





Gray wolf habitat use in response to visitor activity along roadways in Yellowstone National Park

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Abstract. Understanding the behavioral responses of large carnivores to human activity in protected areas is important for conserving top predators. Roads and associated vehicle traffic have a range of impacts on wildlife, including mortality from vehicle collisions and behavioral changes from increasing traffic levels. Roads concentrate human activities and may be particularly impactful when located adjacent to high-quality habitat for wildlife. However, people often overlook road impacts in protected areas because of relatively low road densities. From 1979 to 2017, annual visits to Yellowstone National Park increased from 1.9 to 4.1 million, with many visitors in the last 25 yr focusing on the opportunity to view wild wolves (*Canis lupus*) in their natural habitat from the roadway. To better understand how human activity interacts with landscape attributes and prey availability to shape wolf habitat use, we developed seasonal and diel-specific step selection functions (SSF) for wolves. Wolves responded to increased human activity by using areas farther from roadways during the day and during peak visitation in summer. Prey availability, as estimated by an elk SSF, did not significantly alter habitat selection patterns by wolves. The strength of habitat selection in relation to roads varied among wolf packs. The most heavily viewed wolf packs exhibited less road avoidance, suggesting increased tolerance, which could lead to increased vulnerability to human harvest if they leave the park. Federal and state managers have implemented several measures to mitigate disturbance effects to wolves and curtail habituation. These results may inform adaptive management strategies that seek to continue to conserve natural wolf behavior.

Key words: *Canis lupus*; elk; protected area; road ecology; step selection function; wildlife management; wildlife tourism.

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INTRODUCTION

Road corridors can have significant impacts on terrestrial wildlife communities. Habitat fragmentation and increased road use cause individual mortality from vehicle collisions, population-level behavioral changes from increasing traffic levels, and genetic flow disruptions among populations of animals (Forman and Alexander 1998, Riley et al. 2006, Ament et al. 2008, Monz et al. 2016).

Road impacts also stem from the increased access they provide for humans to undeveloped areas. In some areas, roads can facilitate access by hunters, increasing pressure on animal populations through legal hunting and illegal poaching (Trombulak and Frissell 2000, Noss et al. 2003, Zimmermann et al. 2014). On the other hand, roads can benefit local economies by improving access to scenic, protected areas through ecotourism infrastructure for wildlife viewing (Ament et al. 2008)

and providing recreational hunting opportunities (Smith et al. 2016).

In addition to direct mortality from vehicle collisions, the impacts of roads may stem largely from concentrating human activity in wildlands. Changes in habitat selection through avoidance of areas of higher human use have been documented across taxa in terrestrial and marine ecosystems (Chruszcz et al. 2003, Berger 2007, Lesmerises et al. 2012, Northrup et al. 2012, D'Amico et al. 2016, Bateman and Fleming 2017, Penteriani et al. 2017). Such behavioral responses to humans can manifest in activity changes, whereby animals shift times of peak activity or use areas with higher landscape cover and concealment when closer to humans (Ordiz et al. 2011, Wilmers et al. 2013, Zimmermann et al. 2014, Llana et al. 2016, Gaynor et al. 2018, Suraci et al. 2019b). In some locales, animals subjected to higher rates of visitation have displayed higher field metabolic rates (Barnett et al. 2016) and lowered reproductive success and growth rates of dependent young (McClung et al. 2004, French et al. 2011). Further evidence demonstrated altered large carnivore behavior from the sound of human voices, leading to cascading community-level effects (Suraci et al. 2019a). These effects can be especially troubling for large carnivores given their relatively low population densities, restricted distributions, and significant roles as keystone predators (Hebblewhite et al. 2005, Ripple et al. 2014). For example, increased visitor activity and the removal of carcasses along roads for traffic or safety reasons have displaced gray wolves (*Canis lupus*) from feeding sites near roadsides in Yellowstone National Park (YNP, unpublished data). Repeated removals of wolf-killed carcasses could lead to changes in trophic relationships and indirect effects on prey similar to those seen in response to kleptoparasitism by dominant scavengers (Krofel et al. 2012, Elbroch et al. 2015). For example, carcass removals by humans are analogous to carcass abandonment, which can precede increases in kill rates and energetic expenditures or loss of feeding opportunities to scavengers (Kerley et al. 2002, Smith et al. 2015). In addition, wolf travel routes can be blocked as they move to and from their den areas to feed pups during late spring and early summer

(Smith et al. 2003). In response, management personnel will often close areas or institute no stopping zones along roadways to allow wolves to freely travel or feed without disturbance (Smith et al. 2003). However, repeated displacements over time could lead to long-term behavioral changes through avoidance, tolerance, or habituation (Knight and Cole 1991, Sirot 2010). In other systems, behavioral changes have led to alterations in individual fitness and disruptions to trophic relationships (Knight and Cole 1991, Hebblewhite et al. 2005, Berger 2007).

The National Park Service (NPS) protects nearly one-quarter of the threatened and endangered species in the USA (Ament et al. 2008) through habitat protection and native species restoration. It also provides critical socio-ecological information for understanding the impacts of regulatory protections under different management jurisdictions (Pressey et al. 2015). Furthermore, national parks can serve as important ecological baselines that help scientists understand and predict changes in other ecosystems, especially those experiencing increased anthropogenic influences (Sinclair 1998, Berger 2007). The NPS's mission is to "conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations" (NPS Organic Act of 1916). This mandate distinguishes the NPS from most other land management agencies and guides its current wildlife policies. However, this mission statement contains objectives of conserving nature unimpaired and providing for enjoyment by people that may conflict at times (Clark and McCool 1985, Wright 1992, Keiter 2013). Understanding how to implement this dual mandate by simultaneously protecting wildlife and facilitating visitation in YNP requires monitoring and research on the impacts of roads and visitation on wildlife behavior, which is broadly applicable for wildlife managers in most protected areas.

Ecotourism provides enjoyment for millions of people and can boost surrounding community economies, but it can also result in some negative impacts to natural resources (Liliehalm and Romney 2000). From 1979 to 2017, visitation to national parks in the United States increased 70%

from 50.4 to 85.5 million visitors annually (NPS 2018). The rise in visitation was even more dramatic in YNP during this time, with a nearly 120% increase from 1.9 to 4.1 million annual visitors, mostly occurring from June to August (Appendix S1: Fig. S1; NPS 2018). For example, in 2017, average monthly visitation from November to April was approximately 4% (27,102/month) of that recorded during May–October (658,985/month; NPS 2018; see Appendix S1: Fig. S1, for monthly visitation examples). Although traffic is restricted to a 500-km road system that dates back to the 1930s and 1940s, the road corridor intersects several prime river valleys and landscape features, providing wildlife viewing opportunities to greater areas of the park (Keiter 2013). Previous research has indicated winter motorized travel can alter the behavior of animals, and possibly affect their physiological condition (Creel et al. 2002, Fortin and Andruskiw 2003). However, many animals appeared to habituate to this travel, and there was no evidence it affected their demography, population dynamics, or resource use (Fortin and Andruskiw 2003, Borkowski et al. 2006). It is possible that summer motorized travel could have similar or more substantial impacts on large carnivores like wolves in YNP since visitation is greater during this time. In recent years, wildlife watching has emerged as a popular recreational pursuit that is thought to be a low-impact activity (Knight 2009). From 1995 to 1997, gray wolves were reintroduced to YNP following a 70-yr absence (Smith and Bangs 2009). In the years following the reintroduction, YNP became a world-class location to see wild wolves in their natural habitat because of their surprisingly high sightability from the roadway (Smith et al. 2016). Over the last two decades, the number of park visitors viewing wolves has increased substantially, which leads to large groups of people congregating at wolf viewing sites. This concentrated human activity could alter wolf behavior given that wolves in Scandinavia often fled when approached by humans and developed more cryptic behavior after interactions with humans (Wam et al., 2012, 2014).

