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Original Research Article

Highways, crossing structures and risk: Behaviors of Greater Yellowstone pronghorn elucidate efficacy of road mitigation

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ABSTRACT

Wildlife crossing structures and accompanying barrier fencing can prevent large mammals from accessing road surfaces and can significantly reduce wildlife-vehicle collisions while allowing animals to move from one side of the road to the other. Little research has been conducted on the behavioral responses of wildlife when encountering these novel structures over time. We used the installation of new wildlife road crossing structures built along a 6000-year old migration route to evaluate behavioral responses of long-distance migrators to the structures. We collected behavioral data during and after construction in order to evaluate individuals' immediate responses to these structures and to investigate how they changed over time using generalized linear mixed-effects models and generalized additive models fit by maximum likelihood. Pronghorn acclimated to the crossing structures and the frequency in which they successfully crossed them increased over time. The probability of pronghorn successfully crossing a structure was not influenced by human presence. Pronghorn spent more time in sustained vigilance behaviors after construction. Pronghorn also spent more time in sustained vigilance behaviors at relatively further distances from a structure and lead individuals spent more time in sustained vigilance behaviors than non-lead individuals. We did not detect any significant factors associated with stress behaviors. Pronghorn still demonstrated high sustained vigilance when approaching the structures after 20 months post construction, despite an increase in crossing success. While we found evidence of risk-avoidance behaviors in pronghorn at crossing structures, this work provides evidence that pronghorn gradually acclimated to wildlife crossing structures built in a historical migration corridor in the Greater Yellowstone Ecosystem. We recommend using task completion chronology (rather than project completion dates) to install wildlife mitigation and we recommend using wildlife friendly fencing when fences are required for multiple use (e.g., cattle) at crossing structure entrances.

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1. Introduction

Roads can have multifaceted detrimental impacts on wildlife in many systems, including the tropics, deserts, temperate and even Arctic systems (Jones, 2000; de Freitas et al., 2015; Wilson et al., 2016). Installing wildlife overpasses has not historically been a frequent practice to mitigate wildlife-vehicle collisions (WVCs) for migrating animals, although several European countries have been employing them for over 50 years (Lavsund and Sandegren, 1991; Bank et al., 2002; Corlatti et al., 2009). However, the recognition of their effectiveness in reducing WVCs while maintaining or improving landscape permeability and a subsequent increase in public support for better mitigation of WVCs, have led to a recent surge in the construction of wildlife overpasses globally (van der Ree et al., 2007; Huijser et al., 2008; Taylor and Goldingay, 2010).

Many studies have documented the benefits of crossing structures to humans and wildlife alike (e.g., Beckmann and Hilty, 2010; McCollister and VanManen, 2010; Clevenger and Barrueto, 2014). Researchers have studied what species most readily use what types of structures or when animals have peaks in activities at structures (Clevenger and Waltho, 2000; Dodd et al., 2007; Sawyer et al., 2016). They have looked at the impact that shared human use has on wildlife use of structures (Clevenger and Waltho, 2000, 2005; Barrueto et al., 2014). Some studies have even looked at intraspecific variations (Ford et al., 2017), but few have attempted to quantify, using in situ behavioral observations, the responses of animals to new crossing structures beyond movement and use data (but see Reed et al., 1975 and Singer and Doherty, 1985 for past mammalian examples). The successful use of a crossing structure by wildlife can be affected by many factors; the size and type of structure, native vegetation, behavior and ecology of the target species and human-use of or near the structure all impact the success of animal use (Lesbarrères et al., 2004; Clevenger and Waltho, 2005; Lesbarrères and Fahrig, 2012). It is important that crossing structures be designed to match the target species' behavior and natural history. Effective barrier fencing (including proper design and length), proper siting of the crossing structure(s) and animal ecology all affect the probability of wildlife using under and overpasses (Clevenger et al., 2001; Clevenger and Huisjer, 2011; Huijser et al., 2016).

Target species may avoid using the structure if it is not large enough or if it is not flanked by barrier fencing (Reed et al., 1975; Clevenger and Waltho, 2000; Schmidt and Zumbach, 2008). For example, 39% of migrating mule deer (*Odocoileus hemionus*) in Colorado, USA would not use a 3.05×3.05 m structure (Reed et al., 1975). Additionally, without proper associated fencing many individuals will continue to cross at the road's surface (Baxter-Gilbert et al., 2015; D'Amico et al., 2015; Huijser et al., 2016). Anurans will not use road culverts designed to accommodate herptiles if they are not excluded from the road surface with amphibian-proof fencing (Cunnington et al., 2014). Further, road mortality of small vertebrates is not mitigated by crossing structures without specific measures to accommodate these species. Crossing structures can become ecological traps due to measures taken to increase the use of a crossing structure by mid-size mammals while failing to prevent small animal access to the road (D'Amico et al., 2015).

