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Warning systems triggered by trains increase flight-initiation times of wildlife

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ABSTRACT

Trains on railways collide with and kill wildlife, incurring economic costs for railway operators and impacting species of conservation concern. We proposed to address this problem with train-triggered warning signals, consisting of flashing lights and bell sounds emitted in the 30 s leading up to train arrival, that animals could learn to associate with train arrival. We installed our warning systems at four sites on an active railway where train-triggered cameras recorded the responses of animals to trains. We contrasted the observed flight initiation times when warning signals were active (treatment) and inactive (control) and when trains approached from straight versus curved track, predicting that animals would be more responsive to warning signals on curved approaches because those trains would be harder for animals to detect. When warning signals were provided, animals left the track earlier. For animals larger than and including coyotes (*Canis latrans*), flight responses were 62% earlier (17.0 s, SE = 1.5 vs. 10.5 s, SE = 1.2); smaller animals initiated flight responses 29% earlier (14.6 s, SE = 1.9 vs. 11.3 s, SE = 1.6). Contrary to our prediction, animals were more responsive to warning signals when trains approached from straightaways (large animals 10.3 s earlier for treatment, SE = 2.6; small animals 4.2 s earlier for treatment, SE = 2.4) than when trains approached from curves (large animals 2.7 s earlier for treatment, SE = 2.8; small animals 2.4 s earlier for treatment, SE = 1.6). Non-aversive warning systems could reduce train collisions by providing additional time for animals to adopt an effective escape trajectory.

1. Introduction

Transportation networks create complex challenges for the management of adjacent natural systems. Roads now influence ecosystems around the world (van der Ree et al., 2015) and have extensive effects on wildlife populations (Benítez-López et al., 2010; Morelli et al., 2014; Rytwinski and Fahrig, 2012) that include the provision of foraging opportunities (Barrientos and Bolonio, 2009; Martinig and Mclaren, 2019), promotion of animal movement (DeMars and Boutin, 2018), and collisions of vehicles with animals (reviewed by Fahrig and Rytwinski, 2009). Railways seem to exert similar effects on wildlife (Borda-de-Água et al., 2017), but their ecological effects have garnered much less attention (Popp and Boyle, 2017). This dearth of information is unfortunate because railways may sometimes kill more animals than adjacent roads (Huber et al., 1998; COST 341 Management Committee, 2000; Waller and Servheen, 2005), with potential for demographic effects and damage to species of conservation concern (Borda-de-Água et al., 2017; Dorsey et al., 2015; van der Grift, 1999). One reason for the lack of attention is that wildlife–train collisions rarely harm people

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(in contrast with wildlife collisions on roads; e.g., Bissonette et al., 2008), although derailments are sometimes caused by collisions with large animals (e.g., Langbein, 2011; Morse et al., 2014). Wildlife–train collisions may nevertheless incur economic costs when mortalities affect threatened species or species with a high value to people (Boyle and Bishop, 1987; Conover, 1997; Huijser et al., 2009).

Despite the problems posed by wildlife–train collisions, few practical mitigation options exist. Wildlife exclusion fencing, an effective means of separating terrestrial animals from vehicles on roads (Clevenger et al., 2001), may not be cost-effective for railways where collisions are of little risk to human safety (Huijser et al., 2009). Fencing may also exacerbate low habitat connectivity and population viability unless the barrier includes gaps in the fence (potentially risking entrapment; e.g., Lehnert and Bissonette, 1997) or wildlife crossing structures (at great expense, reviewed by Glista et al., 2009). An alternative to wildlife exclusion on roads is to create opportunities for vehicle operators to detect and avoid animals (Huijser et al., 2006), but this is not practical for trains, which cannot slow down safely on short notice or change direction to avoid animals. Systematic reduction of train speed has been shown to reduce collision risk (Gundersen and Andreassen, 1998; Visintin et al., 2018), but reduced speed could reduce the economic advantages of railway transport including high throughput and energy efficiency (AREMA, 2003). Animal collisions on railways, as on roads, are also more prevalent in some areas (collision hotspots) than others (e.g., Gundersen et al., 1998; Jasińska et al., 2019; Popp et al., 2018).

The problem of reducing wildlife–train collisions motivated our previous development of a train-triggered, track-mounted warning system which signals, via a flashing light and bell sound, the impending arrival of a train (Backs et al., 2017). The system works by (1) detecting a train as it passes a device containing magnetic and vibration sensors and (2) relaying that information wirelessly to (3) trigger the warning devices installed on a nearby section of track where collision risk is to be mitigated. The relative positions of the train detector and warning devices are determined by prior measurements of train speed to generate a consistent warning time of 30 s. The stimuli generated by the warning devices are assumed to be more predictable in time and space than the sound, light, or vibrations generated by the train itself, which we found to be highly variable both in time and space (J. Backs, unpublished data). Importantly, this system does not attempt to provide an aversive stimulus to deter animals from the area comparable to some similar systems (Babińska-Werka et al., 2015; Shimura et al., 2018; cf. Seiler and Olsson, 2017), only to alert them to the impending arrival of a train and to do so with greater temporal and spatial specificity than can be achieved by vehicle-mounted whistles (Valitzski et al., 2009) or wayside headlight reflectors (D'Angelo et al., 2006).