We sought to quantify wolf behavioral changes to understand current patterns of responses to humans through the implementation of step selection functions (SSFs), which are common

methods of estimating wildlife habitat selection from animal location data (Boyce et al. 2002, Manly et al. 2002). These methods have previously been used to show varying responses by wolves to roads and human activity (Hebblewhite and Merrill 2008). Studies in other systems have shown varying responses by wolves to roads depending on the level and type of human use. Selection for areas close to the road either increased (Courbin et al. 2013, Uboni et al. 2015), decreased (Mladenoff et al. 1995, Latham et al. 2011), or displayed more context-dependent responses (Thurber et al. 1994, Paquet et al. 1996, Whittington et al. 2005, 2011, Houle et al. 2010, Ehlers et al. 2014, Zimmermann et al. 2014). For example, Scandinavian wolves displayed an affinity for certain road types for their ease of travel, but exhibited adaptively cryptic behavior when traveling through areas of higher human activity (Zimmermann et al. 2014). Moreover, higher human activity levels have been related to decreased odds of selection and increased mortality in wolves, but can vary among wolf packs in an area due to relative exposure to human activity (Mladenoff et al. 1995, Hebblewhite and Merrill 2008). Legal wolf harvest is permitted in many areas, and, in these regions, road density has been linked to higher rates of human-caused mortality (Fuller et al. 1992, Person and Russell 2008). The absence of hunting within YNP would suggest that wolves would not associate the road and humans with risk (Baldwin and Bender 2008). However, 33 wolves have been killed by vehicle strikes in YNP since 1995 (YNP, *unpublished data*), and some wolves that live primarily within YNP travel outside of the park, becoming exposed to potentially lethal consequences during hunting season in Montana, Idaho, and Wyoming (Borg et al. 2016, Smith et al. 2016). Since 2009, 44–46 wolves that spent at least 90% of their time inside the park have been harvested when they moved outside the park boundary (YNP, *unpublished data*). The harvest of these wolves affected pack stability, which temporarily reduced denning and recruitment rates, as well as wolf sightings by visitors (Borg et al. 2016). However, harvest mortality and pack dissolution had no significant effects on the longer-term population dynamics of wolves (Borg et al. 2015, 2016, Smith et al. 2016).

In this study, our objective was to understand how increasing visitation and road use in YNP-

affected wolf habitat selection. Specifically, we evaluated whether visitor use associated with the roadway affected wolf resource selection patterns. We also evaluated whether these habitat selection patterns varied across wolf packs, diel periods, and season (spring–fall). We developed seasonal and diel-specific SSFs for wolves and their main prey (elk). We then tested the hypothesis that high human activity would cause wolves to avoid the road corridor more during the day when visitation is high. However, since elk have been known to use areas near human activity as refugia (Hebblewhite et al. 2005, Kauffman et al. 2007), we expected this avoidance would be mediated by possibly greater prey availability near the road, as well as landscape attributes that affect perceived risk from humans (Paquet et al. 1996, Uboni et al. 2015).

MATERIALS AND METHODS

Study area

Yellowstone National Park encompasses 8991 km² of federally protected land in Wyoming, Montana, and Idaho. This study focuses on a 5853-km² area that includes Yellowstone's northern range and extends south into the interior of the park and north beyond park boundaries into Custer Gallatin National Forest (Fig. 1). Vegetation consists primarily of grasslands, sagebrush, and shrublands interspersed with varying sized patches of Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), Engelmann spruce (*Picea engelmannii*), and juniper (*Juniperus occidentalis*). Higher elevations include areas of sagebrush steppe and whitebark pine (*Pinus albicaulis*). Eight different ungulates inhabit YNP: elk, bison, mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), pronghorn (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), and non-native mountain goats (*Oreamnos americanus*; Lemke 2004). Elk are the most abundant ungulate in summer, numbering 25,000–35,000 in eight different herds and are the primary prey for wolves, followed by bison and mule deer (White and Garrott 2005, Metz et al. 2012).

Wolf and elk spatial data

Following wolf reintroduction in 1995–1997, the number of wolves in YNP has ranged

between 21 and 174 individuals in three to 16 packs (Fritts et al. 1997, 2001, Smith et al. 2017). We used GPS data from wolves captured annually during winter from 2001 to 2016 using helicopter darting techniques following protocols approved by NPS Institutional Animal Care and Use Committee (IACUC; Permit: IMR_YELL_Smith_wolves_2012). During this time, various radio collar types were used including both very high frequency (Telonics, Mesa, Arizona, USA) and GPS-enabled (Televilt, Lindesberg, Sweden; Lotek, Newmarket, Ontario, Canada; Vectronic-Aerospace, Berlin, Germany). GPS collars were programmed to take fixes at 30-min, 1-h, or 6-h intervals depending on the season. This study utilized 19,771 locations with 6-h intervals between locations from 37 GPS-collared wolves (17 males, 20 females) from 2002 to 2016 (Mean 2 packs/yr, SD 1.11 packs/yr). These individuals represented 16 different packs (Appendix S1: Table S1).

To understand the primary prey species for wolves, elk were captured across the northern range of Yellowstone from 2012 to 2016 under NPS IACUC 2011-47. Elk were fitted with GPS-enabled collars (Lotek; Vectronic-Aerospace). This study evaluated 74,615 GPS locations at a 5-h fix rate during May–October from 33 adult female elk (Mean 19.2 elk/yr, SD 5.85 elk/yr).

Step selection function covariates

To test the effect of landscape attributes on wolf habitat use, we obtained various habitat and landscape layers that could influence wolf habitat selection based on findings from previous studies (Fortin et al. 2005, Whittington et al. 2005, Hebblewhite and Merrill 2008). We used a Digital Elevation Model with 30-m resolution to attain elevation data for the study area. We calculated slope and aspect using the terrain function in the raster package (v 2.8-19; Hijmans and van Etton 2012).

Land cover characteristics and fire boundaries were supplied by the YNP Spatial Analysis Center and used to identify the spatial distribution of vegetation types. The vegetation data were condensed into a categorical land cover type layer, which included herbaceous grassland, shrubland, unburned conifer forest, burned forest, and other land cover that included various wetland and cultivated land cover types. Barren ground was used as a reference category. Burned forest