Human activity can also significantly influence an individual's success of using crossing structures (Singer and Doherty, 1985; Clevenger and Waltho, 2000). In Glacier National Park, mountain goats (*Oreamnos americanus*) temporarily abandoned seasonal ranges due to construction activity combined with high harvest rates (Chadwick, 1983). Furthermore, roads and the presence of tourists at wildlife-road crossing locations in the same ecosystem increased challenges for mountain goats (Singer, 1978). Highway crossing success increased from 74% to 90% once crossing structures were subsequently installed at an important crossing location (Singer and Doherty, 1985). In this case, controlling anthropogenic disturbances by both traffic and visitors increased crossing success for goats.

In Banff National Park, the actual success of crossing structures compared to predicted rates for carnivores and ungulates was negatively correlated with human activities (i.e., hiking, biking and horseback riding; Clevenger and Waltho, 2000). Such anthropogenic effects can prevent the access of animals to seasonal ranges and mates with consequences for genetic exchange within populations. These effects may be specific to regions in close proximity to intense human development (Clevenger and Waltho, 2005). Fine-scale behavioral changes monitored at an individual level, such as increased stress levels or heightened vigilance behaviors, may also be able to further identify factors that reduce or enhance the efficacy of crossing success.

Nonlethal disturbance stimuli, such as human activities or novel infrastructure in a movement corridor, are hypothesized to trigger predator avoidance responses in prey animals (Walther, 1969; Frid and Dill, 2002). Further, it has been demonstrated that some ungulates perceive roads and traffic as a predation risk, and respond to this with increased vigilance and reduced foraging in areas of high vehicle density (Gavin and Komers, 2006) and avoid areas of dense roads (Beckmann et al., 2012). Such increased antipredator behavior in ungulates can negatively affect reproductive physiology (Creel et al., 2007). It can also lead to reduced fitness and population decreases due to energetic losses from increased stress and reduced foraging opportunities (Frid and Dill, 2002; Gavin and Komers, 2006).

Here we test the hypothesis that risk-avoidance behaviors in response to novel anthropogenic disturbances, specifically during and after construction of wildlife crossing structures, reduce the effectiveness of these structures. To test predictions of this hypothesis, we examined the behavioral effects of novel wildlife crossing structures on migrating pronghorn (*Antilocapra americana*) and evaluated the time for pronghorn to acclimate to those novel structures along their migration route. This research is particularly important for long-distance migrators, such as pronghorn in our study, which only encounter these structures twice a year during their fall and spring migratory movements between discreet summer and winter ranges (Beckmann et al., 2012; Seidler et al., 2015). Understanding behavioral reactions to novel crossing structures will benefit other long-distance migrating species (Colchero et al., 2010; Nyaligu and Weeks, 2013) as well as highlight important construction considerations and ensure conservation goals are met.

We examined both biological and anthropogenic factors that could influence animal behavior and the success of pronghorn using a crossing structure. We investigated whether construction activities would influence crossing success, and predicted that pronghorn approaching crossing structures would have a lower success rate while construction was occurring and when humans were present along the route near the road. We also predicted that pronghorn in larger groups or in a non-lead position within the group would show less stress. Finally, we predicted that pronghorn would exhibit a higher proportion of stress behaviors during construction and shortly thereafter as well as when closer to the crossing structure.

2. Methods

2.1. Study site

Our study area was located near Trapper's Point, along US 191 in the Upper Green River Basin (UGRB) of western Wyoming near the town of Pinedale. The Trapper's Point area is approximately 2195 m elevation. The UGRB is in the southern Greater Yellowstone Ecosystem, where pronghorn migrate from summer range in areas such as Grand Teton National Park, 150 km north, to their winter range in the UGRB (Berger et al., 2006; Sawyer and Lindzey, 2000; Sawyer et al., 2005). This region consists primarily of sagebrush (*Artemisia* spp.) steppe communities in rolling hills punctuated by plateaus. The sagebrush steppe in this region has a strong spatial pattern linked to topography (Burke et al., 1989). The topography also leads to snow being swept off the higher elevation plateaus by wind. This provides crucial winter range for an estimated 100,000 ungulates including pronghorn, mule deer, elk (*Cervus elaphus*) and moose (Berger et al., 2006; Burke et al., 1989; Sawyer et al., 2005). The Bureau of Land Management has primary authority for land management.

Twice each year, between 1000 and 2000 pronghorn and 2500 and 3500 mule deer pass through a migration bottleneck at Trapper's Point Historical Monument where the migration route is bisected by US Highway 191 (US 191) 8 km west of Pinedale, WY, USA (Fig. 1; Sawyer et al., 2005; Berger et al., 2006). Approximately 300–400 of these 1000–2000 pronghorn

