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Determinants of Gray Wolf (*Canis lupus)* Sightings in Denali National Park

Bridget L. Borg,[1,2,3] Stephen M. Arthur,[2,4] Jeffrey A. Falke[5] and Laura R. Prugh[6]

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ABSTRACT Wildlife viewing within protected areas is an increasingly popular recreational activity. Management agencies are often tasked with providing these opportunities, yet quantitative analyses of factors influencing wildlife sightings are lacking. We analyzed locations of GPS-collared wolves and wolf sightings from 2945 trips in Denali National Park and Preserve, Alaska, USA, to provide a mechanistic understanding of how viewing opportunities are influenced by attributes of wolves and physical, biological, and harvest characteristics. We found that the presence of masking vegetation, den site proximity to the road, pack size, and presence of a wolf harvest closure adjacent to the park affected wolf sightings, and the influence of den proximity on sightings depended on harvest management. Wolf sightings increased with den site proximity to the road in years with a harvest closure adjacent to the park but not in the absence of the closure. The effect of the harvest closure on sightings was similar in magnitude to an increase in pack size by two wolves or a more than a two-fold decrease in masking vegetation. These findings were consistent across a 10-fold change in spatial resolution. Quantitative analysis of the factors influencing wildlife sightings provides valuable insight for agencies tasked with managing viewing opportunities.

Key words: Alaska; *Canis lupus*; gray wolf; Denali National Park; national parks; non-consumptive use; protected areas; spatially explicit; wildlife viewing; wildlife sightings

RÉSUMÉ. L'observation de la faune dans les aires protégées est un loisir qui prend de plus en plus d'ampleur. Souvent, les organismes de gestion ont le mandat d'offrir de telles activités et pourtant, il n'y a toujours pas d'analyses quantitatives des facteurs qui exercent une influence sur les observations fauniques. Nous avons analysé les emplacements de loups munis de colliers GPS et les observations de loups découlant de 2 945 déplacements au parc national et à la réserve de Denali, en Alaska, aux États-Unis afin d'obtenir une compréhension mécaniste de la manière dont les activités d'observation sont influencées par les attributs des loups ainsi que par les caractéristiques physiques, biologiques et de récolte. Nous avons remarqué que la présence de végétation masquante, la proximité des tanières de la route, la taille des meutes et la présence d'une interdiction de récolte de loups dans le secteur adjacent au parc ont eu un effet sur les observations de loups, et que l'influence de la proximité des tanières par rapport aux observations dépendait de la gestion des récoltes. Les observations de loups augmentaient en fonction de la proximité des tanières par rapport à la route au cours des années pendant lesquelles il y avait interdiction de récolte de loups dans le secteur adjacent au parc, mais ce n'était pas le cas en l'absence d'interdiction. L'ampleur de l'effet de l'interdiction de récolte sur les observations était semblable à une augmentation de la taille de la meute correspondant à deux loups ou plus, ou à la diminution de plus du double de la végétation masquante. Ces constatations se recoupaient dans un changement correspondant au décuple dans la résolution spatiale. L'analyse quantitative des facteurs influençant les observations fauniques offre une importante perspective aux organismes dont le mandat consiste à gérer les activités d'observation.

Mots clés : Alaska; *Canis lupus*; loup gris; parc national de Denali; parcs nationaux; utilisation sans consommation; aires protégées; spatialement explicite; observation de la faune; observations fauniques

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[1] University of Alaska Fairbanks, Institute of Arctic Biology, 323 Murie Building, Fairbanks, Alaska 99775, USA
[2] National Park Service, Denali National Park and Preserve, PO Box 9, Denali Park, Alaska 99755, USA
[3] Corresponding author: bridget_borg@nps.gov
[4] Current address: U.S. Fish and Wildlife Service, Arctic National Wildlife Refuge, 101 12th Ave, Fairbanks, Alaska 99701, USA
[5] U.S. Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, PO Box 757020, Fairbanks, Alaska 99775, USA
[6] University of Washington, School of Environmental and Forest Sciences, Box 352100, Seattle, Washington 98195, USA