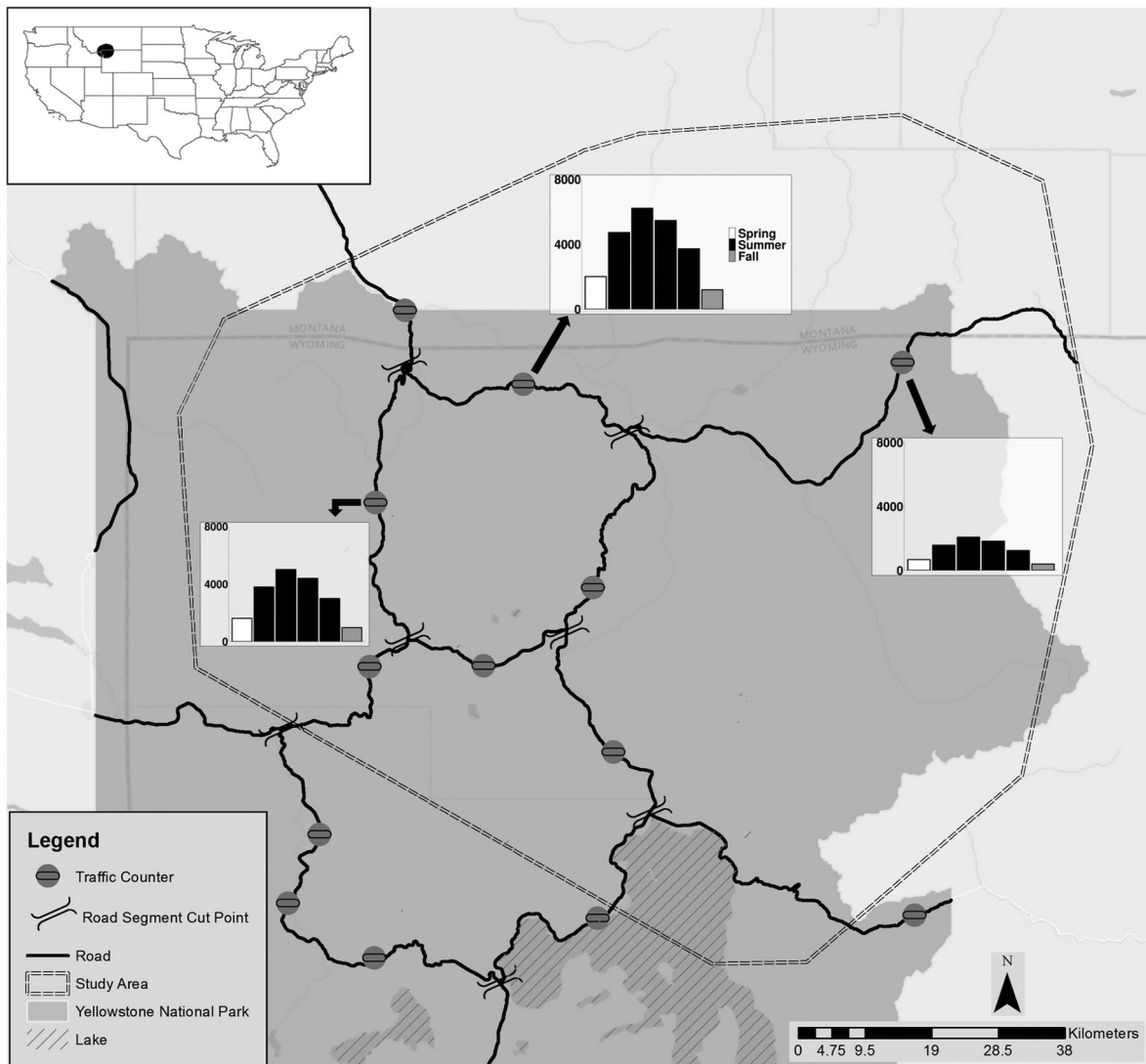


Fig. 1. Study area map in the Greater Yellowstone Ecosystem. The red polygon outlines the 5853 km² where we calculated step selection functions for wolves and elk. The dark gray-shaded area delineates the boundaries of Yellowstone National Park. Circles show the placement of automatic traffic counters. Data from automatic traffic counter in August 2015 were used to generate estimates of average daily traffic (ADT) for each road segment. Inset bar graphs show ADT estimates averaged over all years of the study where shaded bars represent different months within the three seasons used in this study: white bars for spring (May), black bars for summer (June–September), and gray bars for fall (October). All bar graph *y*-axes are scaled from zero to 8000 vehicles per day. See *Results* section for exact dates included in each season.

boundaries were identified using fire boundary layers dating back to the 1960s. These categorical land cover layers were used in both wolf and elk SSF models. Finally, we transformed the spatial distribution of perennial watercourses to a distance raster.

In addition to spatial heterogeneity in vegetation, forage quality changes temporally and has been shown to drive patterns in seasonal elk habitat selection (Hebblewhite and Merrill 2008, Merkle et al. 2016). We obtained normalized-difference vegetation index, a measure of primary

productivity, from Moderate Resolution Imaging Spectrometer (MODIS) satellites, which gives 500-m imagery resolution every 16 d (Didan 2015). Normalized-difference vegetation index imagery at 500-m resolution was downloaded for the entire study area using tools in the R package MODISsp (v1.3.3.9; Busetto and Ranzhetti 2016).

To test the effect of road use for visitation on wolf resource selection, we collected average daily traffic (ADT) estimates from the Transportation and Vehicle Mobility report (Otak 2017). The study placed automatic traffic counters along every major road segment of the park for 3 d in August of 2015 (Fig. 1). These road counter data coupled with data on individual visitor driving habits were used to estimate the relative difference in use on each road segment in the park (Otak 2017). We combined this information with known visitation numbers from each park entrance to scale ADT estimates for the rest of the time period within this study following Eq. 1:

$$\frac{\text{ADT}_{x,t}}{v_t} = \frac{\alpha_{x,2015}}{v_{2015}} \quad (1)$$

where the ratio of ADT for road segment x , during month t , to park visitation estimate from entrance station vehicle counts v , during month t , is proportional to the ratio between estimated vehicle volumes from road traffic counters α or road segment x in August of 2015 to the estimated total park visitation from entrance station vehicle counts v in August 2015. Therefore, ADT was spatially assigned to each road segment in the study area and these estimates are temporally distinct by month and year. To estimate vehicle traffic at night, we examined hourly vehicle counts from entrance stations and found that average night traffic was approximately 5% of daytime traffic (NPS, unpublished data). Thus, nighttime ADT was multiplied by 0.05 to reflect this temporal change. For each used and available wolf location, we identified the closest road segment and assigned the corresponding ADT values based on the month in which the GPS fix occurred.

We also included a road view metric that would account for the wolves' ability to see or hear the roadway. This also predicted locations where visitors were more likely to be positioned

watching or looking for wolves. The road view metric was created by calculating the average openness value along a line identified by the Euclidean distance between each used or available location and the closest site on the road. Openness values ranged from 0 (deep forest) to 289 (open grassland) and were calculated from the sum of non-forested pixels within a 500-m² moving window centered on each pixel (see Kohl et al. 2018 for more information).

To control for the possible influence of prey availability on wolf habitat selection, we built an SSF for elk and used the output as a covariate in our wolf SSF model. We applied the same methodology to generate available locations as we did for wolf GPS locations (see *Wolf step selection function*; Forester et al. 2009, Thurfjell et al. 2014). We evaluated the effect of spatial and temporal variables on elk resource selection following similar methods described for wolves, using conditional logistic regression models via the clogit call in the survival package (Therneau 2015), and fitting generalized estimating equations to account for autocorrelation (Prima et al. 2017). Elk resource selection results, including model selection tables (Appendix S2: Tables S1–S9), beta parameter plots from top models (Appendix S2: Fig. S1), fivefold cross-validation results (Appendix S2: Tables S2–S9), and prediction surface maps (Appendix S2: Figs. S2–S10), can be found in supplemental information sections.

Wolf step selection function

Wolf resource selection can be predicted by topographic attributes, habitat type, prey availability, and anthropogenic influences (Thurber et al. 1994, Mladenoff et al. 1995, Whittington et al. 2005, Hebblewhite and Merrill 2008, Uboni et al. 2015). We applied a used-available framework common in SSF analyses, setting wolf GPS locations from collared wolves as used and matching each to four randomly generated available locations to form matched-case-control sets (Thurfjell et al. 2014). Available points were generated using random sampling of step lengths and turning angles from the used GPS data set (Forester et al. 2009). This matched-case-control method for generating available locations can minimize autocorrelation issues common in temporal and spatial data (Whittington et al. 2005, Craiu et al. 2008). Since Hebblewhite and Merrill

(2008) displayed significant correlation among wolf resource selection between individuals within the same pack, we modeled random slopes and intercepts at the pack level using mixed effects conditional logistic regression (MCLR) models in the R package *coxme* (Hebblewhite and Merrill 2008, Duchesne et al. 2010, Therneau 2018). Akaike's information criterion (AIC) was used to select the most parsimonious MCLR model, and parameter estimates were averaged for models $\leq \Delta 4$ AIC of top models (Appendix S1: Tables S3–S8).

We investigated wolf habitat selection during May–October because 96% of annual human visitation to YNP takes place during this time (NPS 2018). We partitioned our data and modeling procedure into nine temporal divisions (Hebblewhite and Merrill 2008, Kohl et al. 2018). Since elk are the primary prey for wolves (Metz et al. 2012) and ungulates display seasonal shifts in resource selection (Mao et al. 2005, Basille et al. 2013), we expected seasonal changes in predator and prey resource selection to correspond (Barnett and Semmens 2012). These included three diel periods (day, night, and crepuscular) in each of the three seasons we considered (spring, summer, and fall). The cut points for these seasons were identified by closely inspecting each individual elk's yearly movement to identify the day(s) of the year they migrated to and from their respective summer ranges. We then averaged these elk migration dates to identify the mean ordinal date that elk shifted to and from their summer ranges to subset the data into three seasons: spring, summer, and fall. Spring migration began on May 24. The summer season started on May 31 and ended on October 4. The fall season began on October 13 and extended through the end of our study period November 1. We used these average elk migration dates to determine the break points for seasons in the wolf SSF. Diel periods were identified by assigning dawn and dusk times, based on astronomical twilight, for each GPS location using the *maptools* package in R (Bivand et al. 2016). For the crepuscular periods, we placed a 1-h buffer before and after these dawn and dusk times. Day hours took place from dawn until dusk, and night hours took place from dusk until dawn, accounting for those 1-h buffers.