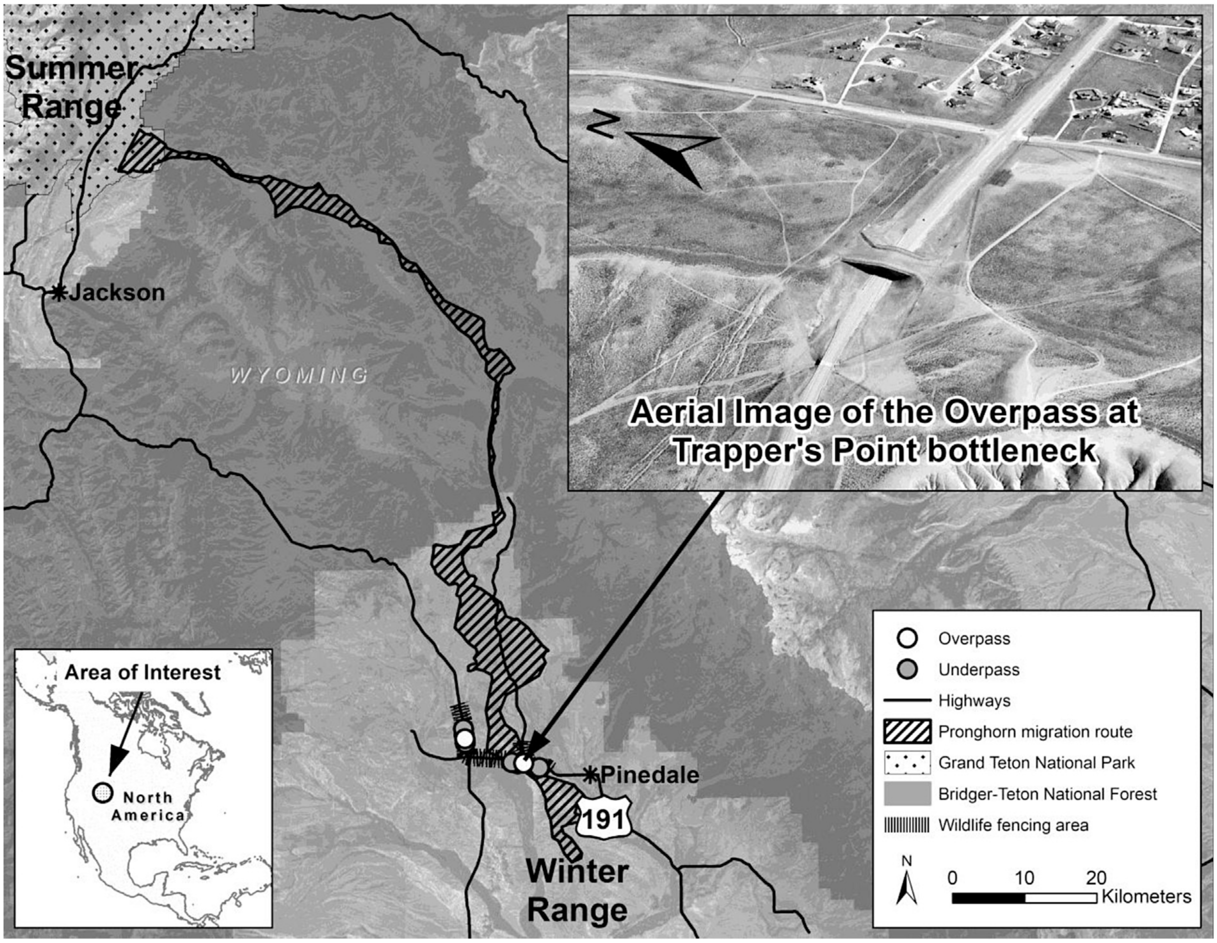

Fig. 1. Map of the study system showing the pronghorn migration route to Grand Teton National Park (Berger et al., 2006; Beckmann et al., 2012). Inset is an aerial view of the Trapper's Point bottleneck and wildlife overpass. Image by Lisa Robertson.

make annual spring and fall migrations to Grand Teton National Park along the Park's sole remaining pronghorn migration route (Berger et al., 2006; Grand Teton National Park, 2010). Archaeological evidence suggests that pronghorn have been migrating through Trapper's Point for 6000 years (Miller et al., 1999). A Forest Plan Amendment in 2008 provided some protections for the migration route through the designation of the Pronghorn Migration Corridor (Bridger-Teton National Forest, 2008).

Recorded ungulate-vehicle collisions on US 191 during seasonal migrations averaged 85/year along a 20 km stretch of this road (Sawyer et al., 2016) and average annual daily traffic were 2578 vehicles/day in 2007 (Wyoming Department of Transportation). US 191 was a two-lane highway with no median. In 2011, the Wyoming Department of Transportation began the construction of wildlife crossing structures along this section of road to increase the safety of motorists and decrease wildlife mortality rates. Two wildlife overpasses and six wildlife underpasses along US 191 with associated 2.4 m (8 feet) high woven-wire fence were completed in 2012 (Fig. 2). Wildlife underpasses were constructed from simple span bridges that were approximately 20 m wide, 13 m long and 4 m high (Sawyer et al., 2016). Fences were completed prior to the completion of the crossing structures. The wildlife overpasses were constructed as a concrete arch system that resulted in a 46 m wide wildlife bridge that, at Trapper's Point, spanned 24 m across the highway (Contech Engineered Solutions, 2013, Figs. 1 and 3a). Associated infrastructure included a gated 3-strand barbed wire cattle fence with wooden top rails and a smooth bottom wire at either end of the wildlife overpass. The Wyoming Department of Transportation considered data on wildlife movement (e.g., Sawyer et al., 2005; Beckmann et al., 2011), local geology and archaeological resources when determining siting of this wildlife overpass. Landmark completion dates of construction can be found in Appendix A of the Supplementary material.