Here, we tested the ability of this warning system to modify the responses of animals to trains. We used remote cameras to observe wild, free-ranging animals on a live railway track at locations where the warning system was installed (treatment) or not (control) for periods of 2–4 weeks and then reversed treatment assignments. Based on the hypothesis that animals would learn to associate warning signals with trains, passages of which we assumed were already aversive, we predicted that animals would leave the railway track sooner (relative to train arrival) when warning signals were provided. Increasing this escape time would be expected to reduce the risk of collisions, particularly if earlier departures lessened the likelihood of panic-like responses or erratic flight paths (Mobbs and Kim, 2015; Rea et al., 2010; Lee et al., 2010). If the presence of intervening topography or vegetation made it more difficult to detect approaching trains, we predicted that animals would flee later (during controls) and exhibit greater responsiveness to the warning signals (during treatments) when trains were approaching from around curves in the track. To facilitate this comparison, warning systems were installed at the intersections of curves and straightaways, such that trains approached from straight track in one direction and curved track in the other direction.

2. Methods

2.1. Study area

We conducted the study on the Canadian Pacific main line railway, which bisects the Bow River valley within Banff National Park, Alberta (hereafter, Banff) in the Canadian Rocky Mountains. In the western half of Banff, the railway runs adjacent to subalpine forests dominated by lodgepole pine (*Pinus contorta*); in the eastern half, the lower-elevation montane eco-region is characterized by wetlands, grasslands, and mixed forests dominated by white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*) (Holland and Coen, 1983). The railway parallels the four-lane Trans-Canada Highway (TCH) as well as the two-lane Bow Valley Parkway through much of Banff. Traffic volumes on the TCH averaged near 23 000 vehicles per day in 2016–2017, ranging from less than half of this average in November 2016 to more than double this average over the July 2017 long weekend (measured 1.6 km west of Banff park gates; Alberta Transportation, 2019). This traffic, together with the nearby Bow River and the mountainous terrain, exposed the railway corridor and adjacent forest to diverse conditions of acoustic noise (J. Backs, unpublished data). The ballast-covered portion of the right-of-way typically extended 3 m to 5 m from the track on both sides, outside of which vegetation and topography often limited visibility around curves. Ambient temperatures during our study ranged from −36.7 °C (January 2017) to +31.4 °C (July 2017) with snow accumulation present but varying in depth from November 2016 to April 2017 with a maximum of 39 cm in March 2017 (Environment and Climated Climate Change Canada, 2019); wind and precipitation conditions often changed hourly. Snow on the railway track was plowed routinely and melted earlier (via sun exposure) on the dark-coloured rails and ballast rock than in the surrounding forest.

In Banff, collisions with trains have become a major source of mortality for grizzly bears (*Ursus arctos*; Bertch and Gibeau, 2009), a threatened species in Alberta. Trains also kill annually up to several dozen individuals of other species of mammals including black bears (*Ursus americanus*), wolves (*Canis lupus*), elk (*Cervus canadensis*), moose (*Alces alces*), and deer (*Odocoileus* spp.; Gilhooly, 2016; Gilhooly et al., 2019) as well as smaller mammals and birds.

Table 1
Test site summary. Treatment pairs define sites that shared warning devices during the experiment: when MLS was in the treatment condition, 5MS was in the control condition and vice versa. Topography height is the difference in elevation between the track bed at the intersection of the track curve and straightaway and the elevation at the highest point inside the curve, both derived from LiDAR data. Sample sizes (*n*) were those used for analyses. Site locations are in Universal Transverse Mercator (UTM) coordinates for NAD83 zone 11 N (EPSG:26911). A map of these sites is provided in Appendix A.

Site name (abbrev.)	Treatment pair	UTM Easting	UTM Northing	Test zone to curve direction	Topography height (m)	*n* large animals	*n* small animals
Muleshoe (MLS)	1	589728	5670054	East	2.4	7	20
Five Mile S (5MS)	1	593279	5669582	East	2.9	8	27
Five Mile C (5MC)	2	594293	5669496	West	4.7	7	97
Stables (STB)	2	602264	5673880	East	11.9	3	5

2.2. Site choices

We chose test sites on the eastern half of the railway within Banff (from the eastern park boundary to Castle Junction, 45.6 km west), where train collisions with wildlife are most common (Gilhooly et al., 2019). Using a digital elevation model, we identified all sites within this region where the railway curved around an area of raised topography and where this curve ended in a long straightaway (> 300 m). These sites were expected to have the greatest contrast in train detectability by direction because trains arriving from around such a curve are often obscured by both vegetation and topography. Of ten such sites identified within the study area, we chose a subset of four where we expected to observe animals on the track most frequently (Table 1, Appendix A; P. Busse, Canadian Pacific, December 2016 pers. comm.; S. Cherry, A. Forshner, D. Gummer, and J. Whittington, Parks Canada, December 2016 pers. comm.).

2.3. Experiment design

Each warning system comprised four types of self-contained electronic devices connected through a wireless radio-frequency network, which we termed train detectors, warning devices, camera controllers, and signal repeaters (Appendix B; Backs et al., 2017). These devices were deployed along the railway track to coordinate the activation of warning signals and cameras (for observing animal responses) with the arrival of a train. We targeted a warning time of 30 ± 5 s, in contrast to our previous work that targeted 20 ± 5 s (Backs et al., 2017), based on our desire to ensure that conditioned (warning) stimuli were typically presented to animals before unconditioned (train) stimuli (Domjan, 2005).