We investigated the relative probability of selection for landscape patches by wolves based on ecologically informed combinations and interactions of covariates resulting in 17 distinct model formulations for the nine diel period and season combinations (Appendix S1: Table S2). All models included a log-transformed distance to road covariate, along with different combinations of the covariates described in the following section. We also included interaction terms between the elk SSF and slope or habitat type to understand if wolf foraging behavior for elk is connected to terrain attributes (Kohl et al. 2018). In addition, we included an interaction between elk SSF values and distance to road to see whether wolves were directly weighing foraging opportunities with potential risks associated with the roadway. In addition to the spatial variation in the use of areas close to the human-dominated roadway, we expected selection to vary based on the amount of vehicle and wildlife watching use. Average daily traffic (see *SSF covariates* section) was used in an interaction term with the log-transformed road distance to account for the conditional effect of varying road use. We tested for an interaction between road view (see *SSF covariates* section) and log-transformed road distance. Prior to fitting models, we standardized all continuous covariates (distance to road, ADT, slope, distance to water, probability of prey encounter [from elk SSF], and road view) to mean = 0 and standard deviation = 1 (Schielzeth 2010). We tested collinearity of model covariates by creating correlation matrices. We only used variables with correlation values less than 0.60. This was particularly important for the elk SSF layer, which was not collinear with any of the other covariates used in the wolf SSF.

RESULTS

We found a significant effect of road attributes on wolf habitat selection. Wolves were more likely to select habitat closer to the road when there was low visibility to the road (road view was low) but avoided the road when bordering habitat was open (road view was high; Fig. 2). However, the level of attraction or avoidance to the road given varying road view values exhibited significant variation among the diel periods and seasons. We found better model fit when taking the natural

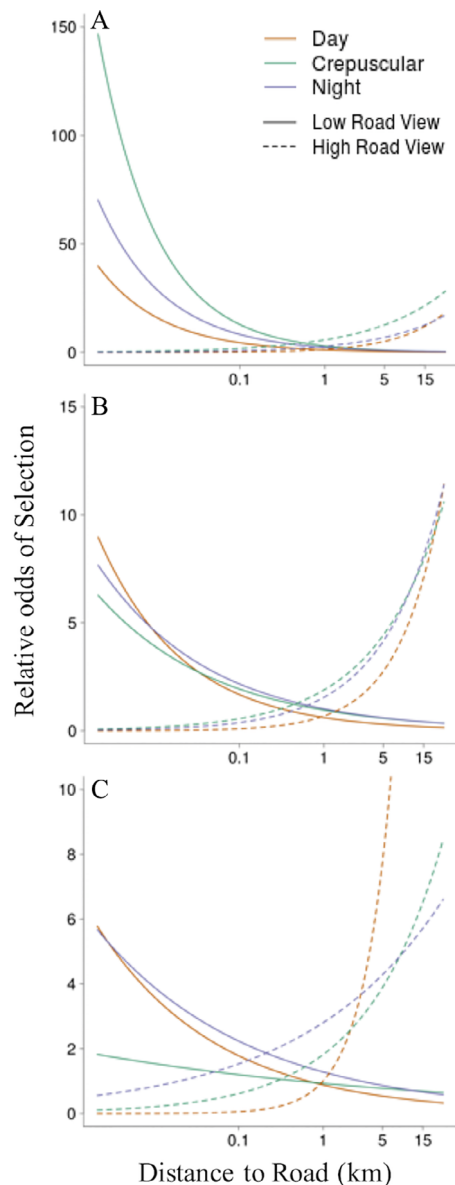


Fig. 2. Plot showing relative odds of selection based on the wolf's distance to road and the road view value. Panels represent different seasons: spring (A), summer (B), and fall (C). Orange lines represent day, green lines represent crepuscular, and purple lines represent night hours. Solid lines represent the odds of selection given Road View is low (habitat is closed), the dashed lines represent selection when Road View is high (habitat is open). Selection for lower x -axis values (smaller distances to road) indicates selection for areas closer to the road. It is important to note that y -axes value ranges differ between seasonal plots.

log-transformation of the distance to road covariate, which adequately accounted for the nonlinear relationship. The most parsimonious MCLR model across all seasons and diel periods included an interaction term between log-transformed distance to road and road view (Table 1; Appendix S1: Tables S3–S5).

We calculated odds ratios for selection coefficients at 50 m because current YNP regulations prohibit humans to approach or remain within 100 m of wolves, allowing direct insight on current protections against wolf habituation. During both summer and fall, wolves were more likely to select areas closer to the road when the road view was blocked during day and night when compared to crepuscular hours. During summer days, when the road view was blocked, wolves were 41.7 (95% CI: 40.6, 42.9) times more likely to use an area 50 m from the road than if the road view was open. When human activity lessened during crepuscular and night hours, the odds ratio changed to 6.0 (95% CI: 4.6, 7.5) and 10.6 (95% CI: 9.6, 11.6), respectively, for an area with the same distance to road and road view metrics. This trend persisted until odds ratios were equivalent for open and blocked road views at around 1 km, 750 m, and 850 m during day, crepuscular, and night hours, respectively (Fig. 2). Further, when the road view was open, wolves were 3.5 (95% CI: 2.5, 4.4) times more likely to select for an area 1 km instead of 50 m from the roadway. Relative to spring, the differences were not as pronounced. In spring, the odds of an animal choosing a patch closer to the road with high vegetative cover blocking the view to the road were considerably lower during the day and increased during the night and into crepuscular times (Fig. 2; Appendix S1: Tables S6–S8). For example, during spring days, wolves were 67.3 (95% CI: 66.5, 68.1) times more likely to use an area 50 m from a road if the road view was blocked than if the road view was open. During crepuscular and night hours, odds of selection for this type of habitat changed to 19.9 (95% CI: 17.8, 22.0) and 29.0 (95% CI: 27.8, 30.2), respectively. This decline in the spring season odds ratios during crepuscular and night hours is due to the overall higher odds of selection for closer distances to the road, diminishing the differences between open and closed road views.

Table 1. Model selection results for MCLR models demonstrating the relationship between wolf resource selection and seven spatial and/or temporal landscape metrics.

Model rank	Model specification	Season	Diel period	AIC	Δ AIC
1	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Slope + Road View + Distance to Road \times Road View	Spring	Day	4914.88	0
2	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Habitat Type + Road View + Distance to Road \times Road View			4931.63	16.75
3	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance to Road \times Road View			4936.4	21.52
1	Distance to Road + Slope + Aspect + Habitat Type + Road View + Distance to Road \times Road View	Spring	Crepuscular	911.17	0
2	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Slope + Road View + Distance to Road \times Road View			911.95	0.78
3	Distance to Road + Slope + Aspect + Road View + Distance to Road \times Road View			912.53	1.35
1	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Habitat Type + Road View + Distance to Road \times Road View	Spring	Night	6040.36	23.41
2	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Slope + Road View + Distance to Road \times Road View			6040.36	23.41
3	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance to Road \times Road View			6059.84	42.89
1	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Slope + Road View + Distance to Road \times Road View	Summer	Day	16,494.96	0
2	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance to Road \times Road View			16,511.96	16.99
3	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Slope + Road View + Distance to Road \times Road View			16,513.85	18.89
1	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance to Road \times Road View	Summer	Crepuscular	3875.35	0
2	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Slope + Road View + Distance to Road \times Road View			3876.81	1.46
3	Distance to Road + Slope + Aspect + Habitat Type + Road View + Distance to Road \times Road View			3876.99	1.64
1	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Habitat Type + Road View + Distance to Road \times Road View	Summer	Night	21,211.62	0
2	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Slope + Road View + Distance to Road \times Road View			21,217.85	6.23
3	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance to Road \times Road View			21,219.22	7.6
1	Distance to Road + Slope + Aspect + Elk RSF + Road View + Distance to Road \times Road View	Fall	Day	1034.65	0
2	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance to Road \times Road View			1038.09	3.44
3	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Slope + Road View + Distance to Road \times Road View			1040.07	5.42
1	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance to Road \times Road View	Fall	Crepuscular	1054.18	0
2	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Slope + Road View + Distance to Road \times Road View			1056.18	2
3	Distance to Road + Slope + Aspect + Habitat Type + Road View + Distance to Road \times Road View			1057.93	3.75

(Table 1. Continued.)