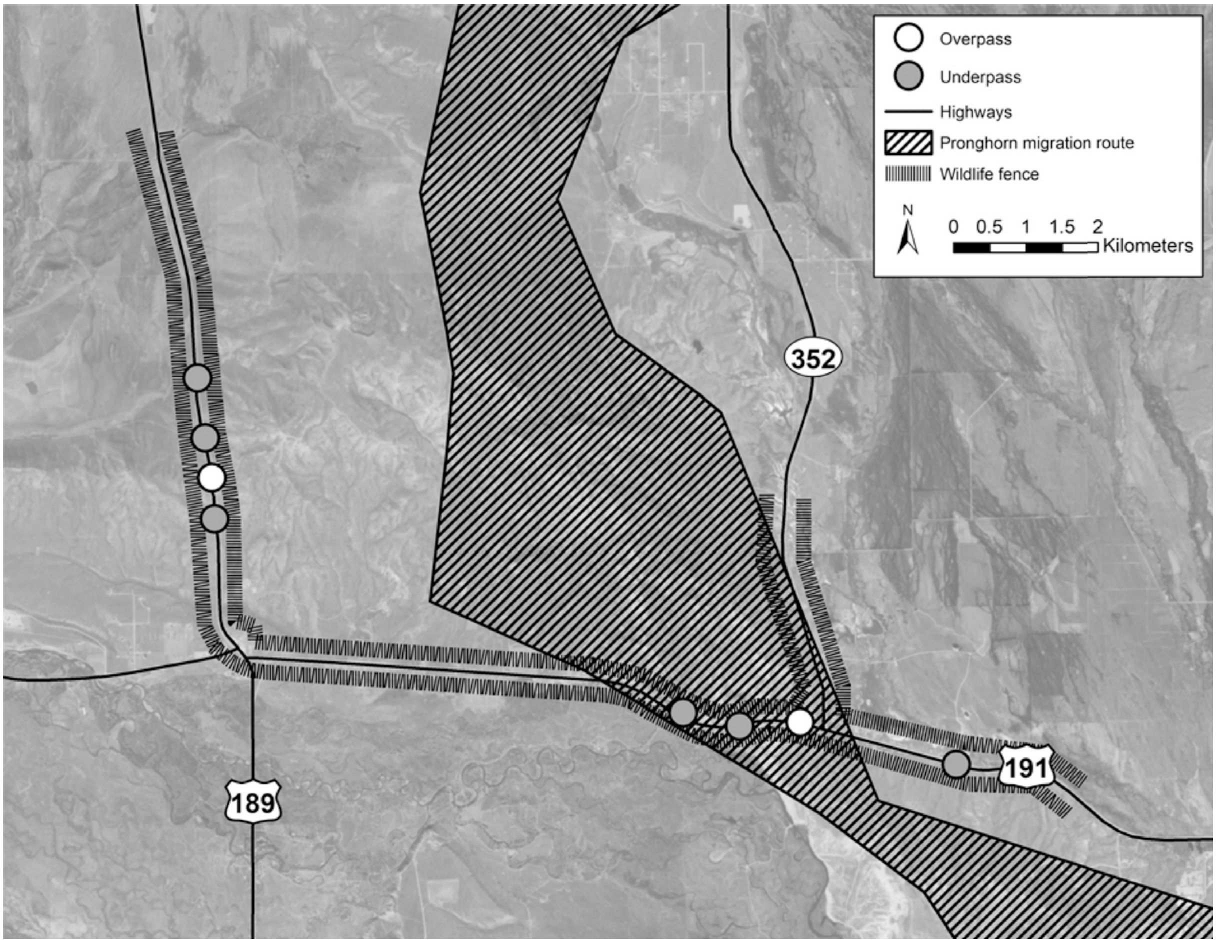

Fig. 2. This map provides a zoomed view of the mitigated section of highway east of Pinedale, Wyoming. Our study focused at the Trapper's Point wildlife overpass (white circle) just west of the junction of State Highway 352 and US 191. The pronghorn migration route represents the general movement path of pronghorn before the mitigation was installed (Berger et al., 2006).