At each site, a 200 m length of track was designated for our experimental treatment (hereafter, the test zone), which began at the point where the curved track met the straightaway and continued 200 m along the straightaway (Fig. 1). Train detectors were

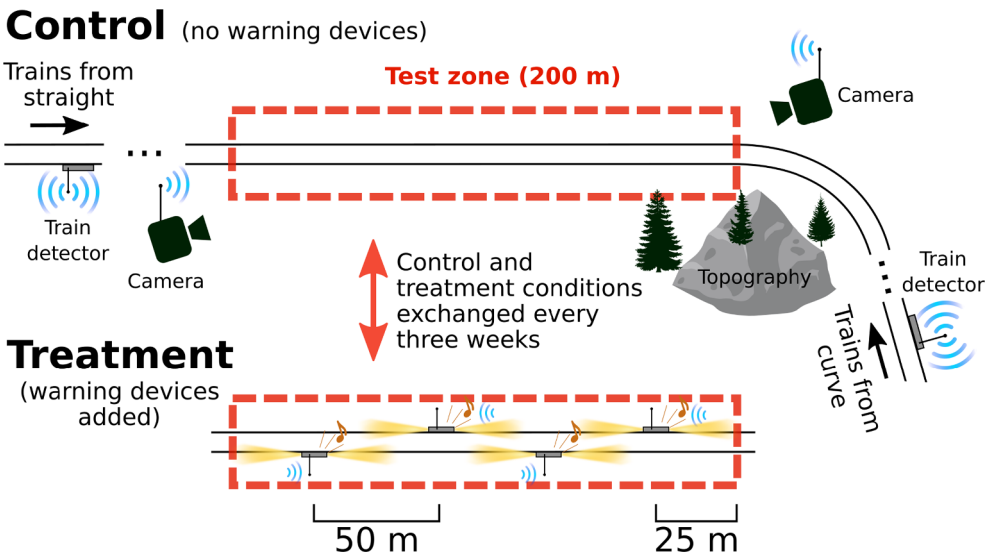

Fig. 1. Equipment layout at test sites. Sites were chosen where a section of straight track met a section of track that curved around topography and vegetation. Cameras were placed at each end of the test zone; train detectors were placed 40 s (at mean train speed) from the center of the test zone in both directions. When a train passed a train detector, wireless signals were transmitted to activate cameras that recorded the presence and subsequent responses of wildlife. During treatment periods, warning devices activated 30 s before trains arrived. Warning devices were not present during control periods.

mounted on the track 40 s away at mean train speed (measured previously with sound recorders) in both directions from the test zone center. When a train moving towards the test zone passed a detector, this device sent a radio signal to all other devices in the network. This signal was received by camera controllers (two per site) mounted in trees on either side of the test zone, where they triggered trail cameras (HP900 with external trigger, Reconyx, USA) facing the test zone to take 90 photographs at up to two frames per second, yielding at least 45 s of footage. The radio signal was also received by warning devices (four per site) within the test zone, which emitted the warning signals (flashing amber lights and bell sounds; Appendix B) after a 10 s delay for a period of 35 s (30 s before and 5 s after train arrival at the test zone center). While the warnings were active, one or both of the light and sound signals were conspicuous to us at all locations within the test zone. Signal repeaters were placed as needed (one to four per site) between the train detectors and camera controllers to ensure network connectivity. Following activation, all devices were programmed to wait six minutes while the train passed.

We deployed warning systems at two sites (treatment pair 1, Table 1) for the first six treatment rotations (November 2016–February 2017) and expanded to the remaining sites (treatment pair 2, Table 1) for the remaining six rotations (February 2017–July 2017). At any given time, only one of the sites in each treatment pair was deployed with warning devices (hereafter, the treatment condition), while the other site was deployed without warning devices (hereafter, the control condition). The treatment and control conditions were swapped within treatment pairs every 2–4 weeks to control for seasonal effects. Warning systems were inactive between experimental periods when the batteries in the devices were depleted.

2.4. Image analysis

We recorded calibration images at each site where the experimenters were standing at known locations within the test zone. These images provided references for the locations of animals and trains captured in subsequent image sequences. Location references remained accurate enough throughout the experiment to identify the near edge of the test zone to within 5 m. These references further allowed estimation of train speed to within $\pm$ 4 km h^{-1} to $\pm$ 10 km h^{-1} (Appendix C).

For sites under the treatment condition, we verified the correct operation of the warning signals by observing the flashing warning lights in camera images (Fig. 2(b)). Occasionally, flashes were not observed in a treatment sequence because of snow accumulation in front of the lights or because the capture rate of the cameras was similar to the flash rate of the warning lights. In these cases, we judged that the treatment was likely delivered (even if only aurally) when sequences recorded before and after the sequence in question showed flashing lights. If this condition was not met, we excluded the sequence from further analysis because the treatment