Model rank	Model specification	Season	Diel period	AIC	Δ AIC
1	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Elk RSF \times Slope + Road View + Distance to Road \times Road View	Fall	Night	2283.92	0
2	Distance to Road + Slope + Aspect + Elk RSF + Road View + Distance to Road \times Road View			2284.65	0.73
3	Distance to Road + Slope + Aspect + Habitat Type + Elk RSF + Road View + Distance to Road \times Road View			2285.46	1.54

Notes: AIC, Akaike's information criterion; MCLR, mixed effects conditional logistic regression. This table shows only the top three models for each of the nine seasons and diel period combinations. Full model selection tables can be seen in Appendix S1: Tables S2–S5. All models include a random intercept and slope for each wolf pack's habitat selection relationship to distance to road. The covariate combination used in each model's specification, AIC, and change in AIC from top model (Δ AIC) is shown for each season and diel period.

We found significant variation across wolf packs in their response to the road corridor. Two packs within the study area (Blacktail Plateau and Lamar Canyon) displayed significantly different selection, favoring areas closer to the road, while other packs avoided areas near the road (Fig. 3). During the spring, the Blacktail Plateau pack was 5.2 (95% CI: 4.8, 5.7) times more likely than the Junction Butte pack (representative of most of the other wolf packs besides Blacktail Plateau and Lamar Canyon) to be 50 m instead of 1 km from the road. While all wolf packs increased selection closer to the road in spring crepuscular and night hours (Fig. 3), the Blacktail Plateau wolves displayed greater preference for these closer distances and were 2.4 (95% CI: 2.0, 2.8) and 3.9 (95% CI: 3.3, 4.5) times more likely to select these areas when compared to the Junction Butte pack. Compared to spring, summer selection displayed a considerable shift to farther distances from the roadway for all packs when visitation numbers are at their peak (Fig. 3; NPS 2018). The Lamar Canyon pack displayed the most affinity for close distances to the road during summer where they were 4.2 (95% CI: 3.5, 4.9) and 4.2 (95% CI: 3.6, 4.8) times more likely than the Junction Butte pack to select an area 50 m from the road during day and night hours, respectively. Interestingly, there was no significant variation in distance to road selection during summer crepuscular hours, with wolf packs 1.6 (95% CI: 0.23, 3.0) times more likely to use an area 1 km than 50 m from the roadway (Fig. 3). In the fall, the variation among packs in the effect of the road lessened and wolves were on average 4.9 (95% CI: 2.8, 7.0), 1.8 (95% CI: 0,

3.7), and 1.1 (95% CI: 0, 2.5) more likely to select an area 1 km instead of 50 m from the road in day, crepuscular, and night hours, respectively (Fig. 3). Further, neither ADT nor the elk SSF significantly influenced wolf resource selection.

DISCUSSION

We found that wolves selected against habitat close to the road corridor in YNP when there was insufficient vegetative cover blocking their view of the roadway. Wolves selected areas closer to the road at night and crepuscular times when human activity decreased (Figs. 2, 3). In addition, wolves avoided the road more during the day than at night and crepuscular hours when road traffic decreased substantially. This pattern was most dramatic in spring when snow levels limit efficient wolf movement into the farther reaches of the study area, drawing them toward the low-cost movement path of the road corridor (Whittington et al. 2005). This season also takes place prior to elk spring migration, and wolves may be able to maximize encounter rates with prey closer to the road since elk have been shown to select road corridors in other studies (Kauffman et al. 2007, Whittington et al. 2011, Courbin et al. 2013).

The impact of roads and their associated human activity on wildlife in protected areas is often overlooked because road densities are low compared to more human-dominated landscapes. However, the availability of high-quality habitat adjacent to roads can lead to greater vulnerability of local wildlife to negative impacts of the road (Bernardino and Dalrymple 1992,

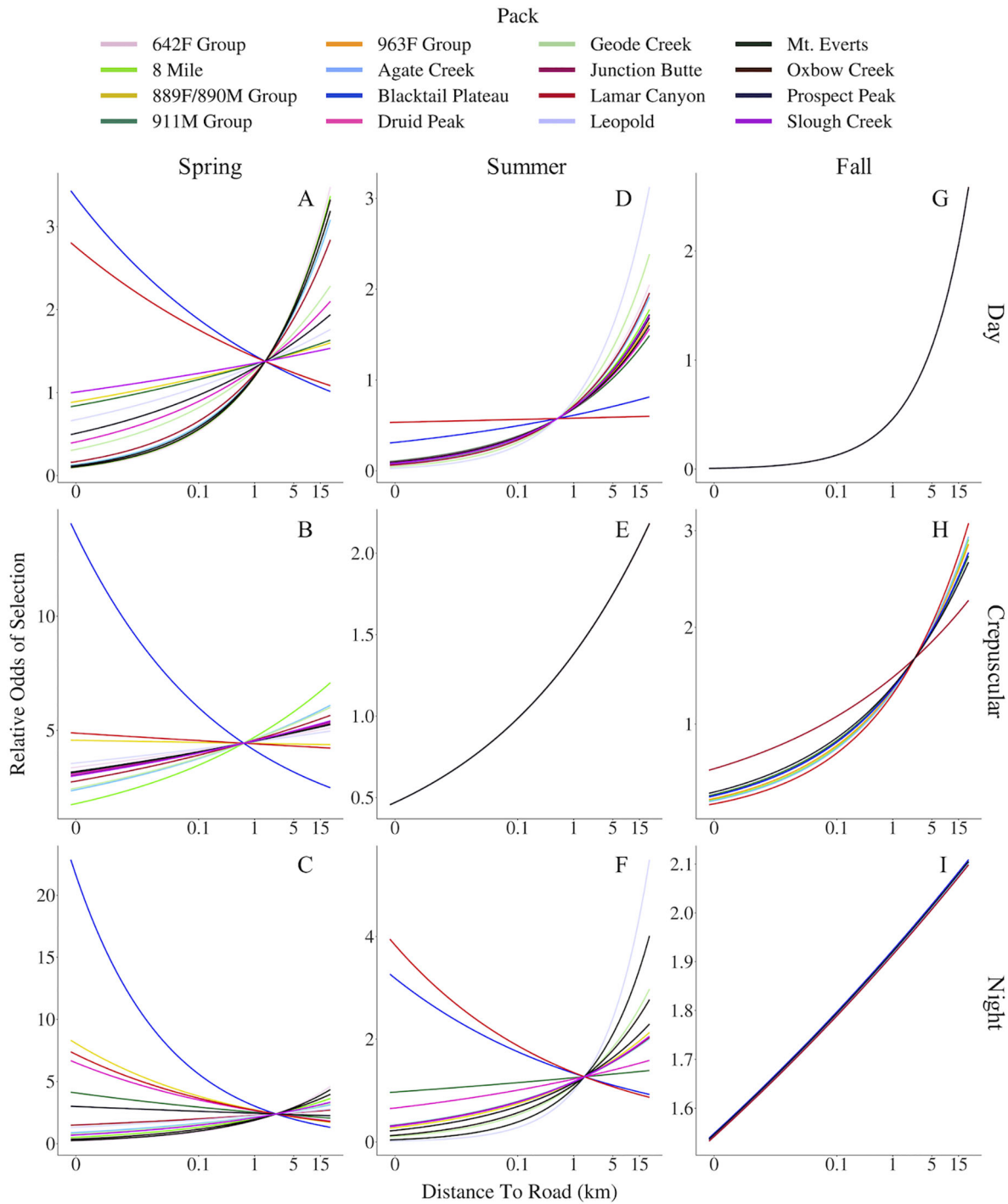


Fig. 3. Results from mixed effects conditional logistic regression modeling with random intercepts and slopes for each pack's distance to road relationship. Panels represent different seasonal and diel period combinations. Seasons are aligned in columns: spring selection in panels A–C, summer in panels D–F, and fall in panels G–I. Diel periods are separated by rows: day panels in A, D, and G; crepuscular in B, E, and H; and night in panels C, F, and I.

Drews 1995, Kline and Swann 1998, Ament et al. 2008, Garriga et al. 2012, Bateman and Fleming 2017). In the Bow River Valley of Banff National Park, wolves began to change habitat use patterns when visitation exceeded 100 people per month, and wolves abandoned favorable habitat when visitation topped 10,000 people per month (Paquet et al. 1996). We expected ADT to be a reasonable approximation of human activity along the roadway that would help explain wolves' spatial and temporal relationship with the road corridor. However, ADT was not chosen through model selection routines in any seasonal and diel period combination. Though the inclusion of the ADT covariate did not provide significant adjustment on wolf selection coefficients for differing distances to the road, the inherent fluctuations in diel-specific visitor use (high during the day and low during the night) may be sufficient to draw conclusions on the impact of human activity along the road (Figs. 2, 3). Nevertheless, this pattern is not homogeneous across all wolf packs and our results show that two packs responded differently to human activity associated with the roadway.