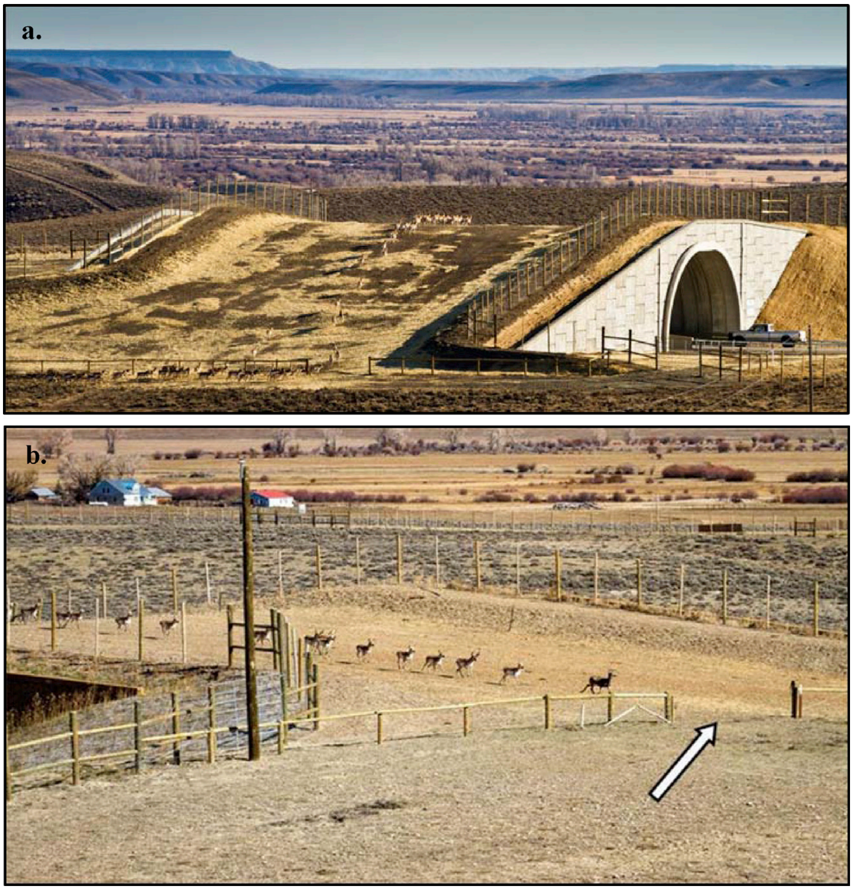

Fig. 3. Pronghorn at the Trapper's Point bottleneck: a) successfully crossing the wildlife overpass at Trapper's Point, fall 2012. b) Following a single mule deer over the Trapper's Point wildlife overpass in October 2013. Note the solitary gate (white arrow) in the fence. The fence is open. Images by Jeff Burrell.

2.2. Data collection

We observed pronghorn behavior near the Trapper's Point wildlife overpass and two nearby wildlife underpasses during spring and fall migrations from September 2011 to May 2014 to understand the effects that crossing structures may have on wildlife over time. The construction of the crossing structures was initiated in March 2011 so our observations started after construction had begun. Observers used a 48 × 60 mm spotting scope (Nikon Prostaff) to collect data. Observer locations changed among seasons to accommodate constraints on visibility due to topography and direction of animal travel. Observations were made from a vantage point 0.66 km north and 0.72 km southeast of the Trapper's Point wildlife overpass in the fall and spring, respectively. All attempts were made to observe an individual's behavior continuously from their initial detection until they crossed the highway or crossing structure or, in the case of evening sampling, until it was too dark for an observer to record behaviors accurately.

At the start of our observation, we estimated the individual's distance from the highway or crossing structure and noted its sex, the type of structure that the individual was approaching (i.e., highway, wildlife underpass, or wildlife overpass) and whether humans were present along the migration path (i.e., the presence of construction workers, tourists, hikers or off-road vehicles in the general area). While pronghorn behaviors might be relatively consistent within a group (i.e., the group generally mimics the lead animal; O'Gara and Yoakum, 2004), intra-group differences likely impact behavioral responses so we also collected information on the individual's location in the group (i.e., lead or not lead) and total group size.

We collected focal behavioral data on individual pronghorn during our observations (see Appendix B of the Supplementary material for an ethogram). We selected an individual in the group and alternated between lead and non-lead individuals across groups to collect data on individuals occupying both locations within different groups. Focal observations were made for a minimum of 3 min. We ended focal observations if the individual went out of sight or successfully crossed the structure or road. Successful crossings were defined as an individual crossing the road surface, a wildlife overpass or a wildlife underpass without returning to the approach side of the road.

2.3. Data analysis

To look at the changing behavior of pronghorn over time, we coded each season and year of observations as a time series based on five distinct observation periods: fall 2011, spring 2012, fall 2012, spring 2013, and spring 2014. We used generalized linear mixed-effects and generalized additive models to investigate factors influencing pronghorn crossing success and behavior near Trapper's Point. We conducted two separate analyses to 1) determine any change in crossing success of pronghorn over time, and 2) investigate the behavioral responses of pronghorn to these crossing structures and associated infrastructure. We first modeled the dependent variable of whether an individual successfully crossed the structure or road as a function of the fixed effects of human presence and season coded as a time-series variable, and of the random effect of group identity; we included this random effect on the intercept to account for any unobserved differences among groups. We performed this analysis using a binomial distribution and the ‘glmer’ function from the lme4 package in R v. 3.3.2 (Bates et al., 2015; R Development Core Team, 2016). Observations were only included if we could determine whether an individual successfully crossed, or did not cross, the structure or road during the observation period and for individuals in which the focal observation spanned 3 min or more.