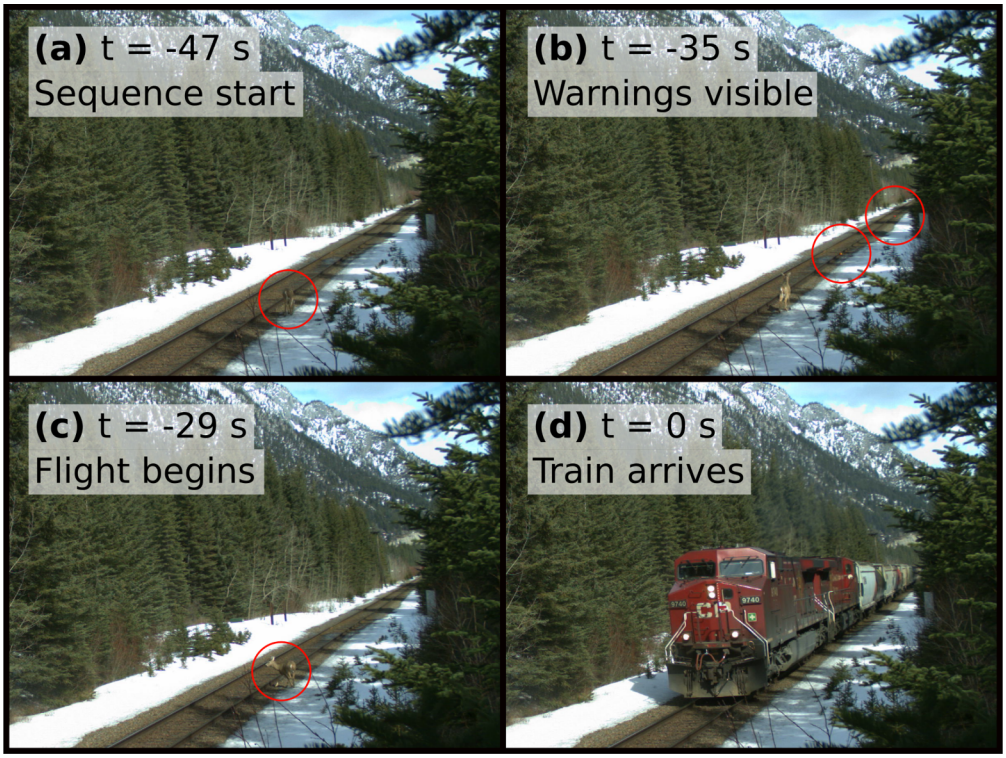

Fig. 2. Example of key events in an animal sequence. (a) A deer (circle added) was visible foraging near the track in the first image. (b) 12 s following system activation, flashes of light from two warning devices were visible (likely not the first flashes). The deer raised its head from foraging one image (1 s) earlier. (c) 6 s later, the deer turned to flee and continued to move perpendicular to the track until it was no longer visible. (d) 29 s (the flight initiation time) later, the train arrived where the deer began its retreat.

was likely not delivered (e.g., when batteries were depleted).

To support analysis and interpretation, we recorded several environmental variables that could have affected the responses of animals to trains. These included weather conditions (rain, snow, and wind), light level (dawn, day, dusk, night), and foliage presence (off, emerging, on) that might have visually or aurally obscured train approaches and snow cover (none, light, moderate, heavy) that can affect the retreat behaviours of animals (e.g., Rea et al., 2010).

2.5. Behavioural coding

A team of six observers reviewed all images retrieved from the cameras by viewing them on computer screens. In each sequence of 90 images, we recorded the number of animals visible for each species present. We identified duplicate events from opposing cameras to prevent double counting. A single observer then reviewed all sequences with animals to eliminate inter-observer variation in the interpretation of behaviours. These processes together required an estimated 200 person-hours.

We designated the first animal to flee (regardless of species) within the field of view of either camera at a site as the focal animal (Fig. 2(a)). We classified the initial behaviour of this animal as one of foraging (small, occasional movements with head down), travelling (steady movement along the track), alert (head up, ears erect, face oriented towards the train), flight (fast movement along or away from the track), crossing/approaching/leaving (movement perpendicular to the track), or unknown (behaviour not discernable). Image numbers were recorded where this animal changed its behaviour to alert (if observed) and flight. We did not consider further the timing of alert responses because too few clear alert responses were observed. We also excluded sequences where an animal was initially fleeing. To increase the sample size for larger species, we chose a large animal as focal over an earlier-fleeing small animal if independence of the flight response seemed likely (e.g., substantial interposing vegetation and distance).

When the focal animal initiated flight behaviour (i.e., changed to flight from a different classification of initial behaviour), we noted the position of the animal, and the image for which the train was closest to this position. The time stamp of this image revealed the time between the initiation of the animal's flight response (Fig. 2(c)) and train arrival at the location where retreat began (Fig. 2(d)). We termed this time difference the flight initiation time t_{FIT}, related to the more common flight initiation distance d_{FID} (reviewed by Stankowich and Blumstein, 2005) as

$$d_{\mathrm{FID}} = v_{\mathrm{T}} t_{\mathrm{FIT}} \tag{1}$$

where v_{T} is the train speed. We excluded treatment sequences from further analysis where the flight response was observed before the warning signals were active (i.e., within 8 s of the first image in the sequence). We also excluded sequences where flight behaviour did not have a discrete beginning, where flight did not lead an animal to leave the ballast (rock-covered) area or to seek cover within the ballast area without stopping its movement, or where the animal returned to the ballast area within the same image sequence.

We only used animal sequences for our analyses where we were confident that we had correctly coded the flight response, that the warning signals activated (during treatment periods), and that a flight response did not occur before we expected the warning signals to activate (during treatment periods; together, the high-confidence criteria). To increase our sample size, we did not exclude sequences where the focal animal began outside the test zone as long as the sequences otherwise met the high-confidence criteria. We chose not to analyze small animal sequences recorded after April 20, 2017 because a sufficient sample of small animals was obtained from earlier months.