INTRODUCTION

Wildlife viewing is one of the most popular outdoor recreational activities (Higginbottom, 2004). Approximately one in three people over the age of 16 participate in wildlife viewing activities each year; in 2011 alone, people spent over 54 billion dollars on these activities (U.S. Census Bureau, 2011). Protected areas are destinations for people seeking opportunities to view wildlife in natural settings (Stander, 2008; Knight, 2009), and some agencies such as the National Park Service are mandated to protect wildlife viewing opportunities as an important component of visitor experience (Manfredo, 2002). Despite the growing importance of wildlife viewing as a recreational activity, few studies have looked at wildlife sighting opportunities as a quantifiable resource or examined how natural and anthropogenic influences might affect this resource (Schultz and Bailey, 1978; Singer and Beattie, 1986; Burson et al., 2000; Manfredo, 2002; Borg et al., 2016).

Several factors can influence wildlife viewing opportunities in protected areas, such as wildlife movements and behavior, surrounding vegetation, topography, and anthropogenic activity (reviewed in Knight, 2009). Visitation to parks has increased in recent years (Thomas et al., 2020), as has the intensity of human disturbance and activity outside of park boundaries (Radeloff et al., 2010). This increased anthropogenic activity could reduce some wildlife sighting opportunities and increase others. Depending on the level and type, human activity or development may displace species spatially or temporally (Gill et al., 1996; Beale, 2007; Hebblewhite and Merrill, 2008; Stankowich, 2008) or may attract or habituate wildlife (Schultz and Bailey, 1978; Thurber et al., 1994; James and Stuart-Smith, 2000; Whittington et al., 2005; Knight, 2009; Steyaert et al., 2016). Additionally, climate change is increasing shrub cover across many northern and high elevation areas (Sturm et al., 2001; Tape et al., 2006), which may reduce the visibility of wildlife to visitors (Duffus and Dearden, 1990; Orams, 1996). Understanding the importance of these factors is needed to inform policies aiming to maintain wildlife viewing opportunities in protected areas (Manfredo, 2002; Borg et al., 2016). Here, we quantify how anthropogenic and natural factors influence sightings of gray wolves (*Canis lupus*) using a unique dataset from Denali National Park and Preserve (DNPP), Alaska.

Viewing any large mammal species is an important experience for visitors to protected areas (Skibins et al., 2012), and observing a wolf in the wild is a rare and highly valued experience (Montag et al., 2005; Keller, 2019). DNPP is one of the best places in the world to see wolves in their natural habitat, but sightings have declined in recent years (Borg et al., 2016). To our knowledge, DNPP is the only protected area in the world that systematically records wildlife sightings in a spatially explicit database, resulting in a dataset of wildlife sightings from thousands of trips along the Denali Park Road. In addition, DNPP controls visitor access through a shuttle bus system along the 148 km long Denali Park Road (NPS, 1986). This dataset, in combination with relatively controlled and consistent traffic levels and visitor activity, presents a unique opportunity to examine how the probability of seeing a wolf is affected by spatiotemporal variation in physical and biological factors.

Additionally, data from GPS-collared wolves were collected as part of a long-term wolf-monitoring program within DNPP during the study period. In conjunction with the wolf sighting data, these two unique and concurrent datasets allowed us to use a two-pronged approach to determine factors that influenced (1) the proximity of a wolf to the road, making it "available" to be detected and (2) whether a wolf was detected along a road segment. We hypothesized that factors increasing the probability of a wolf being near the Denali Park Road would similarly increase sightings.

