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Original Article

Wildlife Warning Reflectors and White Canvas Reduce Deer–Vehicle Collisions and Risky Road-Crossing Behavior

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ABSTRACT Collisions between wildlife and vehicles are detrimental to both wildlife and human safety. A variety of mitigation methods have been deployed with the intent of increasing ungulate awareness of approaching vehicles. Wildlife warning reflectors are one such method. Roadside reflectors are designed to reflect headlights into the right-of-way and alert ungulates to approaching vehicles. Studies of the effectiveness of these reflectors have yielded mixed results. We conducted a robust test of reflectors in central Wyoming, USA, during 2013 and 2014, and unexpectedly discovered a potentially more effective method than the reflectors for reducing collisions between vehicles and mule deer (*Odocoileus hemionus*). In our initial experiment, we manipulated 10 1.6-km segments of highway by leaving their reflectors exposed or covering them with a white canvas bag with the intention of neutralizing the reflector. The treatment configuration was swapped monthly. We counted deer carcasses under each treatment for 1 year and observed deer road-crossing behavior using thermal video cameras. Carcass rates were 33% less in the white canvas treatment relative to uncovered reflectors. Deer in the white canvas treatment also stopped before entering the road 20% more often, ran into the road from the right-of-way 11% less often, and fled from the road 12% more often than when reflectors were uncovered. In a follow-up experiment, we found that deer carcass rates were 32% less when reflectors were exposed versus covered with black canvas. We further found that deer road-crossing behavior was least risky in a white canvas treatment, intermediate in a reflectors treatment, and most risky when reflectors were removed from posts. Taken together, these results indicate that, although reflectors were moderately effective, white canvas was substantially more effective in reducing deer–vehicle collisions. This unexpected finding suggests that new vigilance-enhancing mitigation methods should be explored as a way to reduce wildlife–vehicle collisions. © 2018 The Wildlife Society.

KEY WORDS mule deer, *Odocoileus hemionus*, road ecology, Strieter-Lite reflectors, wildlife–vehicle collisions, Wyoming.

Collisions between large mammals and vehicles pose a threat both to wildlife and highway safety (Bissonette et al. 2008, Huijser et al. 2008). Across the United States, an estimated 1–2 million collisions between large mammals and vehicles occur every year, and this number continues to climb as road networks expand and traffic volumes increase (Huijser et al. 2009). The vast majority of these collisions involve deer (*Odocoileus* spp.; Huijser et al. 2009). Highways and wildlife–vehicle collisions can have a significant negative effect on wildlife by reducing population numbers and impeding animal movements through home ranges and along migratory corridors (Forman and Alexander 1998, Beckman and Hilty 2010). In the western United States, roads are considered one of the most significant threats to mule deer (*O. hemionus*; Wakeling et al. 2015), which have declined in many parts of their range (de Vos et al. 2003). Wildlife–vehicle collisions are also expensive and dangerous; they are estimated to cost US$6–12 billion/year in the United States (Huijser et al. 2009) and in Wyoming, USA, account for 15–18% of all reported vehicle collisions per year (Wyoming Department of Transportation, 2016). As a

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consequence, wildlife managers and transportation engineers continue to invest considerable resources to determine how best to prevent wildlife–vehicle collisions from occurring.

Wildlife–vehicle collision mitigation measures range widely in both cost and effectiveness. Highway crossing structures such as overpasses and underpasses, when coupled with extensive wildlife-exclusion fencing to funnel animals toward the crossings, typically reduce wildlife–vehicle collisions by >80% (Huijser et al. 2009, 2016; Huijser and McGowen 2010; McCollister and Van Manen 2010; Sawyer et al. 2012). They are also very effective at maintaining habitat connectivity for large mammals. However, they typically cost hundreds of thousands to millions of dollars to install and require years of planning (Huijser et al. 2009). Further, they rely on excluding wildlife from the road, which may be difficult to do in more developed areas where there are many driveways or access roads that require a break in the wildlife exclusion fencing.

A number of much less expensive mitigation measures have been developed in an attempt to modify ungulate behavior to reduce wildlife–vehicle collisions. These are generally designed to increase the level of vigilance and awareness of vehicles among target animals. Measures such as deer whistles, olfactory repellents, mirrors, and model deer in alarm posture have generally proven ineffective at reducing wildlife–vehicle collisions (Romin and Dalton 1992, Romin and Bissonette 1996, Brown et al. 2000, Ujvári et al. 2004, Valitzski et al. 2009).

Wildlife warning reflectors, also known as Strieter-Lite® (Strieter Corporation, Rock Island, IL, USA) reflectors or Swareflex (Swareflex GmbH, Vomp, Austria) reflectors, are another mitigation method designed to increase ungulate vigilance and awareness of vehicles (Fig. 1). Reflectors are mounted on a series of roadside posts so that vehicle headlights reflect in a moving pattern both across the road and into the roadside vegetation. The intent is that approaching deer or other ungulates will notice the reflected light and halt or flee away from the road until the vehicle and lights have passed and then cross safely. Reflectors are visually subtle to drivers. Despite numerous studies, the effectiveness of these reflectors has remained the subject of debate. The Strieter Corporation (Rock Island, IL, USA) reports a 78–90% reduction in deer–vehicle collisions based on an unpublished meta-analysis that they commissioned (Grenier 2002). However, results of studies within this meta-analysis and in the broader literature are mixed. Although many studies have found no effect of reflectors on collision rates, as measured via carcass counts (Woodard et al. 1973, Waring et al. 1991, Armstrong 1992, Ford and Villa 1993, Reeve and Anderson 1993), other studies have found that reflectors reduced collision rates by anywhere from 19–90% (Gladfelter 1984, Schafer and Penland 1985, Pafko and Kovach 1996, Gulen et al. 2006). A recent meta-analysis of all light-reflecting devices, including reflectors and mirrors, found no consistent effect of these devices on collision rates (Brieger et al. 2016). Study designs have been highly variable among these studies. Many studies have relied upon before–after comparisons, which is problematic given that wildlife–vehicle collision rates can vary from year to year at a specific location because of annual fluctuations in deer activity (Brieger et al. 2016). Other studies have used case-control designs with questionable controls, such as substantially fewer carcasses at the control site relative to the treatment site before the reflectors were installed (Gladfelter 1984).