2.6. Statistical analysis

We tested our hypotheses on two groupings of the data: coyotes and larger animals (hereafter, large animals) and animals smaller than coyotes (hereafter, small animals). Although we were primarily interested the effect of treatment on large animals, for which mortality records are kept by both Parks Canada and Canadian Pacific, many more samples were obtained for small animals. We also expected large and small animals to respond differently to trains based on expected differences in their perceptual ranges (Mech and Zollner, 2002; Blumstein, 2006).

For each species group, we developed a regression model for flight initiation time testing for the effects of treatment and track curvature while controlling for potential confounding factors (Gelman and Hill, 2007; Hoef and Boveng, 2015; Harrell, 2015). Our experimental design suggested the inclusion of a random effect of test site (Zuur et al., 2009), but the severe imbalance of high-confidence samples among sites caused singularity in mixed model fits where test site was included as a random effect (Bates et al., 2015). Sites were instead pooled for large animals as the smaller sample permitted the inclusion of at most three parameters (Harrell, 2015, p. 72), while for the larger sample of small animals test site was included as a fixed factor (i.e., no pooling; Gelman and Hill, 2007, p. 275). Generalized linear models (GLMs) were fitted with Gamma-distributed errors due to the positive continuous nature of the response (Zuur et al., 2009) and with an identity link function for convenience of interpretation. We report Wald *t*-statistics for each parameter estimate with the understanding that they are generally conservative (Dunn and Smyth, 2018), and we infer importance of the parameters to the model fit using the corresponding *p*-values (Murtaugh, 2014a, 2014b). Model fits were assessed by likelihood ratio *F*-tests comparing the model of interest with the null model (Dunn and Smyth, 2018). Where averaged comparisons between factor levels were desired, contrasts were calculated by estimating the marginal means (Lenth, 2019) with significance estimated with Wald *t*-statistics (Dunn and Smyth, 2018). Dispersion estimates for our models were generally greater than recommended for the use of Wald statistics (Dunn and Smyth, 2018, p. 277), but parameter values and standard errors nevertheless agreed closely with estimates obtained by other techniques (e.g., bootstrapping; Appendix D).

For large animals we modelled treatment, approach curvature, and their interaction only due to the small sample size. For the

larger sample of small animals, we modelled these effects while controlling for train speed (centered and scaled to zero mean and unity SD) and Boolean effects of noise-generating weather, snow cover, and animals beginning their sequences foul of the track (i.e., within 1.2 m of the nearest rail; Canadian Pacific, 2010). We excluded from further analysis variables with under-represented categories (initial behaviour of the focal animal, whether the focal animal crossed the track during its flight, whether vision-obscuring weather was present) or that showed collinearity with treatment (number of days since start of experiment; Zuur et al., 2010). We excluded from all analyses the small number of samples for which train speeds were less than 45 km h^{-1}, both to prevent their undue influence on the small-animals regression (Harrell, 2015, p. 90) and because slow trains traversing curves tend to emit loud, high-frequency noise (Rudd, 1976) that would likely change their acoustic detectability for animals. We included only the treatment-with-curvature interaction term in each model because we had hypothesized its importance; we did not find any explanatory interactions among the remaining variables (Zuur et al., 2010).

All statistical analyses were performed in R version 3.5.1 (R Core Team, 2018).

3. Results

Sampling for a total of 520 site-days, we recorded 1.6 million images in 17 679 sequences capturing 9 628 unique events with and without animals present, suggesting that an average of 19 trains passed each site per day. Animals were visible in 838 sequences (711 unique events; 90 large animals, 619 small animals, 2 of unknown size) involving 1 942 individual animals (Appendix E), predominantly deer, elk, red squirrels (*Tamiasciurus hudsonicus*), and unidentified birds. No animals were visibly struck by trains, and all animals (where the train did not obscure the camera view before the animal retreated) were observed to flee in response to train approach. Of the 711 unique events in which animals were visible, 280 were interpretable with our behavioural coding: e.g., our cameras recorded the focal animal initiating a flight response as well as the train reaching the animal's position of first flight. Within these 280 events, animals initially appeared to be foraging in 74% of events, travelling in 4% of events, alert in 11% of events, and engaging in other behaviour in 11% of events. Focal animals were observed to begin their flight responses foul of the track in 35% of sequences and crossed the track during their flight responses in 18% of sequences. Retaining from these 280 events only high-confidence sequences (27 large, 157 small) with train speeds greater than 45 km h^{-1} (see Section 2), $n = 25$ large animal sequences and $n = 149$ small animal sequences remained (Appendix F).

Large animals displayed earlier flight initiation times in the presence of warning signals (Fig. 3). Our model fit was better than the null model (df = (3, 24), $F = 4.9$, $p = 0.010$) and suggested that the treatment parameter had a strong effect on flight initiation time with marginally significant but large parameters for track curvature and its interaction with treatment (Table 2). The model predicted a mean increase in flight initiation time of 6.5 s (SE = 1.9, $t = -3.4$, $p = 0.003$) from 10.5 s (SE = 1.2) for control to 17.0 s (SE = 1.5) for treatment, averaged across curved and straight approaches. The mean difference between flight initiation times for trains from curves and straightaways was negligible (est. 0.8 s lower for straightaways, SE = 1.92, $t = -0.4$, $p = 0.695$), but the treatment effect was substantially stronger when considering only trains approaching from straightaways (est. 10.3 s earlier flight for treatment, SE = 2.6, $t = -4.0$, $p < 0.001$) and weaker when considering only trains approaching from curves (est. 2.7 s earlier flight for treatment, SE = 2.8, $t = -0.9$, $p = 0.34$).