We hypothesized that den site location, breeding status of individual wolves, and pack size would influence wolf movement patterns and sightings. Specifically, we predicted that the probability of a wolf being near the road would increase with proximity of a wolf den site to the road because wolves' movements often radiate from a central den site location in the summer (Packard, 2003). We also predicted that breeding pairs (i.e., breeders) would have a lower probability of being observed relative to non-breeders, because breeders may be more likely to attend to pups and remain near den sites (Thurston, 2002; Tsunoda et al., 2009, but see Potvin et al., 2004). Den site attendance and associated movements are also influenced by pack size (Ballard et al., 1991; Tsunoda et al., 2009). We expected that larger packs would increase the probability of wolf sightings, because additional wolves would be foraging, and individuals could have longer foraging bouts (Ruprecht et al., 2012). We expected that failed recruitment (i.e., denning failure or early mortality of pups) would decrease the probability of wolf presence and sightings near the road because movements would no longer be tied to the den site.

The role of a wolf harvest closure adjacent to DNPP on wolf sightings was also of particular interest. Typically, two to four wolf packs in the eastern portion of DNPP occupy territories spanning both the Denali Park Road corridor and areas outside of the park to the northeast (Borg and Taylor, 2018). These packs provide for the majority of wolf sightings because of their proximity to the Denali Park Road (Borg and Burch, 2014). However, wolves from these packs also use habitat outside of the park where they are subject to harvest. Harvest (i.e., legal hunting and trapping) of wolves was permitted on all state land adjacent to DNPP until 2000, when a harvest closure was enacted by the Alaska Board of Game (AKBOG) in areas outside of the northeast boundary of DNPP (Fig. 1). The closure changed in spatial extent during the first two years and was removed in its entirety in 2010. When the closure was rescinded, members of the AKBOG requested more information and research into the relationship between the harvest of wolves