The Lamar Canyon and Blacktail Plateau packs exhibited less avoidance of the road than other packs in the study area (Fig. 3). The Lamar Canyon pack resides primarily in Lamar Valley, a famous wildlife watching area in the northeastern section of the park (N. Varley et al., *unpublished manuscript*). Historically, this area has received the most wolf watching use and the Lamar Canyon wolves have been exposed to substantial human presence at close distances to the road. In addition, this wolf pack often established natal den sites close to the roadway leading to frequent habitat selection close to the road. Similarly, the Blacktail Plateau pack received relatively high visitor viewing pressure compared to most packs used in this study. Moreover, the founding members of the Blacktail Plateau pack originated from packs that utilized areas similar to Lamar Canyon wolves, possibly carrying over some of these learned responses. These repeated human-wolf interactions without adverse consequences, sometimes with hundreds of people at a time, likely led to greater tolerance of humans at close distances to the road. This habituation may have contributed to greater harvest vulnerability because several

individuals from these packs were harvested or illegally shot outside the park in 2011, 2012, and 2018 (Smith et al. 2016).

In addition to testing for anthropogenic influences, we wanted to understand if prey availability would be a driving force in determining wolf habitat use. Optimal foraging theory suggests individuals will select habitat that provides access to food resources (Pyke et al. 1977). Interestingly, the addition of the elk SSF did not significantly help explain wolf habitat-use patterns. Future research will incorporate tri-axial accelerometer data to examine wolf behavior-specific SSF in relation to the elk SSF.

CONCLUSIONS

Wolves' reactions to human activity are shaped by the cumulative sum of repeated interactions with humans and the consequences of these interactions (Whittaker and Knight 1998, McNay 2002, Bejder et al. 2009). For some wolves in YNP, innocuous interactions with humans occur regularly as wolves traverse portions of the landscape along roadways where human use is concentrated and has increased. Nonetheless, an extensive study on YNP visitor values in 2016 found that 83% of respondents stated viewing wildlife in their natural habitat as a primary reason for visiting the park and half of all visitors surveyed rated wolves as "extremely important" to their experience in the park (Resource Systems Group 2017). In addition, wolf-centric ecotourism continues to increase in the Yellowstone area and generates tens of millions of dollars annually in the regional economy (Duffield et al. 2008; N. Varley et al., *unpublished manuscript*). However, our findings indicate human activity along roads in YNP can influence habitat selection decisions by wolves. Thus, visitor use, wolf management, and regional socioeconomics are inextricably entwined. In addition, our findings suggest high visitor use along roads in YNP may result in some wolves becoming less wary of people, which could increase their risk of being harvested if they leave the park during hunting seasons in surrounding states. Moreover, these patterns are broadly applicable beyond national parks and protected areas where roads may intersect high-quality habitat, leading to alterations in wolf behavior.

Because most of YNP is managed as wilderness (92% of land area) with no public roads, relatively low and stable human backcountry use (Gunther et al. 2017), and designated campsites, many animals have limited exposure to people. For wolves living in YNP, some packs occupy territories largely in remote areas removed from human activity, while other packs' territories overlap extensively with the road corridor resulting in more frequent human encounters. We suggest that due to both variation in human exposure and individual wolves' tolerance to human activity, impacts on wolf behavior in YNP vary in significance.

Park managers have implemented several measures to mitigate specific disturbance effects to wolves, including closed areas around dens, no-stopping areas along roadways frequently crossed by wolves, and requiring people to stay at least 100 m from wolves. They have implemented a management plan to discourage excessive habituation and, in collaboration with Yellowstone Forever (an official non-profit education and fund-raising partner), supervised two employees to monitor wolves and manage visitor behavior in key wolf-watching areas. Park managers also coordinate regularly with state managers to discuss the trans-boundary management of wolves. These discussions have contributed to modest quotas and harvests of wolves in hunting areas along the boundary of YNP (Smith et al. 2016). Even though population-level impacts were not identified in our study, nor were individual-fitness impacts evaluated, our results provide new information on wolf responses to human activity along the roadways. This knowledge may aid both future researches on visitor impacts, as well as guide adaptive management that seeks to continue conserving natural wolf behavior, while providing positive visitor experiences.

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LITERATURE CITED

- Ament, R., A. P. Clevenger, O. Yu, and A. Hardy. 2008. An assessment of road impacts on wildlife populations in U.S. national parks. *Environmental Management* 42:480–496.
- Baldwin, R. A., and L. C. Bender. 2008. Den-site characteristics of black bears in Rocky Mountain National Park, Colorado. *Journal of Wildlife Management* 72:1717–1724.
- Barnett, A., N. L. Payne, J. M. Semmens, and R. Fitzpatrick. 2016. Ecotourism increases the field metabolic rate of whitetip reef sharks. *Biological Conservation* 199:136.
- Barnett, A., and J. M. Semmens. 2012. Sequential movement into coastal habitats and high spatial overlap of predator and prey suggest high predation pressure in protected areas. *Oikos* 121:882–890.
- Basille, M., D. Fortin, C. Dussault, J.-P. Ouellet, and R. Courtois. 2013. Ecologically based definition of seasons clarifies predator–prey interactions. *Ecography* 36:220–229.
- Bateman, P. W., and P. A. Fleming. 2017. Are negative effects of tourist activities on wildlife over-reported? A review of assessment methods and empirical results. *Biological Conservation* 211:10–19.
- Bejder, L., A. Samuels, H. Whitehead, H. Finn, and S. Allen. 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. *Marine Ecology Progress Series* 395:177–185.
- Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters* 3:620–623.
- Bernardino, F. S., and G. H. Dalrymple. 1992. Seasonal activity and road mortality of the snakes of the Pahay-okee wetlands of Everglades National Park, USA. *Biological Conservation* 62:71–75.
- Bivand, R., et al. 2016. Tools for reading and handling spatial objects: package “mapproj”. R Documentation. <https://cran.r-project.org/web/packages/mapproj/index.html>
- Borg, B. L., S. M. Arthur, N. A. Broman, K. A. Cassidy, R. McIntyre, D. W. Smith, and L. R. Prugh. 2016.