Small animals also displayed earlier flight initiation times in the presence of warning signals, but to a lesser degree than large animals (Fig. 3). Our model fit was better than the null model (df = (10, 148), $F = 2.5$, $p = 0.010$) and suggested a small but important effect for track curvature, a marginally significant effect of treatment, and no significant interaction (Table 2). Averaged over levels of all other variables, the model predicted that treatment increased flight initiation time of small animals by 3.3 s (SE = 1.5, $t = -2.2$, $p = 0.03$) from 11.3 s (SE = 1.6) for control to 14.6 s (SE = 1.9) for treatment. The model also predicted a decrease in average flight initiation time from straightaways at 14.9 s (SE = 1.9) to curves at 11.1 s (SE = 1.7) (difference of 3.9 s, SE = 1.4, $t = 2.7$, $p = 0.007$). The model predicted treatment effects that were stronger for trains approaching from straightaways (4.2 s greater for treatment, SE = 2.4, $t = -1.7$, $p = 0.085$) and weaker for trains approaching from curves (2.4 s greater for treatment, SE = 1.6, $t = -1.5$, $p = 0.137$).

4. Discussion

Wildlife mortality from collisions with trains might be reduced without train speed reductions or animal exclusion measures if animals more consistently left the track before trains arrived. We tested a track-mounted wildlife warning system designed to encourage the avoidance of trains by animals. We expected that animals would have earlier flight initiation times in response to warning signals, especially when trains were otherwise difficult to detect, which we assumed to apply when trains approached from curves. When warning signals were present, animals had earlier flight initiation times on average, but contrary to our prediction, the effect was most pronounced when trains approached from straight sections of track. If flight initiation time is related to collision risk, our results suggest that train-triggered warning systems could mitigate collision risk for wildlife and offer insight into where warning systems may be most useful.

When we provided warning signals, both large and small animals retreated earlier from trains than when signals were not provided. Averaged across trains approaching from curves and straightaways, large animals retreated 6.5 s earlier and small animals retreated 3.3 s earlier. Although apparently small, these differences represent 62% and 29% increases over the mean flight initiation time with no warning signals, respectively. At the mean train speed in our analyzed sample (60.5 km h^{-1}), these time differences correspond to increased separations between animal and train of 110 m (large animals) and 55 m (small animals) at the moment of flight initiation. Perhaps the most comparable study to date used a track-side warning system that emitted a sequence of animal alarm

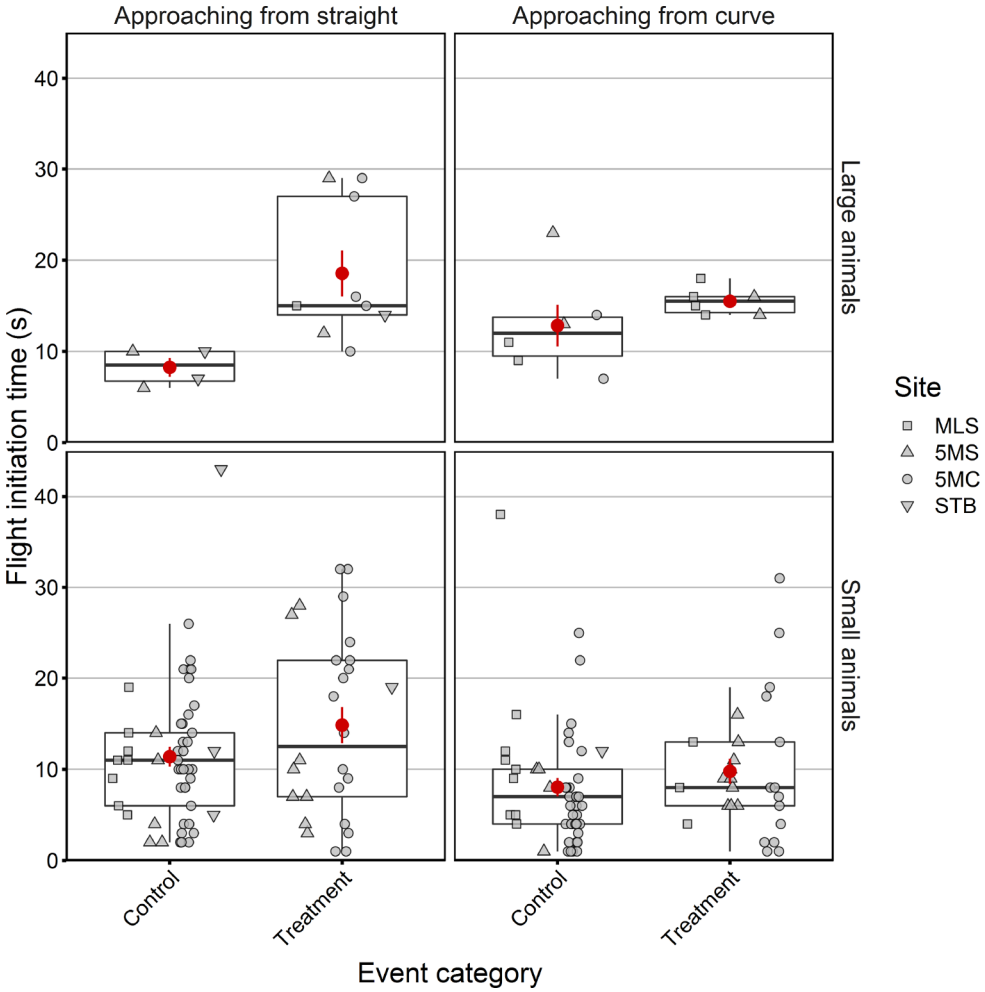

Fig. 3. Effect of treatment on flight initiation time for four groupings of approach curvature and animal size. Box plots indicate medians, first and third quartiles, and range to 1.5 times the interquartile range. Means and standard errors are indicated by the filled circles with ranges. All data points are shown with test site indicated by shape and position grouping. A summary of these data by species is provided in Appendix F.

