Inc, 2017. *Multiwildschutzwarner* (Accessed 6 December 2017). <https://www.wildwechsel-unfall-vermeiden.de/index.html>.
- Mueller, J.E., 1968. An introduction to the hydraulic and topographic sinuosity indexes I. *Ann. Assoc. Am. Geogr.* 58, 371–385.
- Mysterud, A., Larsen, P.K., Ims, R.A., 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., Hjernmann, D.Ø., 1999b. 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. *Med. Microbiol. Lett.* 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. Wildl. 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? *Wildl. 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, pp. 10.
- 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 Schlaw: 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.
- 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., Muyltermans, 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, pp. 157.
- Rowden, P., Steinhart, D., Sheehan, M., 2008. Road crashes involving animals in Australia. *Accid. 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. Saf. Res.* 19, 99–100.
- Schilderwerk Beutha Inc, 2017. *Der Wildwarnreflektor* (Accessed 6 December 2017). <http://www.halbkreisreflektor.de/>.
- 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. Forschung Straßenbau und Straßenverkehrstechnik. Bundesministerium für Verkehr und digitale Infrastruktur, Hrsg 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. *Microsc. Res. Tech.* 35, 445–462.
- Team, R.Core, 2018. *URL: R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- 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. *Wildl. Soc. Bull.* 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.R., 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.