In one of the few comprehensive studies of the effects of reflectors on deer road-crossing behavior, there was no

Figure 1. Wildlife warning reflectors (left), reflectors covered with white canvas (center), and reflectors covered with black canvas (right) in central Wyoming, USA.

significant effect of reflectors on deer road-crossing behavior (D'Angelo et al. 2006). In another study, deer were found to react to reflectors initially but became increasingly habituated over a period of 17 days, suggesting no long-term effect of the reflectors on deer behavior (Ujvári et al. 1998). The lack of consistent deer behavioral responses to reflectors, coupled with inconclusive or weak evidence from carcass counts, has led some to conclude that reflectors are ineffective (D'Angelo and van der Ree 2015, Brieger et al. 2016).

Between 2007 and 2010, the Wyoming Department of Transportation (WYDOT) installed Strieter-Lite® wildlife warning reflectors along 30.6 km of highway in central Wyoming with deer–vehicle collision rates ranging spatially from 2.5 to 12.5/km/year. We initially set out to ask whether these reflectors were effective in terms of reducing 1) the number of deer–vehicle collisions; and 2) risky road-crossing behavior among deer in the real-world setting of high-speed rural roads in Wyoming. After the first year of the study, we discovered that our "control" treatment, which was reflectors covered with white canvas, had a greater effect than the reflectors on both collision rates and deer behavior. It was clear that the white canvas was not functioning as a neutral control, so we implemented 2 additional experiments in the second year of the study to test the effectiveness of both reflectors and white canvas against more neutral treatments. Thus, an unanticipated but key objective of the study became testing the effectiveness of white canvas as an alternative to reflectors.

STUDY AREA

The WYDOT installed red Strieter-Lite wildlife warning reflectors between 2007 and 2010 in 3 general areas (Fig. 2):

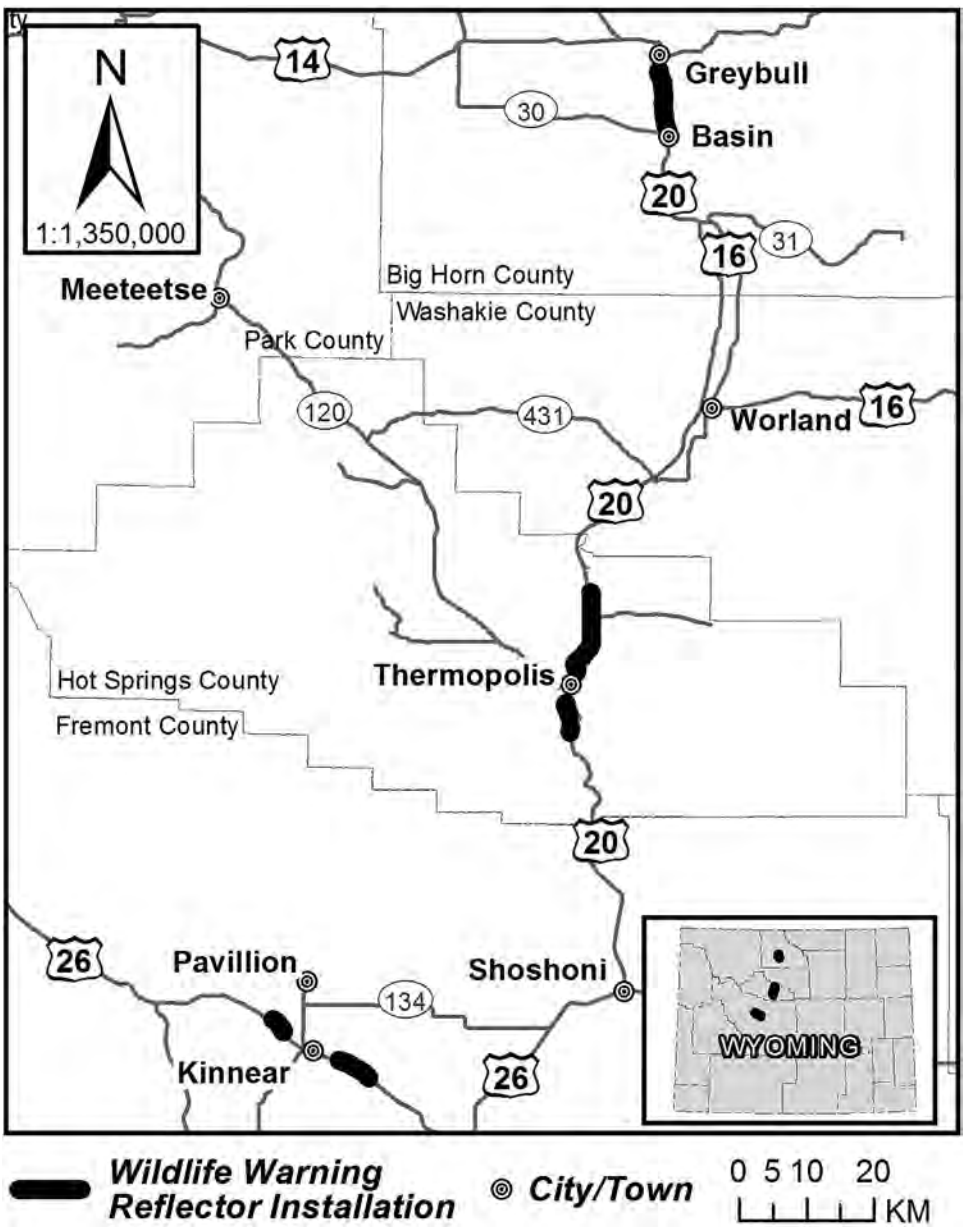

Figure 2. Road stretches on 3 highways in central Wyoming, USA, where wildlife warning reflectors were tested in 2013–2014.

1) on US 26 east and west of the small settlement of Kinnear (9.2 km); 2) on US 16/20 between the towns of Basin and Greybull (9.7 km); and 3) on US 20 north and south of the town of Thermopolis (19.6 km). Reflectors were installed and maintained according to manufacturer's specifications, taking in account road curvature, slope of embankment, and height above road surface. All 3 reflector areas were situated on 2-lane highways with speed limits of 105 km/hr (65 miles/hr) and annual average daily traffic ranging from 1,853 (Kinnear) to 3,281 (Basin) vehicles. Adjacent land-cover types consisted primarily of sagebrush (*Artemisia* spp.) and saltbrush (*Atriplex* spp.) scrub (32–45%), irrigated cropland (23–29%), and wetland (10–26%). An active railroad ran parallel to US 16 and US 20, ranging from 20 to 400 m from the road.