In the second analysis, we investigated how pronghorn behaviors changed at the crossing structures over time and whether they were a function of the independent variables of human presence, season coded as a time-series variable, location in the group (lead or non-lead), group size (number of individuals), and initial distance from the structure. We grouped the behaviors we observed during focal observations into two categories for this analysis: 1) sustained vigilance (walking or running towards the crossing location in a direct line while looking at the crossing location with ears erect), and 2) stress (piloerection, head-bobbing and pacing along a fence; see Appendix B of the Supplementary material). All other behaviors were classed as a reference category that we called nominal behaviors. Group size and distance to the structure were standardized to have a mean of 0 and a standard deviation of 1. We modeled the proportion of time spent in each behavior for observations between 3 and 5 min using a beta distribution and the ‘gamlss’ package in R (Stasinopoulos and Rigby, 2007). We fit this model using the beta inflated distribution (‘BEINF’) to accommodate observations in which individuals spent all or none of the allotted time in a specific behavior category (i.e., an individual was exhibiting sustained vigilance behaviors for the entire duration of the focal observation). Human presence was coded as a binary variable in both analyses ($0 = $ absent, $1 = $ present). We examined model fit for both analyses by investigating residual plots for homogeneity of variance and by calculating pseudo R^2 values.

We quantified the number of crossing attempts an individual made by counting the clusters of sustained vigilance behaviors. All descriptive statistics are expressed as means ± SE [minimum, maximum]. Model results for continuous variables are presented as parameter effect sizes (*b*), SE, and *p*-values from our models. All models were fit by maximum likelihood estimation. References made to a “structure” mean the highway, a wildlife overpass or underpass. Data available from the Dryad Digital Repository.

3. Results

We observed 293 pronghorn from 154 groups approaching the crossing structures when construction was occurring and after construction was complete ($n = 133$ during the spring migration and $n = 160$ during the fall migration). Group size was 32.28 ± 1.88 [1, 207]. Average distance that a group was to a structure when observations began was 1913.12 ± 111.77 m [0, 11960]. The average number of attempts an individual pronghorn made to cross a structure during an observation was 2.23 ± 0.18 [0, 19]. Observations were made on 134 lead animals, 116 non-lead animals and 43 animals whose location in their group was unknown due to topography obscuring some of the observer's range of view. Pronghorn successfully reached the other side 95 times out of 285 crossing attempts (Fig. 3a and b). Of these, 35% were made on the highway's surface, 59% were on the wildlife overpass, 4% were through either of the two wildlife underpasses and 2% we were unable to observe because we lost sight of the group during the crossing event. All crossings on the highway surface that we observed were made before the crossing structures were completed (i.e., occurred before the fall of 2012).

Due to missing data in some of our covariates, we used observations of 146 and 147 individual pronghorn to determine the factors that influenced success of crossing and behaviors at crossings, respectively. The number of individuals monitored from each group was 1.86 [1, 6].

Human presence did not influence the crossing success of migrating pronghorn at the structures between 2011 and 2014 ($b = -0.06$, $SE = 0.78$, $p = 0.94$; Table 1). However, crossing success of migrating pronghorn was correlated with time period (Fig. 4a). Successful crossings increased in frequency over time ($b = 0.98$, $SE = 0.34$, $p = 0.004$; Table 1). Group identity accounted for 26% of the variation (conditional $R^2 = 0.53$).

Pronghorn behaviors around the crossing structures and associated infrastructure also changed over time. Pronghorn were more likely to exhibit increased sustained vigilance behaviors over time ($b = 0.3$, $SE = 0.07$, $p < 0.001$), but stress behaviors did not significantly change over time ($b = -0.04$, $SE = 0.1$, $p = 0.71$; Table 2 and Fig. 4b). Together, these results indicate a decrease in the quantity of nominal behaviors occurring over time (Fig. 4b).

Pronghorn spent more time exhibiting sustained vigilance behaviors when they were further from crossing structures ($b = 0.39$, $SE = 0.11$, $p < 0.001$; Table 2) and lead animals spent more time exhibiting sustained vigilance behaviors than non-lead animals ($b = 0.62$, $SE = 0.21$, $p = 0.003$; Table 2). The presence of humans during migration and group size did not significantly influence pronghorn behavior, and no independent variables were significant in predicting the proportion of

Table 1
Results from the generalized linear mixed-effects model investigating the factors influencing the probability of crossing success for pronghorn. Group identity was coded as a random effect on the intercept and explained 26% of the variation in our data. Time indicates the change in crossing success over the five seasons of observations. Significant values, not including the intercept, are noted in bold ($p < 0.05$).

	Estimate (SE)	P-value
Intercept (No humans)	−4.86 (1.51)	0.001
Human presence	0.06 (0.78)	0.94
Time	**0.98 (0.34)**	**0.004**

time in stress behaviors ($p \geq 0.1$). Our models explained 23% of the variation in our data for sustained vigilance behaviors ($R^2 = 0.23$). Our model for stress behaviors poorly described the variation in our data ($R^2 = 0.02$).