calls and predator vocalizations for 60 s leading up to train arrival (Babińska-Werka et al., 2015), in contrast to the 30 s warning time targeted in our study. These authors achieved a larger increase in escape time from control to treatment conditions (26 s for roe deer), although the variation they measured in escape time under the treatment condition (mean ± SD = 35 ± 38.3 s) was much larger than in the present study (mean ± SD = 17.3 ± 6.0 s for large animals). This difference could be attributable to the larger interval between stimulus onset and train arrival (60 s versus 30 s in this work; Babińska-Werka et al., 2015) or the use of aversive warning stimuli (Babińska-Werka et al., 2015). Our warning stimuli appeared to cause earlier retreats without the use of aversive stimuli (Backs et al., 2017).

Track curvature had differing effects for large and small animals. For large animals, flight initiation times for curves and straightaways did not differ meaningfully; for small animals, the mean decrease in flight initiation time from straightaways to curves was 3.9 s, comparable to the mean difference between treatment and control for the same species group. The small animals difference appears to be consistent with our prediction that animals would respond later to trains approaching from curves. Studies of wildlife–vehicle collisions on both roads and railways have highlighted the association of collisions with curves (Gunson et al., 2011; Jasińska et al., 2019; Popp et al., 2018), citing visibility as an issue for drivers (Bashore et al., 1985) and potentially animals (Hamr et al., 2019), and recommending vegetation clearing as a potential means of reducing collision risk (Andreassen et al., 2005). Acoustic detectability of trains might also be reduced where the track curves around steep topography (J. Backs, unpublished data). Contrary to our expectation, both large and small animal models revealed decreases in the effect of treatment for curves compared to straightaways. We speculate that this could occur if animals were more likely to initiate early flight responses when both warning signals and train stimuli were presented together, which would in general occur earlier for trains approaching from straightaways. Animals appear to flee earlier in response to multiple as opposed to single predator-like stimuli (Geist et al., 2005), and so may also flee earlier in response to the combination of a predator-like stimulus and the novel warning stimulus. From this perspective, our warning signals may have sometimes functioned more like an animal deterrent (cf. Babińska-Werka et al., 2015; Muzzi and Bisset,

Table 2
Parameter estimates (est.), standard errors (SE), and Wald t statistics from two Gamma generalized linear models with identity links for which the response variable was animal flight initiation time in seconds. Reference categories (Ref.) for categorical variables are indicated in parentheses. ":" indicates interactions. Boldface lines (excluding intercepts) indicate statistical significance at $\alpha = 0.05$. Train speed was centered and scaled to aid interpretation (original mean ± SD = 60.5 ± 4.6 km h^{-1}).

	Est.	SE	t	p
Large animals				
Intercept	8.3	1.4	5.8	< 0.001
Treatment (Ref. control)	10.3	2.6	4.0	< 0.001
Approaching from curve (Ref. straight)	4.6	2.3	2.0	0.060
Treatment:curve	−7.6	3.8	−2.0	0.060
Small animals				
Intercept	9.2	1.5	6.2	< 0.001
Treatment (Ref. control)	4.2	2.4	1.7	0.085
Approaching from curve (Ref. straight)	−3.0	1.4	−2.2	0.030
Auditory weather present (Ref. absent)	1.0	1.2	0.8	0.411
Heavy snow (Ref. light)	0.5	1.2	0.5	0.638
Animal starts on track (Ref. off track)	3.2	1.7	1.9	0.061
Train speed (km h^{-1}; scaled)	−0.5	0.6	−0.9	0.383
Site, 5MS (Ref. 5MC)	−2.1	1.5	−1.4	0.164
Site, MLS (Ref. 5MC)	1.9	2.1	0.9	0.373
Site, STB (Ref. 5MC)	5.1	6.0	0.9	0.391
Treatment:curve	−1.8	2.8	−0.6	0.533

1990; Shimura et al., 2018) than the learning instrument we had intended (Backs et al., 2017; Domjan, 2005). It could also be that the warning signals increased animal alertness in a way that encouraged their detection of the train, as the gaze of the focal animal sometimes appeared to be drawn by the warning signals towards an approaching train (e.g., Fig. 2).