Deer populations in this region were mostly mule deer, although we observed one group of approximately 10 white-tailed deer (*O. virginianus*) north of Thermopolis. Both species were primarily resident, and deer–vehicle collision rates were greatest during autumn (Riginos et al. 2016).

METHODS

Experiment I: Reflectors Versus White Canvas

In February 2013, we set up a cover–uncover experiment in the Thermopolis reflector area. We used white canvas sample bags to cover reflectors on 10 alternating 1.6-km (1-mi) segments of road for 1 month at a time, then switched the bags to cover the previously uncovered segment. We used white canvas bags because they were a durable and economical material (~US$1.50/bag) that could be used to cover the reflectors and stop them from reflecting. Bags were custom-made from unbleached cotton duck canvas for WYDOT by Commercial Bags and Textile, Inc. (Des Moines, IA, USA), and measured 35 × 61 cm. We folded bags and tied them tightly onto reflector posts to prevent them from flapping or blowing off in the wind. Starting in October 2013, we extended the experiment to include the Kinnear and Basin–Greybull reflector areas. October–January is the peak deer–vehicle collision season, so we alternated the experimental configuration every 2 weeks until the end of February 2014, when we terminated the experiment. We did this to ensure that all 1.6-km road segments experienced both treatments through the peak collision season, because the timing of peak deer road crossing activity varied somewhat from location to location.

We worked with highway maintenance crews to record all deer carcasses that occurred within the experimental area. Although carcass counts likely underestimate the actual number of deer–vehicle collisions because some animals leave the right-of-way before dying, we assumed that this fraction would be similar across treatments, allowing us to use carcass counts as a relative index of collisions in each treatment. Maintenance crews surveyed roads and mowed right-of-ways every 45 days; when a crew member encountered a carcass, he or she recorded the Global Positioning System location, date, and what treatment (reflector exposed vs. covered) was applied to that road segment at that time. This enabled us to accurately assign each carcass to a highway segment and treatment.

In addition to carcass counts, we also observed deer road-crossing behavior at 16 sites within the experimental areas between November 2013 and January 2014. Sites were spread across all 3 reflector areas (Kinnear = 2, Basin–Greybull = 6, Thermopolis = 8) and located in places where we had previously observed frequent deer crossing events. We collected behavioral data using 2 automated recording systems between dusk and dawn, which is the time window when most deer–vehicle collisions occur and reflectors are expected to be most effective. Each system consisted of a FLIR® Scout PS32 Thermal Handheld Camera (FLIR Systems, Wilsonville, OR, USA) wired to a laptop and deep-cycle battery. In the field, we mounted the FLIRs to the end of 3-m-long poles placed in the road right-of-ways. We directed the camera parallel to the road, with a field of view that included the road, both shoulders, and right-of-ways.

We recorded deer behavioral observations in 5 "cycles," each 8 nights long, between 19 November 2013 and 21 January 2014. Each night, one FLIR system was set up in a reflector-exposed road segment and the other was set up in a nearby white canvas covered segment. Cameras recorded footage continuously to the laptop. We moved the FLIR system after each night so that all 16 sites were sampled once per cycle.

We could reliably observe behavior for deer that were less than approximately 100 m from the camera. We scored deer behavior as follows. Each time a deer moved to the edge of the shoulder, within approximately 3 m of the road, and showed intent to cross the road by moving consistently toward the road with head up, we considered this to be a "deer–road interaction." For each deer–road interaction, we noted whether a vehicle was present or not. In cases where deer were crossing in a group, we only scored the behavior of the first animal that approached the road. For each deer–road interaction, we scored deer behavior using the following categories: whether the deer 1) stopped on the shoulder before entering the road; 2) lifted and/or turned its head before entering the road, hereafter, "exhibited vigilance"; 3) fled away from the road; or 4) ran into the road.

Experiment II: Reflectors Versus Black Canvas

We conducted a second cover–uncover experiment between May and December 2014 using black canvas to cover the reflectors. We used black canvas in an effort to neutralize the reflectors with something far less visible than either the white canvas or reflectors because it was clear that white canvas was having an effect on deer behavior (see Results). We considered removing and reinstalling reflectors, but concluded that it was not logistically feasible to do this over a large enough area to get reliable carcass data. Other means of covering the reflectors that we tried resulted in either a surface that was still somewhat reflective or dirtied the reflectors beyond repair. After several efforts we settled on painting canvas bags using black spray paint (Flat Black color, Rust-Oleum Corp, Vernon Hills, IL, USA). This proved nonreflective and durable under intense sun and weather conditions but required one can of paint for every 2 bags. Given the very large amounts of paint involved, we limited the experiment to 2 adjacent 1.6-km stretches just north of Thermopolis that had consistently high deer–vehicle collision rates. We swapped treatments monthly between the 2 stretches until October 2014, and then every 2 weeks until December 2014.

We collected carcass data as above between May and December 2014. We collected deer road-crossing behavior data between October and December 2014 at one location within each of the 2 stretches of the experiment. Over the course of 5 9-night cycles, we mounted the FLIR system in one or the other of these 2 stretches, on alternating nights. We assessed deer behavior as described above.

Experiment III: Reflectors Versus White Bags Versus Empty Posts

Between October and December 2014, we deployed a third experiment to directly compare deer road-crossing behavior in the presence of reflectors, reflectors covered with white canvas, and empty posts (reflectors removed). Due to the challenges of removing and replacing reflectors, we deployed treatments only in the viewshed, or the extent of roadway visible in the daytime from the position where each FLIR system was mounted, with an additional buffer of 100 m beyond the viewshed and behind the FLIR. Treated areas averaged 734 m (range = 686–922 m). We implemented these treatments at 6 of the 16 sites used in Experiment I: 2 in Thermopolis and 4 in Basin–Greybull. At any one time, each site was configured in one of 2 possible treatments (reflectors vs. empty posts, or white bags vs. empty posts). We changed treatments every 2 weeks.