- Implications of harvest on the boundaries of protected areas for large carnivore viewing opportunities. *PLOS ONE* 11:e0153808.
- Borg, B. L., S. M. Brainerd, T. J. Meier, and L. R. Prugh. 2015. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. *Journal of Animal Ecology* 84:177–187.
- Borkowski, J. J., P. J. White, R. A. Garrott, T. Davis, A. R. Hardy, and D. J. Reinhart. 2006. Behavioral responses of bison and elk in yellowstone to snowmobiles and snow coaches. *Ecological Applications* 16:1911–1925. [https://doi.org/10.1890/1051-0761\(2006\)016\[1911:BROBAE\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1911:BROBAE]2.0.CO;2)
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modelling* 157:281–300.
- Busetto, L., and L. Ranghetti. 2016. MODISTsp: An R package for automatic preprocessing of MODIS Land Products time series. *Computers & Geosciences* 97:40–48.
- Chruszcz, B., A. P. Clevenger, K. E. Gunson, and M. L. Gibeau. 2003. Relationships among grizzly bears, highways, and habitat in the Banff-Bow Valley, Alberta, Canada. *Canadian Journal of Zoology* 81:1378–1391.
- Clark, J., and D. McCool. 1985. Staking out the terrain: Power differentials among natural resource management agencies. State University of New York Press, Albany, New York, USA.
- Courbin, N., D. Fortin, C. Dussault, V. Fargeot, and R. Courtois. 2013. Multi-trophic resource selection function enlightens the behavioural game between wolves and their prey. *Journal of Animal Ecology* 82:1062–1071.
- Craiu, R. V., T. Duchesne, and D. Fortin. 2008. Inference methods for the conditional logistic regression model with longitudinal data. *Biometrical Journal* 50:97–109.
- Creel, S., J. E. Fox, A. Hardy, J. Sands, B. Garrott, and R. O. Peterson. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. *Conservation Biology* 16:809–814.
- D'Amico, M., S. Périquet, J. Román, and E. Revilla. 2016. Road avoidance responses determine the impact of heterogeneous road networks at a regional scale. *Journal of Applied Ecology* 53:181–190.
- Didan, K. 2015. MOD13A1 MODIS/Terra Vegetation Indices 16-Day L3 Global 500m SIN Grid V006. NASA EOSDIS LP DAAC. <https://lpdaac.usgs.gov/products/mod13a1v006/>
- Draws, C. 1995. Road kills of animals by public traffic in Mikumi National Park, Tanzania, with notes on baboon mortality. *African Journal of Ecology* 33:89–100.
- Duchesne, T., D. Fortin, and N. Courbin. 2010. Mixed conditional logistic regression for habitat selection studies. *Journal of Animal Ecology* 79:548–555.
- Duffield, J. W., C. J. Neher, and D. A. Patterson. 2008. Wolf recovery in Yellowstone: park visitor attitudes, expenditures, and economic impacts. *George Wright Forum* 25:13–19.
- Ehlers, L. P. W., C. J. Johnson, and D. R. Seip. 2014. Movement ecology of wolves across an industrial landscape supporting threatened populations of woodland caribou. *Landscape Ecology* 29:451–465.
- Elbroch, L. M., P. E. Lendrum, M. L. Allen, and H. U. Wittmer. 2015. Nowhere to hide: pumas, black bears, and competition refuges. *Behavioral Ecology* 26:247–254.
- Forester, J. D., H. K. Im, and P. J. Rathouz. 2009. Accounting for animal movement in estimation of resource selection functions: sampling and data analysis. *Ecology* 90:3554–3565.
- Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29:207–231.
- Fortin, D., and M. Andruskiw. 2003. Behavioral response of free-ranging bison to human disturbance. *Wildlife Society Bulletin* 31:804–813.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320–1330.
- French, S. S., M. González-Suárez, J. K. Young, S. Durham, and L. R. Gerber. 2011. Human disturbance influences reproductive success and growth rate in California sea lions (*Zalophus californianus*). *PLOS ONE* 6:e17686.
- Fritts, S. H., et al. 2001. Outcomes of hard and soft releases of reintroduced wolves in central Idaho and the Greater Yellowstone Area. Pages 125–147 in D. Maehr, editor. Large mammal restoration. Island Press, Washington, D.C., USA.
- Fritts, S. H., E. E. Bangs, J. A. Fontaine, M. R. Johnson, M. K. Phillips, E. D. Koch, and J. R. Gunson. 1997. Planning and implementing a reintroduction of wolves to Yellowstone National Park and central Idaho. *Restoration Ecology* 5:7–27.
- Fuller, T. K., W. E. Berg, G. L. Radde, M. S. Lenarz, and G. Blair Joselyn. 1992. A history and current estimate of wolf distribution and numbers in Minnesota. *Wildlife Society Bulletin* 20:42–55.
- Garriga, N., X. Santos, A. Montori, A. Richter-Boix, M. Franch, and G. A. Llorente. 2012. Are protected areas truly protected? The impact of road traffic on vertebrate fauna. *Biodiversity and Conservation* 21:2761–2774.

- Gaynor, K. M., C. E. Hohnowski, N. H. Carter, and J. S. Brashares. 2018. The influence of human disturbance on wildlife nocturnality. *Science* 360:1232–1235.
- Gunther, K., D. Tyers, T. Coleman, K. R. Wilmot, and P. J. White. 2017. Current management strategy. Pages 131–151 in P. J. White, K. Gunther, F. Van Manen, and J. A. Jerrett, editors. *Yellowstone grizzly Bears: ecology and conservation of an icon of wildness*. Yellowstone Forever and Yellowstone National Park, Mammoth, Wyoming, USA.
- Hebblewhite, M., and E. Merrill. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* 45:834–844.
- Hebblewhite, M., C. A. White, C. G. Nietvelt, J. A. McKenzie, T. E. Hurd, J. M. Fryxell, S. E. Bayley, and P. C. Paquet. 2005. Human activity mediates a trophic cascade caused by wolves. *Ecology* 86:2135–2144.
- Hijmans, R. J., and J. van Etton. 2012. raster: Geographic analysis and modeling with raster data. R package version 2.0–12. <https://cran.r-project.org/web/packages/raster/index.html>
- Houle, M., D. Fortin, C. Dussault, R. Courtois, and J.-P. Ouellet. 2010. Cumulative effects of forestry on habitat use by gray wolf (*Canis lupus*) in the boreal forest. *Landscape Ecology* 25:419–433.
- Kauffman, M. J., N. Varley, D. W. Smith, D. R. Stahler, D. R. MacNulty, and M. S. Boyce. 2007. Landscape heterogeneity shapes predation in a newly restored predator–prey system. *Ecology Letters* 10:690–700.
- Keiter, R. B. 2013. *To conserve unimpaired: the evolution of the national park idea*. Island Press, Washington, D.C., USA.
- Kerley, L. L., J. M. Goodrich, D. G. Miquelle, E. N. Smirnov, H. B. Quigley, and M. G. Hornocker. 2002. Effects of roads and human disturbance on Amur tigers. *Conservation Biology* 16:97–108.
- Kline, N. C., and D. E. Swann. 1998. Quantifying wildlife road mortality in Saguaro National Park. Pages 23–31 in G. Evink, P. Garrett, D. Zeigler, and J. Berry, editors. *International conference on wildlife ecology and transportation*. FL-ER-69-98, Florida Department of Transportation, Tallahassee, Florida, USA.
- Knight, J. 2009. Making wildlife viewable: habituation and attraction. *Society & Animals* 17:167–184.
- Knight, R. L., and D. N. Cole. 1991. Effects of recreational activity on wildlife in wildlands. *Transactions of the North American Wildlife and Natural Resources Conference* 56: 238–247.
- Kohl, M. T., D. R. Stahler, M. C. Metz, J. D. Forester, M. J. Kauffman, N. Varley, P. J. White, D. W. Smith, and D. R. MacNulty. 2018. Diel predator activity drives a dynamic landscape of fear. *Ecological Monographs* 88:638–652.
- Krofel, M., I. Kos, and K. Jerina. 2012. The noble cats and the big bad scavengers: effects of dominant scavengers on solitary predators. *Behavioral Ecology and Sociobiology* 66:1297–1304.
- Latham, A. D. M., M. C. Latham, M. S. Boyce, and S. Boutin. 2011. Movement responses by wolves to industrial linear features and their effect on woodland caribou in northeastern Alberta. *Ecological Applications* 21:2854–2865.
- Lemke, T. O. 2004. Origin, expansion, and status of mountain goats in Yellowstone National Park. *Wildlife Society Bulletin* 32:532–541.
- Lesmerises, F., C. Dussault, and M. H. St-Laurent. 2012. Wolf habitat selection is shaped by human activities in a highly managed boreal forest. *Forest Ecology and Management* 276:125–131.
- Liliehalm, R. J., and L. R. Romney. 2000. Tourism, national parks and wildlife. Pages 137–152 in R. W. Butler and S. W. Boyd, editors. *Tourism and national parks: Issues and implications*. Wiley, New York, New York, USA.
- Llaneza, L., E. J. García, V. Palacios, V. Sazatornil, and J. V. López-Bao. 2016. Resting in risky environments: the importance of cover for wolves to cope with exposure risk in human-dominated landscapes. *Biodiversity and Conservation* 25:1515–1528.
- Manly, B. F. L., L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. *Resource selection by animals: statistical design and analysis for field studies*. Second edition. Kluwer, Norwell, Massachusetts, USA.
- Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management* 69:1691–1707.
- McClung, M. R., P. J. Seddon, M. Massaro, and A. N. Setiawan. 2004. Nature-based tourism impacts on yellow-eyed penguins *Megadyptes antipodes*: Does unregulated visitor access affect fledging weight and juvenile survival? *Biological Conservation* 119:279–285.
- McNay, M. E. 2002. Wolf-human interactions in Alaska and Canada: a review of the case. *Wildlife Society Bulletin* 30:831–843.
- Merkle, J. A., K. L. Monteith, E. O. Aikens, M. M. Hayes, K. R. Hersey, A. D. Middleton, B. A. Oates, H. Sawyer, B. M. Scurlock, and M. J. Kauffman. 2016. Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences* 283:20160456.
- Metz, M. C., D. W. Smith, J. A. Vucetich, D. R. Stahler, and R. O. Peterson. 2012. Seasonal patterns of