Although our warning system increased flight initiation times for animals, the relationship between flight initiation and collision risk was not clear from our observations. Animals often moved off the track in as little as 1 s to 2 s when they chose to do so, but only infrequently did animals move directly off the track as their first response to a train. For instance, focal animals crossed the track as part of their flight response in 17% of high-confidence sequences (30% for large animals, 15% for small animals), in rare cases missing the train arrival by less than one second. These near-misses tended to occur when animals (especially deer, elk, and pigeons) were present in groups: As one animal moved off the track, its conspecifics often crossed in front of the train to follow. This grouping behaviour in both ungulates and birds may afford some protection from collisions where collective detection of trains enables earlier flight initiation (Elgar, 1989; Beauchamp, 2017), but any benefit of earlier responding appeared to be unimportant in cases where elk continued to cross in front of the train until the train arrived, separating the herd (cf. Altmann, 1952). In one extreme event, a herd of elk appeared unable to detect an approaching train until the train operator turned off the locomotive headlight, after which the elk fled from the train between the rails. This behaviour is known to lead to collisions when the animal continues to retreat along the track until struck (e.g., Rea et al., 2010); an animal's choice of flight response has also been found to precipitate collisions with vehicles on roads (Lee et al., 2010). For both of these collision modes, earlier flight initiation caused by warning signals may plausibly reduce the risk of collisions, although determinants of an animal's choice of flight response are not yet well-understood (reviewed by Lima et al., 2015). We can only speculate about changes in collision risk attributable to the warning system until collision rates are measured experimentally, although future tests of wildlife warning systems may yield more insight (Seiler and Olsson, 2017).

We anecdotally observed other instances where animals ran parallel to the track before moving perpendicular to the track and leaving the right of way. Occasionally, animals used the same escape routes (potentially, game trails) in different retreat sequences, consistent with the idea that animals inform their flight decisions with the locations of refugia (reviewed by Stankowich and Blumstein, 2005). If presence of escape routes determines an animal's escape trajectory off the right-of-way, management of vegetation and topography within the right-of-way could help to reduce collisions (I.G. Pengelly and J.D. Hamer, pers. comm.). Vegetation clearing has also been shown to reduce wildlife–train collisions (Jaren et al., 1991; Andreassen et al., 2005), its effectiveness often attributed to the reduction in attractants along the railway (cf. Pollock et al., 2017). Vegetation clearing might also reduce collisions by increasing the distance to the nearest refuge, encouraging earlier flight responses (Stankowich and Blumstein, 2005). However, vegetation clearing could potentially increase collision risk if uprooted vegetation is left at the edge of the right of way, blocking escape routes that may already be constrained by steep topography or adjacent bodies of water.

The potential effectiveness of vegetation clearing in reducing collisions may also be limited because other factors attract animals to the railway, including opportunities to forage on spilled grain (Gangadharan et al., 2017) or other train-killed animals (Murray et al., 2017) or to travel efficiently (Pollock et al., 2019). We observed that 74% of our 280 codable sequences began with the focal animal displaying foraging behaviour. In 29% of sequences that began with foraging behaviour, animals were present between the rails where vegetation was not generally found, suggesting the animals were foraging on grain. We also observed that carnivores most often appeared to be travelling (in 8 of 9 sequences; cf. Pollock et al., 2019) while other species groups exhibited foraging behaviour more often than any other single behaviour, including ungulates (18 of 40 sequences) and small animals (189 of 230 sequences).

Future implementations of this warning system may benefit from increased warning time. Animals in 13 treatment sequences (3

large animals, 10 small; excluded from our analysis) began to flee before the warning devices were expected to emit signals. Two other large animals (also excluded) appeared to interrupt or delay their retreat from the train to look directly towards the warning devices. An increase in warning time to 35 or 40 s might have allowed the activation of warning signals to precede the flight responses of all observed animals. However, the time between warning activation and train arrival must remain short enough that learning can occur (Cooper, 1991; in humans, cf. Richards and Heathington, 1990).

The positive effect of warning signals on flight initiation time shown in this work may encourage further development and testing. The ability of warning devices to reduce wildlife collisions could be assessed by measuring collisions directly, but the sampling effort would be substantial if a similar experiment design to ours was used. We estimated that 55 000 site-days (compared to the 520 site-days observed in this work) would be required if the present study design were used to collect a statistically useful sample of collision events (Appendix G). Advances in computer vision (Janzen et al., 2017) and more efficient energy management in the warning system devices (Appendix B) would lower the cost of such an effort. Alternative monitoring techniques such as train-mounted cameras may observe more animals per unit effort (Burley, 2015), but they cannot observe the behaviours of animals around track curves. More invasive approaches (such as barrier fencing; Clevenger et al., 2001; Seiler and Olsson, 2017) may be needed to reduce collisions with large groups of ungulates (e.g. elk herds) that take longer than 30 s to cross the track even when given early warning of train approach.

Wildlife warning systems could reduce the needless loss of animals to train collisions, and we suggest that the design studied here warrants a test of its ability to reduce collisions. Warning systems like this one could be implemented as a cost-effective alternative or as a complement to exclusion fencing. Reductions in wildlife collisions would allow railways to remain leaders in safety and stewardship as they serve the ever-growing transportation needs of people.

Data accessibility

Data supporting our analyses are available upon request.

CRediT author statement

Jonathan A.J. Backs: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization, Resources, Project administration, Funding acquisition. **John A. Nychka:** Conceptualization, Methodology, Writing - review & editing, Resources, Supervision. **Colleen Cassady St. Clair:** Conceptualization, Methodology, Writing - review & editing, Resources, Supervision, Project administration, Funding acquisition.

Declaration of competing interests

None.

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Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.trd.2020.102502. The following appendices are included: A. Map of test sites; B. Warning system design; C. Camera calibration; D. Parameter values obtained by bootstrapping; E. Animals observed, total and over time; F. Flight initiation times by species; and G. Encounter rate extrapolation.

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