We collected behavioral observations over the course of 5 9-night cycles during which we rotated 2 FLIR systems nightly among the 6 sites, so that each site was sampled 3 times within each work cycle. We employed this design to provide a balanced representation of each site under different treatment and time-of-year conditions. We evaluated deer behavior using the same methods as in previous experiments. Owing to the short duration and extents of road used in this experiment, we did not collect carcass data.

Data Analyses

We standardized carcass counts from both Experiments I and II to number of carcasses per km per year. This was done to account for the fact that the configurations of treatments were not applied for a completely equal number of days, so total number of days was not always equal among treatments. We calculated carcass rates separately for each 1.6-km road segment in each experiment. For each experiment, we used a paired *t*-test to determine whether treatments differed in carcass rate. We paired data by road segment to control for the fact that deer may cross more frequently and have more opportunities for collisions in some segments than others.

Differences in carcass rates between treatments could be caused by deer crossing the road more carefully in one treatment than the other, or by deer crossing the road less frequently in one treatment than the other. We examined the former possibility using behavioral observations detailed above. For Experiment I (reflectors-exposed vs. covered with white canvas), we conducted 2 additional analyses to investigate whether covering reflectors caused deer to alter their road-crossing frequency or location. If deer were averse to crossing in road segments with white canvas covering reflectors, they might be expected to 1) show different crossing rates in the same segment under white canvas versus reflectors treatments; and 2) be more likely to cross and get hit at the edge of the adjacent segment that would be in a different treatment state. We used a paired *t*-test to test for any differences in crossing rate between the 2 treatments, paired by FLIR location. We determined road crossing rate from behavioral observations and defined it as the total number of deer observed crossing per night, which we log-transformed to normalize these data. To test whether deer were more likely to get hit at the edges of treatments, we categorized each carcass as being located at the edge (first and last 25%) or middle (center 50%) of the segment in which it was hit. We used a Pearson's chi-square (χ^2) goodness-of-fit test to test whether treatment affected the proportion of carcasses found in the edge versus the middle (Zar 1999).

We analyzed deer behavioral data from all 3 experiments using a χ^2 goodness-of-fit test to compare each combination of treatment and vehicle presence versus absence. We then used an analysis of means for proportions to understand which combinations of treatment and vehicle status were influencing significance in the overall chi-squared models (Nelson et al. 2005). The analysis of means provides a visual means to show which group or groups have proportions within or exceeding upper and lower "decision lines" (analogous to confidence intervals); a group that exceeds either decision line is considered significantly different from the overall average of group proportions. We performed all analyses in Program JMP (version 12.0.1, 2015; SAS Institute, Inc., Cary, NC, USA) and Program R (version 3.0.1; R Core Team, 2013).

RESULTS

Carcasses

We recorded 93 carcasses in the Thermopolis experimental area between February 2013 and February 2014. There were 48% more carcasses/km/year when reflectors were exposed compared with when they were covered with white canvas (Fig. 3a; $t_{10} = 3.38$, $P = 0.007$); white canvas reduced the number of carcasses by 33% compared with reflectors. The mean difference in carcass rate between paired road stretches was greater than zero (mean difference = 3.96 carcasses/km/yr; 95% CI = 1.35–6.58). Reflectors, although less effective than white canvas, were more effective than black canvas at reducing deer–vehicle collisions; in a 3.2-km section of the Thermopolis area, reflectors reduced the carcass rate by 32% compared with the black canvas (Fig. 3b; $t_2 = -57.49$, $P = 0.011$). Here, too, the mean difference in carcass rate between paired road stretches was greater than zero (mean difference = 7.55 carcasses/km/yr; 95% CI = 9.23–5.88).

We found no evidence that the treatment affected the number of deer crossing the road at a given site. Deer crossing

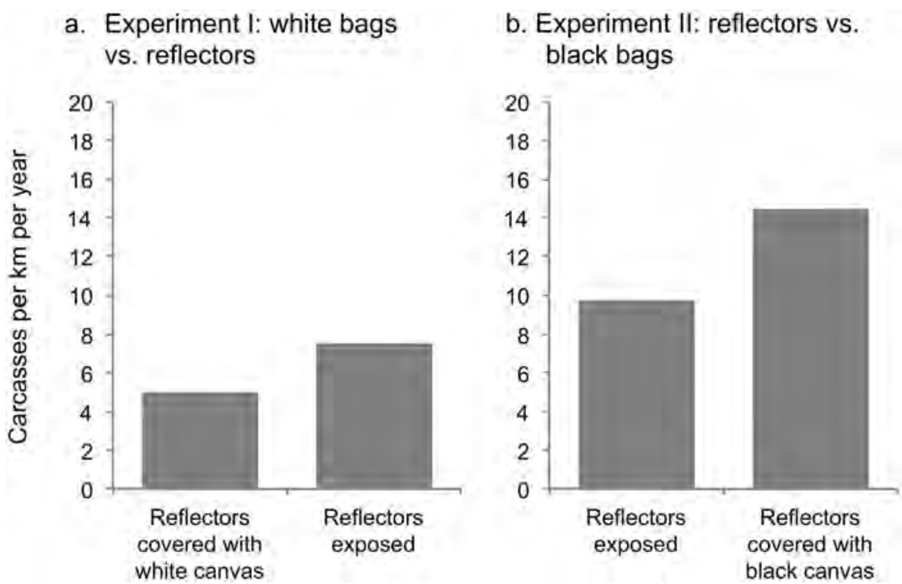

Figure 3. Mean deer carcass rates observed on stretches of highway under different experimental treatments imposed in the area of Thermopolis, Wyoming, USA, from February 2013 to February 2014 (a: Experiment I; $n = 93$ carcasses) and May to December 2014 (b: Experiment II; $n = 20$ carcasses).

rates at behavioral observation sites did not differ between reflector and white canvas treatments ($t_{12} = 0.33$, $P = 0.75$). Further, we found no effect of treatment (reflector exposed vs. white canvas) on the location within each road segment at which deer–vehicle collisions occurred ($\chi^2_{1,121} = 1.33$, $P = 0.72$). Together, these results indicate that the observed effects of treatments on carcass rates were not an artifact of the experiment's 1.6-km treatment configuration.

Road-Crossing Behavior

We observed 407 independent deer–road interactions, 131 with a vehicle present, in Experiment I; 175 deer–road interactions, 47 with a vehicle present, in Experiment II; and 288 deer–road interactions, 134 with a vehicle present, in Experiment III.