- predation for gray wolves in the multi-prey system of Yellowstone National Park. *Journal of Animal Ecology* 81:553–563.
- Mladenoff, D. J., T. A. Sickley, R. G. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology* 9:279–294.
- Monz, C., A. D'Antonio, S. Lawson, J. Barber, and P. Newman. 2016. The ecological implications of visitor transportation in parks and protected areas: Examples from research in US National Parks. *Journal of Transport Geography* 51:27–35.
- National Park Service Organic Act of 1916. <https://uslaw.link/citation/us-law/public/64/235>
- National Park Service. 2018. National Park Service visitor use statistics. <https://irma.nps.gov/Stats/Reports/Park/YELL>
- Northrup, J. M., J. Pitt, T. B. Muhly, G. B. Stenhouse, M. Musiani, and M. S. Boycet. 2012. Vehicle traffic shapes grizzly bear behaviour on a multiple-use landscape. *Journal of Applied Ecology* 49:1159–1167.
- Noss, R. F., H. B. Quigley, M. G. Hornocker, T. Merrill, and P. C. Paquet. 2003. Conservation biology and carnivore conservation in the Rocky Mountains. *Conservation Biology* 10:949–963.
- Ordiz, A., O. G. Støen, M. Delibes, and J. E. Swenson. 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. *Oecologia* 166:59–67.
- Otak. 2017. Yellowstone National Park transportation and vehicle mobility study: data collection and analysis. National Park Service, Wyoming, USA. https://www.nps.gov/yell/getinvolved/upload/Yellowstone-Transportation-Mobility-Study_lo-res.pdf
- Paquet, P. C., J. Wierzchowski, and C. Callaghan. 1996. Effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. *In* J. Green, C. Pacas, S. Bayley, and L. Cornwell, editors. A cumulative effects assessment and futures outlook for the Banff Bow Valley. Banff Bow Valley Study. Department of Canadian Heritage, Ottawa, Ontario, Canada.
- Penteriani, V., J. V. López-Bao, C. Bettega, F. Dalerum, M. M. Delgado, K. Jerina, I. Kojola, M. Krofel, and A. Ordiz. 2017. Consequences of brown bear viewing tourism: A review. *Biological Conservation* 206:169–180.
- Person, D. K., and A. L. Russell. 2008. Correlates of mortality in an exploited wolf population. *Journal of Wildlife Management* 72:1540–1549.
- Pressey, R. L., P. Visconti, and P. J. Ferraro. 2015. Making parks make a difference: poor alignment of policy, planning and management with protected-area impact, and ways forward. *Philosophical Transactions of the Royal Society B: Biological Sciences* 370:20140280.
- Prima, M.-C., T. Duchesne, and D. Fortin. 2017. Robust inference from conditional logistic regression applied to movement and habitat selection analysis. *PLOS ONE* 12:e0169779.
- Pyke, G. H., H. R. Pulliam, and E. L. Charnov. 1977. Optimal Foraging Theory : A selective review of theory and tests. *Quarterly Review of Biology* 52:137–154.
- Resource Systems Group. 2017. Yellowstone National Park visitor use study. Resource Systems Group, White River Junction, Vermont, USA.
- Riley, S. P. D., J. P. Pollinger, R. M. Sauvajot, E. C. York, C. Bromley, T. K. Fuller, and R. K. Wayne. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. *Molecular Ecology* 15:1733–1741.
- Ripple, W. J., et al. 2014. Status and ecological effects of the world's largest carnivores. *Science* 343:1241484.
- Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution* 1:103–113.
- Sinclair, A. R. E. 1998. Natural regulation of ecosystems in protected areas as ecological baselines. *Wildlife Society Bulletin* 26:399–409.
- Sirost, E. 2010. Should risk allocation strategies facilitate or hinder habituation to nonlethal disturbance in wildlife? *Animal Behaviour* 80:737–743.
- Smith, D. W., and E. E. Bangs. 2009. Reintroduction of wolves to Yellowstone National Park: history, values, and ecosystem restoration. Pages 92–125 *in* M. W. Hayward and M. J. Somers, editors. Reintroduction of top-order predators. Wiley-Blackwell, Oxford, UK.
- Smith, D. W., D. R. Stahler, and D. S. Guernsey. 2003. Yellowstone Wolf Project: Annual Report, 2002. Yellowstone National Park, Mammoth, Wyoming, USA.
- Smith, D., D. Stahler, E. Stahler, M. Metz, K. Cassidy, K. Cassidy, L. Koitzsch, Q. Harrison, E. Cato, and R. McIntyre. 2017. Yellowstone Wolf Project Annual Report. Yellowstone National Park, Mammoth, Wyoming, USA.
- Smith, J. A., Y. Wang, and C. C. Wilmers. 2015. Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society B: Biological Sciences* 282: 20142711
- Smith, D. W., P. J. White, D. R. Stahler, A. Wydeven, and D. E. Hallac. 2016. Managing wolves in the Yellowstone area: Balancing goals across

- jurisdictional boundaries. *Wildlife Society Bulletin* 40:436–445.
- Suraci, J. P., M. Clinchy, L. Y. Zanello, and C. C. Wilmers. 2019a. Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. *Ecology Letters* 22:1578–1586.
- Suraci, J. P., L. G. Frank, A. Oriol-Cotterill, S. Ekwanga, T. M. Williams, and C. C. Wilmers. 2019b. Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. *Ecology* 100:e02644.
- Therneau, T. 2015. A package for survival analysis in S. R package version 2.38. <https://CRAN.R-project.org/package=survival>
- Therneau, T. 2018. coxme: mixed effects cox models. R package version 2.2-10. <https://cran.r-project.org/web/packages/coxme/index.html>
- Thurber, J. M., R. O. Peterson, T. D. Drummer, and S. A. Thomas. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin* 22:61–68.
- Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. *Movement Ecology*. 2. <https://doi.org/10.1186/2051-3933-2-4>
- Trombulak, S. C., and C. A. Frissell. 2000. Society for conservation biology review of ecological effects of roads on terrestrial and aquatic communities. *Biology* 14:18–30.
- Uboni, A., D. W. Smith, J. S. Mao, D. R. Stahler, and J. A. Vucetich. 2015. Long- and short-term temporal variability in habitat selection of a top predator. *Ecosphere* 6:1–16.
- Wam, H. K., K. Eldegard, and O. Hjeljord. 2012. From overlooking to concealed: Predator avoidance in an apex carnivore. *European Journal of Wildlife Research* 58:1001–1003.
- Wam, H. K., K. Eldegard, and O. Hjeljord. 2014. Minor habituation to repeated experimental approaches in Scandinavian wolves. *European Journal of Wildlife Research* 60:839–842. <https://doi.org/10.1007/s10344-014-0841-0>
- White, P. J., and R. A. Garrott. 2005. Northern Yellowstone elk after wolf restoration. *Wildlife Society Bulletin* 33:942–955.
- Whittaker, D., and R. L. Knight. 1998. Understanding wildlife responses to human. *Wildlife Society Bulletin* 26:312–317.
- Whittington, J., C. Cassidy, S. T. Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. *Ecological Applications* 15:543–553.
- Whittington, J., M. Hebblewhite, N. J. DeCesare, L. Neufeld, M. Bradley, J. Wilmshurst, and M. Musiani. 2011. Caribou encounters with wolves increase near roads and trails: a time-to-event approach. *Journal of Applied Ecology* 48:1535–1542.
- Wilmers, C. C., Y. Wang, B. Nickel, P. Houghtaling, Y. Shakeri, M. L. Allen, J. Kermish-Wells, V. Yovovich, and T. Williams. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. *PLOS ONE* 8:e60590.
- Wright, R. G. 1992. *Wildlife research and management in the national parks*. University of Illinois Press, Champaign, Illinois, USA.
- Zimmermann, B., L. Nelson, P. Wabakken, H. Sand, and O. Liberg. 2014. Behavioral responses of wolves to roads: Scale-dependent ambivalence. *Behavioral Ecology* 25:1353–1364.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3164/full>