4. Discussion

Migrating pronghorn demonstrated a clear preference for crossing the highway on the actual road surface when accessible and a secondary preference for the Trapper's Point wildlife overpass when compared to the nearby wildlife underpasses. However, they had varying behavioral responses to the construction of highway crossing structures over time. Our results suggest a complex response by pronghorn to these structures.

The increase in sustained vigilance of pronghorn following the completion of construction may be a response to the placement of these novel structures along the historic migration route. For thousands of years, these animals have negotiated this bottleneck to access seasonal ranges, and for over half of a century, this has been done by crossing the highway. In 2012, pronghorn were suddenly compelled to utilize a man-made crossing structure or not cross the road at all. The concomitant increase in sustained vigilance behaviors we observed over a relatively short period reveals that individuals were still adapting to the structures in their migratory path in 2014, despite the fact that the wildlife overpass actually led to a higher probability of successfully crossing the road. This is potential evidence of mal-adaptation by pronghorn. In other words, given time to adjust to US Highway 191, pronghorn were more comfortable crossing on the road surface, despite the high level of WVC risk. However, the increased observation of successful crossings during the final acclimation phase is an encouraging indication that pronghorn may eventually return to spending less time in vigilant behaviors near Trapper's Point during migration. Indeed, there was high variation in the amount of time spent in sustained vigilance behaviors during acclimation, suggesting that individuals were likely acclimating to the wildlife overpass structure at varying rates. Additionally, the fact that pronghorn spent very little time in stress behaviors across all study phases provides some assurances that pronghorn will be able to adjust their behaviors relatively quickly in response to crossing structures, as seen with deer and moose successfully utilizing wildlife crossing structures in Banff, Canada (Clevenger et al., 2009).

We observed that most stress behaviors occurred when individuals were adjacent to fences, roads and crossing structures. For example, the head-bobbing and pacing behaviors only occurred at fence lines. Both behaviors appeared to be a means of

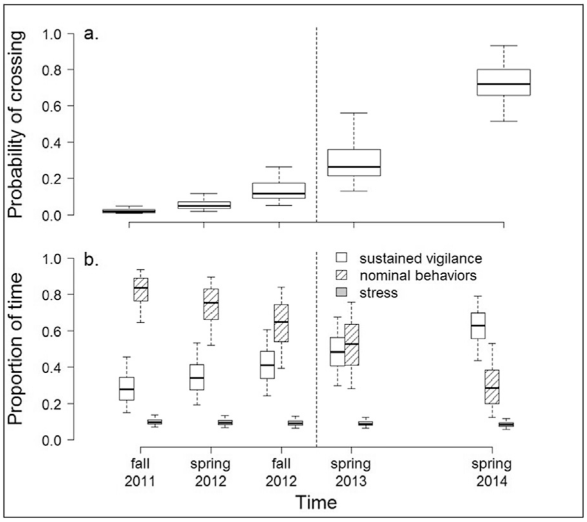

Fig. 4. a) Changes in the probability of pronghorn successfully crossing the highway under or overpass during migration between September 2011 and May 2014 at Trapper's Point wildlife overpass outside of Pinedale, Wyoming. b) Changes in the proportion of time that pronghorn spent in each behavioral category during migration between September 2011 and May 2014 outside of Pinedale, Wyoming. The dashed vertical line in both figures represents the end of the construction of crossing structures.

Table 2

Results from the generalized additive models investigating the ecological and anthropogenic effects on the proportion of time spent by pronghorn in each behavioral category. Parameter estimates (and standard errors) are presented. Significant values, not including the intercept, are noted in bold ($p < 0.05$).

Factor	Sustained vigilance	Stress behaviors
Intercept (No humans, Non-lead)	−1.56 (0.29)	−2.27 (0.39)
Time	**0.3 (0.07)**	−0.04 (0.1)
Human presence	−0.22 (0.25)	−0.01 (0.38)
Lead	**0.62 (0.21)**	0.15 (0.34)
Group size	−0.09 (0.1)	−0.17 (0.19)
Distance to structure	**0.39 (0.11)**	0.14 (0.13)

attempting navigation past the fence. Since our statistical analyses were performed on the first 3−5 min of any focal observation for uniformity, we were often analyzing behaviors farther from crossing structures and associated infrastructure rather than only behaviors occurring immediately adjacent to them. Additionally, the hillier topography immediately adjacent to the crossing structures made it difficult to observe pronghorn that were closer to the structures and associated infrastructure as opposed to those at greater distances, leading to reduced and fragmented observations on individuals that were close to fences and crossing structures. This may have contributed to the observation that pronghorn spent an apparent small proportion of time in stress behaviors. The reduced amount of time spent in stress behaviors may also be an artifact of how we *a priori* defined stress behaviors. While piloerection, pacing and head-bobbing are indicative of high stress in pronghorn, the sustained-vigilance behaviors that we observed may easily be defined as lower-level stress activities. Indeed, pronghorn always approached crossing structures in sustained vigilance behaviors, with erect ears and visually fixed on the structure.