Experiment I.—In Experiment I (reflectors vs. white canvas), all 4 deer behaviors differed among treatment–vehicle presence combinations (Fig. 4; deer that stopped before attempting to cross: $\chi^2_3 = 26.37$, $P \leq 0.001$; deer that exhibited vigilance: $\chi^2_3 = 22.76$, $P \leq 0.001$; deer that ran into the road: $\chi^2_3 = 42.84$, $P \leq 0.001$; deer that fled from the road: $\chi^2_3 = 89.21$, $P \leq 0.001$). Deer were more likely to stop and exhibit vigilance behavior before crossing a road in the white canvas treatment compared with the reflectors treatment. Deer stopped before crossing 81% ($n = 129$) of the time in the white canvas treatment without any vehicle present and 90% ($n = 60$) of the time with a vehicle present, compared with 60% of the time in the reflectors treatment without any vehicle ($n = 135$) and 68% of the time with a vehicle present ($n = 68$; Fig. 4a). Similarly, deer exhibited vigilance behavior before crossing 82% ($n = 129$) of the time in the white canvas treatment without any vehicle present and 90% ($n = 60$) of the time with a vehicle present, compared with 64% ($n = 135$) of the time in the reflectors treatment without any vehicle present and 68% ($n = 68$) with a vehicle present (Fig. 4b).

In the absence of a vehicle, deer ran, rather than walked, into the road from the right-of-way at low rates in both treatments: 11% ($n = 133$) of the time in the white canvas treatment and 13% ($n = 138$) of the time in the reflectors treatment (Fig. 4c). Similarly, in the absence of a vehicle, deer fled from the road at low rates in both treatments: 4% ($n = 133$) of the time in the white canvas treatment and 2% ($n = 138$) of the time in the reflectors treatment (Fig. 4d). However, in the presence of a vehicle, deer ran into the road less in the white canvas treatment (35% of the time, $n = 60$) compared with the reflectors treatment (46% of the time, $n = 69$; Fig. 4c) and fled from the road more in the white canvas treatment (45% of the time, $n = 60$) compared with the reflectors treatment 33% of the time, $n = 69$; Fig. 4d). Thus, overall, white bags were associated with more safe, less risky deer road-crossing behavior than were reflectors.

Experiment II.—In Experiment II (reflectors vs. black canvas), vigilance was the only deer behavior that did not differ among treatment–vehicle presence combinations (Fig. 5; deer that stopped before attempting to cross: $\chi^2_3 = 12.08$, $P = 0.007$; deer that exhibited vigilance: $\chi^2_3 = 4.58$, $P = 0.20$; deer that ran into the road: $\chi^2_3 = 31.33$, $P \leq 0.001$; deer that fled from the road: $\chi^2_3 = 38.48$, $P \leq 0.001$). In general, deer exposed to reflectors in the presence of a vehicle exhibited different behaviors from other treatment–vehicle combinations. Deer stopped before entering the road 86% ($n = 28$) of the time when reflectors were exposed and a vehicle was present compared with 59% ($n = 17$) when reflectors were covered with black canvas and a vehicle was present; 53% ($n = 51$) when reflectors were exposed and no vehicle was present; and 51% ($n = 67$) when reflectors were covered with black canvas and no vehicle was present (Fig. 5a). Vigilance behavior showed a similar, though not statistically significant, pattern: deer exhibited vigilance 89% ($n = 28$) of the time when reflectors were

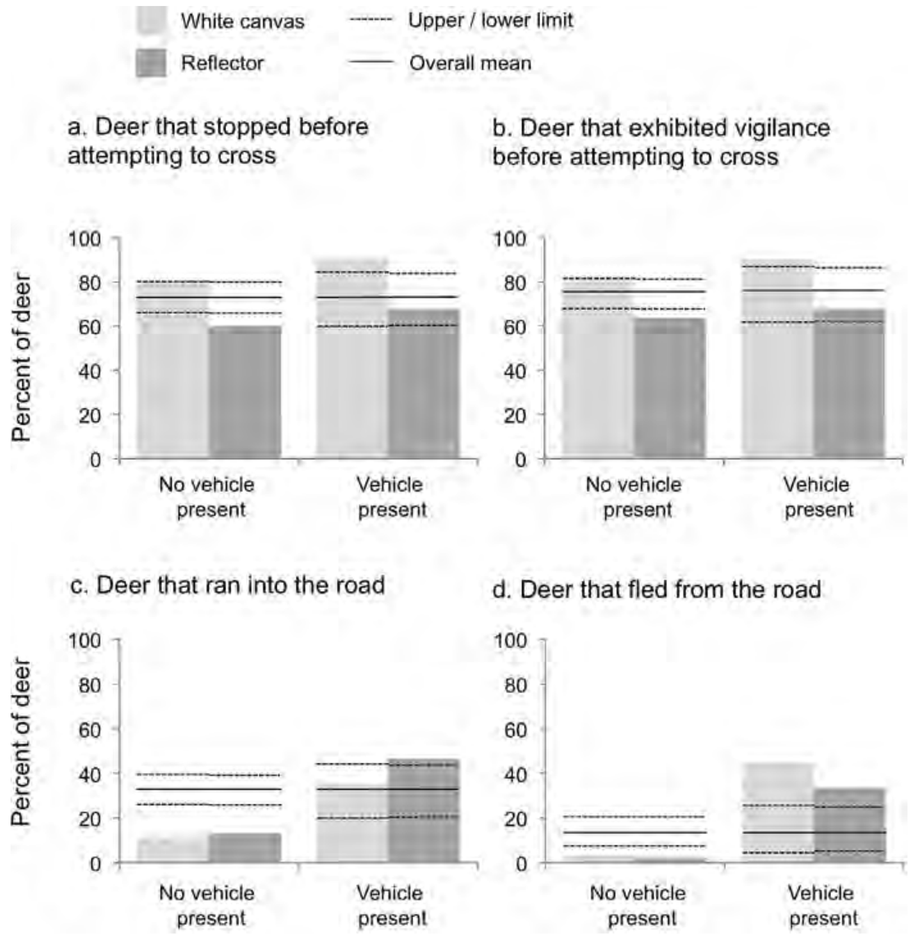

Figure 4. Percent of deer that exhibited 4 key behaviors: (a) stopping at edge of road, (b) vigilance, (c) running into the road, and (d) fleeing from the road, when attempting to cross segments of highway with wildlife warning reflectors versus white canvas covering reflectors (Experiment I; $n = 407$) and in the presence versus absence of an oncoming vehicle. Solid lines indicate overall means and dashed lines indicate upper and lower limit lines from analysis of means. Data were collected in central Wyoming, USA, between November 2013 and January 2014.