While the presence of human activity at and around crossing structures did not seem to influence the eventual success or failure of an individual crossing a structure, this may be because most human activities in the area were ephemeral and occurred at relatively low levels. These results align well with previous research that identified the distance to dense human developments as an important factor contributing to the reaction of animals to human presence at structures (Clevenger and Waltho, 2005). Additionally, the Wyoming Department of Transportation, under the advice of the Wyoming Game and Fish Department and other biologists, ceased major construction activities on the wildlife overpass during migration and this likely alleviated otherwise stressful passage for pronghorn.

Group identity played a large role in pronghorn crossing success, accounting for 26% of the unexplained variation. Thus, something specific about group identity or composition (e.g., behavior, genetics, group size) affected crossing. Future studies should investigate the group-specific factors that may lead to crossing success.

The large amount of inter-group variation and lack of fit in our models is likely due in part to pronghorn behavioral ecology. Pronghorn tend to be flighty and as a group they follow the movements and behavior of the lead individual (O'Gara and Yoakum, 2004; Beckmann and Berger, 2005). Factors such as the specific location of the group, weather, time of day, group size, sex and age of the lead individual have the capacity to influence behavior as individuals cue off the group leader, other conspecifics, and other environmental variables. Although our models, not including the stress behaviors, explained >20% of the variation in our data, future models that include additional factors are likely to result in stronger model fit. Had we been able to collect larger sample sizes, we also may have been able to better detect variation in pronghorn behaviors. We believe additional research should collect more data on the inter-group variation that was unexplained in the current research. Additionally, we suggest a re-assessment of crossing success and behaviors of this pronghorn herd at this site when pronghorn may have further adapted to the structures.

4.1. Management implications

This study provides useful information both to modify existing structures and to plan for the future mitigation of WVCs. We never observed pronghorn crossing the highway surface once construction was completed. This major finding points to the success these structures had in significantly reducing the risk of WVCs (Sawyer et al., 2016). Our results also suggest that while pronghorn were behaviorally challenged during our observations, the probability of successfully crossing the structures increased over time potentially indicating that the landscape is increasing in permeability for pronghorn as the animals acclimate to the structures.

Our research indicates that several modifications in construction planning, completion timing and design could have decreased the amount of time pronghorn took to successfully cross the highway and ultimately acclimate to novel crossing structures. Our recommendations are applicable across a broad spectrum of species and geography, providing global implications for conserving wildlife that must cross roads and increasing the efficiency of road mitigation for wildlife.

Pronghorn struggled with fences while they were attempting to use the crossing structure. Multiple fence lines, meant for cattle management, cross the path that pronghorn must take to access the wildlife overpass. One set of fences in particular, located at both ends of the completed wildlife overpass, presented unnecessary challenges for wildlife (Fig. 3b). Each of these fence lines had a gate, but the seasonal opening of these gates relied on a human action every season to open and close them. These 3-strand wire fences with a 16″ high smooth bottom wire, two barbed middle wires, and a wooden top rail are not designed for easy wildlife navigation. We occasionally witnessed nervous pronghorn tangle themselves in the fence when a gate was not open, an open gate was not found, or the gate was lying on the ground. These issues are exacerbated by snow. This unnecessary added stress and hazard for migrating wildlife could be alleviated by installing temporary removable fencing, lay-down fence, or by raising the bottom wire to 18–20″ while keeping 12” between the top and second wire, replacing the barbed wire with smooth wire and removing the wooden rail (Paige, 2012; Christine Paige and Paul Jones, personal communication). When cattle are not present and if removable fencing is not an option, clipping the bottom wire to the middle wire to create more space under the fence will greatly improve the ability of pronghorn to navigate through (Paige, 2012). In this study system, we recognize the need to accommodate multiple users (e.g., an important seasonal cattle drive occurs through the bottleneck) and offer solutions that will work for both cattle and wildlife; in other systems, the detriment to wildlife of fences and gates across the openings of crossing structures should be avoided. Fences likely contributed to the increasing levels of sustained vigilance documented in this study.

Finally, multiple sections of barrier fence were installed before crossing structures were available for pronghorn to use. To reduce the number of animals trapped on the road during construction, transportation departments should create infrastructure (crossing structures and barrier fences) completion chronologies (rather than landmark dates) for individual contractors.

Despite concerns over the necessity for multi-use access and issues with fences, this highway mitigation effort for wildlife is an overall conservation success (Fig. 3a). Pronghorn in this system must be migratory given the severe winters and thus have a strong drive to move between discreet summer and winter ranges, aspects of their behavioral ecology that are key factors contributing to the success of these crossing structures. A robust understanding of the ecology of local migrating wildlife populations, such as this example from the Greater Yellowstone Ecosystem, will provide decision makers tools to determine how and where mitigation could significantly reduce WVCs while also accommodating the continued passage by migrating wildlife. Future studies should address whether the behavioral changes we document here occur at other sites, with other species, and whether they affect success of road mitigation, individual fitness, and ultimately population demographics.

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Appendix A. Supplementary data

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