exposed and a vehicle was present compared with 69% ($n = 16$) when reflectors were covered with black canvas and a vehicle was present, 78% ($n = 50$) when reflectors were exposed and no vehicle was present, and 71% ($n = 62$) when reflectors were covered with black canvas and no vehicle was present (Fig. 5b). In the absence of a vehicle, deer ran into the road 10% ($n = 72$) of the time in the black canvas treatment and 13% ($n = 54$) of the time in the reflectors treatment (Fig. 5c). In the presence of a vehicle, however, deer ran into the road from the right-of-way 63% ($n = 19$) of the time in the black canvas treatment compared with 43% ($n = 28$) of the time in the reflectors treatment (Fig. 5c). In the absence of a vehicle, deer fled from the road 3% ($n = 74$) of the time in the black canvas treatment and 4% ($n = 54$) of the time in the reflectors treatment. Whereas in the presence of a vehicle, deer fled from the road 21% ($n = 19$) of the time in the black canvas treatment compared with 50% ($n = 28$) of the time in the reflectors treatment (Fig. 5d). Thus, overall, reflectors were associated with more safe, less risky deer road-crossing behavior than were black canvas.

Experiment III.—In Experiment III (reflectors vs. white canvas vs. posts), deer stopping behavior differed somewhat in relation to treatment–vehicle combinations (Fig. 6a; $\chi^2_5 = 10.97$; $P = 0.05$). In the presence of a vehicle, deer stopped 79% ($n = 53$) of the time in the white canvas treatment compared with 70% ($n = 33$) of the time in the reflectors treatment and 63% ($n = 41$) of the time in the empty posts treatments. In the absence of a vehicle, deer stopped 81% ($n = 26$) of the time in the white canvas treatment compared with 56% ($n = 41$) of the time in the reflectors treatment and 59% ($n = 78$) of the time in the empty posts treatment. Vigilance behavior did not differ across treatment–vehicle combinations ($\chi^2_5 = 2.13$, $P = 0.83$) but showed the same rank order of responses as stopping behavior, with vigilance greatest in the white canvas treatment and least in the empty posts treatment both with and without a vehicle present (Fig. 6b). Consistent with the previous 2 experiments, deer in Experiment III were more likely to run into the road ($\chi^2_5 = 59.65$, $P \leq 0.001$) and flee from the road ($\chi^2_5 = 78.01$, $P \leq 0.001$) in the presence of a vehicle than when there was no vehicle present. However, treatment influenced these deer behaviors in the presence of a vehicle (Fig. 6c and d). In the absence of a vehicle, deer ran into the road at similarly low rates across treatments: 10% ($n = 29$) of the time in the white canvas treatment, 7% ($n = 42$) of the time in the reflectors treatment, and 6% ($n = 78$) of the time in the empty posts treatment. In contrast, in the presence of a vehicle, deer ran into the road

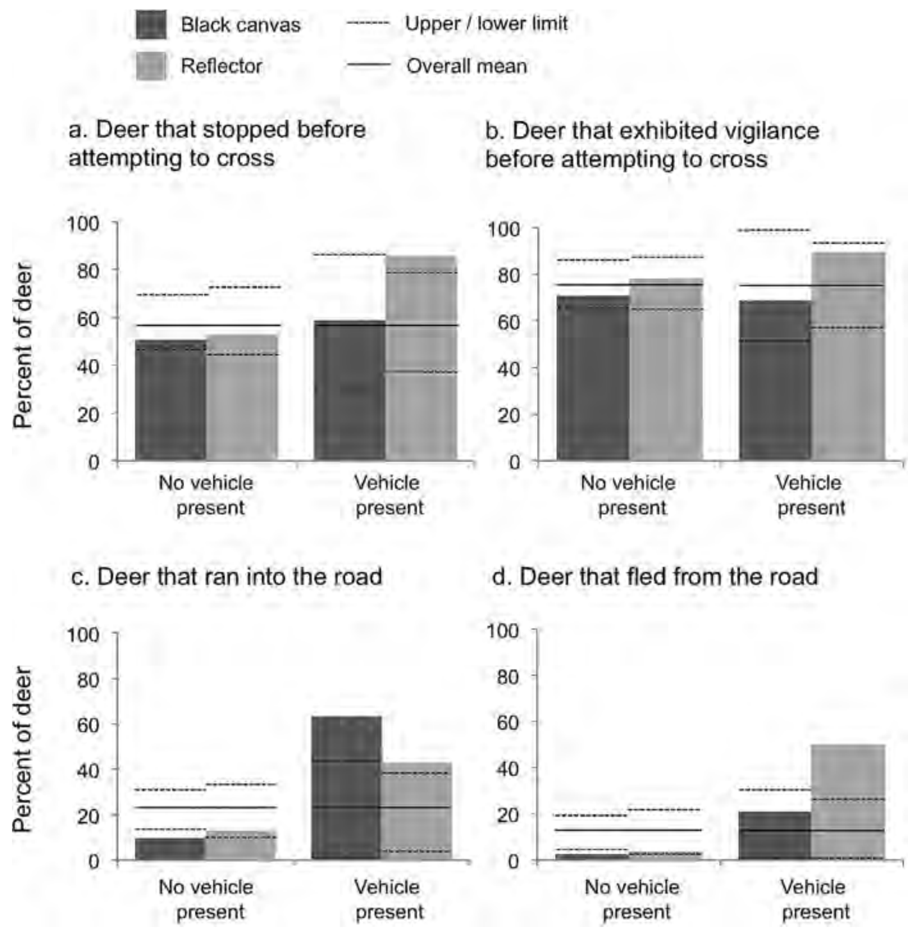

Figure 5. Percent of deer that exhibited 4 key behaviors: (a) stopping at edge of road, (b) vigilance, (c) running into the road, and (d) fleeing from the road, when attempting to cross segments of highway with wildlife warning reflectors versus black canvas covering reflectors (Experiment II; $n = 175$) and in the presence versus absence of an oncoming vehicle. Solid lines indicate overall means and dashed lines indicate upper and lower limit lines from analysis of means. Data were collected in central Wyoming, USA, between October and December 2014.

substantially less frequently in the white canvas treatment (33%, $n = 52$) compared with the reflectors treatment (57%, $n = 33$) and empty posts treatment (48%, $n = 44$). In the absence of a vehicle, deer also fled from the road at similarly low rates across treatments: 3% ($n = 30$) in the white canvas treatment, 5% ($n = 42$) of the time in the reflectors treatment, and 1% ($n = 81$) of the time in the empty posts treatment. In contrast, in the presence of a vehicle, deer fled from the road substantially more frequently in the white canvas treatment (50%, $n = 54$) compared with the reflectors treatment (41%, $n = 34$) and empty posts treatment (30%, $n = 44$).

DISCUSSION

Transportation and wildlife managers have attempted a variety of measures to reduce wildlife–vehicle collisions while ensuring habitat connectivity for ungulates and other large mammals, with mixed success. Several of the more costly methods are moderately to highly effective. Crossing structures coupled with extensive (>5 km) wildlife exclusion fencing have consistently averaged >80% effectiveness, while crossing structures with short wildlife exclusion fencing have averaged 50% effectiveness with much variation around this average (Huijser et al. 2016). Systems that detect animals as they enter the right-of-way and warn drivers have averaged 65% effectiveness with much variation around this average (Huijser et al. 2015). In many places, the cost of these mitigations or practical constraints prohibiting extensive wildlife fencing have led managers to turn to inexpensive, fenceless methods. These typically attempt to modify driver or animal behavior and include driver warning signs, reduced speed limits, deer whistles, mirrors, and reflectors. Yet studies of these methods have mostly shown limited to zero effectiveness (D'Angelo and van der Ree 2015, Huijser et al. 2015, Brieger et al. 2016).

We originally set out to test the effectiveness of deer warning reflectors using a robust experimental design. Our intent was that white canvas would negate the effects of reflectors by physically covering them, serving as a control for the reflectors. To our surprise, we instead introduced a novel treatment that had strong and distinct effects on deer–vehicle collision rates and road-crossing behavior. Although the reflectors themselves were moderately effective in reducing deer–vehicle collision rates and risky deer behavior compared with 2 nonreflective treatments (black canvas and removing reflectors), the white canvas treatment was consistently more effective than the reflectors or either of the nonreflective treatments.

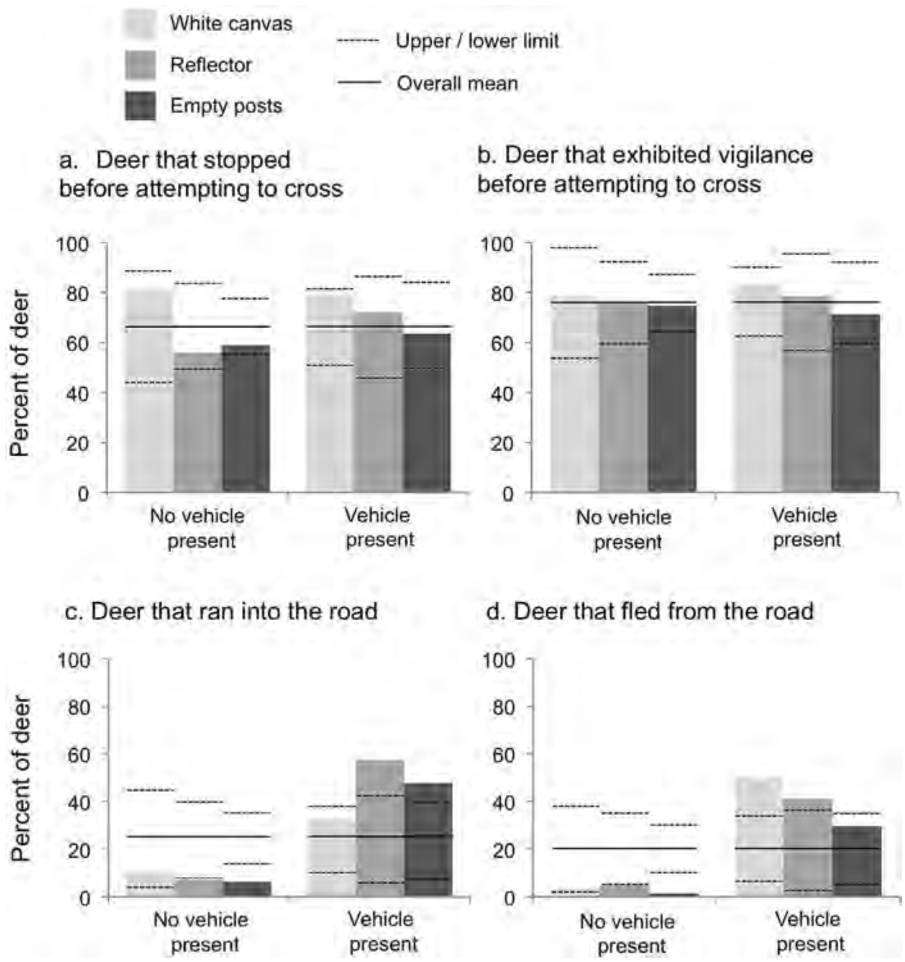

Figure 6. Percent of deer that exhibited 4 key behaviors: (a) stopping at edge of road, (b) vigilance, (c) running into the road, and (d) fleeing from the road, when attempting to cross segments of highway with wildlife warning reflectors versus white canvas covering reflectors versus empty posts (reflectors removed) and in the presence versus absence of an oncoming vehicle (Experiment III; $n = 288$). Solid lines indicate overall means and dashed lines indicate upper and lower limit lines from Analysis of Means. Data were collected in central Wyoming, USA, between October and December 2014.

Wildlife Warning Reflectors

Previous studies of the effectiveness of wildlife warning reflectors have produced results ranging from no effect to 97% reduction in carcass rates (Table 1). This wide variation has led to a general conclusion that wildlife warning reflectors are not reliably effective (D'Angelo and van der Ree 2015, Brieger et al. 2016). We found that reflectors reduced deer–vehicle collisions by 33% compared with when reflectors were covered with nonreflective black canvas, which was a moderate reduction but considerably less than the 50–97% reported in some previous studies (Schafer and Penland 1985, Pafko and Kovach 1996, Grenier 2002).

There are many possible explanations for the wide range of results among different studies, including traffic volume, speed limit, deer species, other road and ecological factors, and differences and deficiencies in study design. Studies of wildlife warning reflectors have generally relied on before–after or case–"control" comparisons. In before–after comparisons, carcass rates for the same stretches of highway are compared across one or multiple years before and after the reflectors were installed. The disadvantage of this approach is that it is difficult to account for inter-annual variation in carcass rates due to fluctuations in deer or vehicle activity at that specific site. Even at the same location, deer activity can fluctuate from year to year as a result of different weather and forage-availability patterns (Monteith et al. 2011), and traffic volumes can change over time. At our study sites, a before–after comparison indicated that carcass rates significantly increased, significantly decreased, or stayed the same after reflectors were installed, depending on which reflector area was in question (Riginos et al. 2015). Case-control studies avoid this problem by comparing carcass rates in the same period of time, but in different spatial locations. The challenge with this approach is that reflectors are typically installed in locations with high deer–vehicle collision rates, and finding an untreated control with similar collision rates can be challenging. For example, in at least one prior study, collision rates were substantially lower in the control sites even before the reflectors were installed (Gladfelter 1984). Many of these previous studies also had low initial or nonreflector carcass rates, making it difficult to determine whether reflectors affected carcass rates. A before–after-control–impact study design would address some of the challenges of the before–after and case-control designs but

Table 1. Summary of major studies of the effects of wildlife warning reflectors on mule and white-tailed deer, indicating (where applicable) percent decrease in carcasses attributed to reflectors.

Location	Type of deer	Study design	Conclusion	Reference
CO, USA	Mule	Cover–uncover	No effect	Woodard et al. (1973)
IL, USA	White-tailed	Before–after	No effect	Waring et al. (1991)
WY, USA	Mule	Cover–uncover and case-control	No effect	Reeve and Anderson (1993)
CA, USA	Not specified	Before–after	No effect	Ford and Villa (1993)
ON, Canada	Not specified	Cover–uncover	No effect	Armstrong (1992)
VA, USA	White-tailed	Case-control	Ineffective at most sites, highly effective at 2 sites	Cottrell (2003)
IN, USA	White-tailed	Case-control	19% decrease	Gulen et al. (2006)
IA, USA	White-tailed	Case-control	41% decrease	Gladfelter (1984)
MN, USA	White-tailed	Before–after	50–97% reduction in rural areas, no effect in suburban areas	Pafko and Kovach (1996)
WA, USA	White-tailed and mule	Cover–uncover	88% decrease	Schafer and Penland (1985)
WY, USA	Mule	Cover–uncover	33% decrease	This study

can be logistically challenging and has only been used in a handful of studies (Brieger et al. 2016).

We measured effects of reflectors on both carcasses and deer behavior. Although our experimental tests of reflectors against our best available controls, black canvas and empty posts, were limited to relatively short stretches of road, results were consistent. In Experiment II, the effect of reflectors on carcass rates was almost identical in the 2 road stretches. Further, carcass results were supported by concordant behavioral results; deer engaged in less risky behavior in the reflectors treatment compared with both the black canvas and empty posts treatments. Only 2 other studies have examined the effects of reflectors on both carcass rates and behavior in the same system, and these included very few observations of deer behavior (i.e., <20; Waring et al. 1991, Armstrong 1992). One study included observations of a large number of deer road crossings ($\sim$200/treatment) and concluded that reflectors had no effect on deer behavior (D'Angelo et al. 2006). That study, however, was conducted on a road with a 40 km/hr (25 miles/hr) speed limit. It is possible that the faster-moving traffic at our study site had a greater influence on deer, either because the reflectors were more visible to deer, deer were more wary of moving stimuli, or both.

Effectiveness of White Canvas

Although we found reflectors to be somewhat effective, white canvas covering the tops of posts was considerably more effective in terms of reducing both carcass rates and accident-causing deer behaviors. It is not entirely clear why the white canvas substantially reduced the likelihood of deer getting hit by vehicles, but it is consistent with our understanding of deer visual capabilities. At low light levels, deer are best able to detect colors at shorter (green, blue, and ultraviolet) wavelengths (VerCauteren and Pipas 2003, Cohen et al. 2014). If white canvas was highly visible to deer, the reflection from car headlights may have caused the deer to startle or be more wary before crossing. Additionally or alternatively, it is possible that the white canvas covering posts resembled a raised deer tail or rump patch, which is generally viewed as an alarm cue or pursuit deterrent (Hirth and McCullough 1977, Stankowich 2008).

It is also possible that deer responded more strongly to the white canvas than the reflectors because they were habituated to the reflectors (Ujvári et al. 1998), which were installed as much as 6 years prior to the beginning of the experiment, whereas the white canvas was a more novel stimulus. However, we did not find any change in deer behavior over the 3 months of behavioral observations in Experiment I (reflectors vs. white canvas) at any of the experimental sites. The length of time needed for deer to habituate to a novel environmental feature is unknown. It is possible that the effectiveness of the white canvas might have decreased over time had the experiments been run for a longer time period.

Another alternative explanation for the effectiveness of the white canvas is that they affected driver awareness and behavior. The white canvas was likely noticeable and unusual to drivers, and it is possible that drivers responded by themselves being more vigilant and cautious. This could explain the reduced deer carcass rates that occurred in the presence of white canvas, but it does not explain the effects of white canvas on deer behavior. Future research could include measures of vehicle speed and surveys of drivers to assess the effects of white canvas on their behavior.

MANAGEMENT IMPLICATIONS

Regularly spaced white canvas covering the tops of roadside posts altered deer road-crossing behavior, resulting in substantially fewer deer–vehicle collisions along a fast-moving highway. This suggests that mitigations that increase ungulate vigilance and alter their road-crossing behavior have the potential to be more effective than previously thought. Considerably more research is necessary before we can conclude that any technology inspired by the "white canvas effect" is consistently effective; however, our surprising initial results indicate that there is potential for low-cost mitigation measures that modify ungulate behavior to reduce wildlife–vehicle collisions and allow animals to more safely cross roads in areas where traffic volume does not restrict road permeability for these animals. Long-term implications are unknown.

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