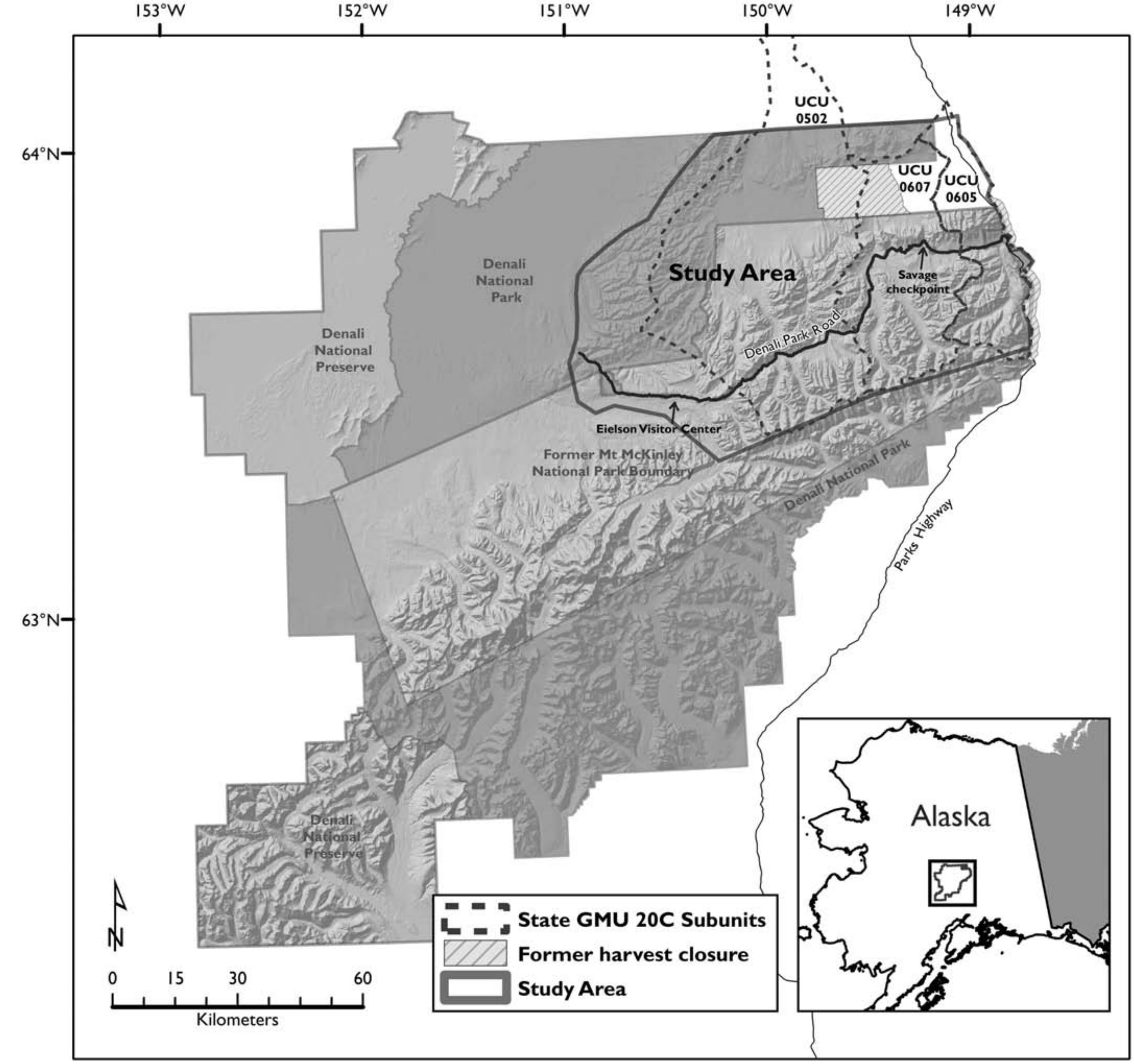

FIG. 1. Map of study area and Denali Park Road in Denali National Park and Preserve, Alaska, USA. Uniform Coding Units (UCUs) within Game Management Unit 20C and the former closed area where wolf hunting and trapping was prohibited from 2000 to 2010 are shown. The harvest closure was first established in 2000 and expanded in 2001 and 2002. The full closure extent (2002–10) is depicted.

adjacent to DNPP and wolf sightings within DNPP (ADFG, 2010), which was a primary motivation for the current study. We tested for an effect of the presence of a harvest closure on wolf sightings near the road, hypothesizing that increased harvest or harvest activity during years without the closure may cause wolves to avoid areas of human activity (Kitchen et al., 2000; Theuerkauf et al., 2003). Finally, we also hypothesized that factors increasing the probability of a wolf being near the Denali Park Road would increase sightings along the road corridor.

Previous analysis of annual variation in wolf sightings in DNPP and Yellowstone National Park indicated that wolf sightings were affected by pack size, den location, and harvest outside of the park (Borg et al., 2016). However, it is unknown how these factors compare in importance to physical features such as vegetation and topography. Previous analysis indicated that both wolf population size and den occurrence near the road were greater during a period when the harvest closure was in place, potentially confounding the relative effects of the closure and den location on wolf sightings (Borg et al., 2016). The annual metric of sightings used in Borg et al. (2016), while useful for capturing changes in sightings from year to year, did not account for spatial variation in sightings along the Denali

Park Road. Here, we use a spatially explicit framework to account for additional sources of variation, such as physical features of the environment, to further elucidate the relative impacts of wolf demography, harvest, and den site location on wolf sightings.

Ecological patterns can vary with spatial scale (Wiens, 1989; Levin, 1992); therefore, we investigated the importance of spatial grain size on inferences regarding factors influencing wolf sightings. We anticipated that individual animal behavior and social group dynamics would be most important at fine and intermediate spatial grains (e.g., 1.6 to 8 km), and population-level factors would be most important at a coarse spatial grain (16.2 km). We further hypothesized that biological factors influencing individual behavior, such as successful reproduction and movements associated with den sites, would be more important in explaining variation in wolf sightings at a fine spatial grain, whereas factors describing the physical characteristics affecting visibility of wildlife would be equally important across varying levels of spatial analysis. Although we hypothesized that the harvest of wolves adjacent to the park would reduce sightings (Borg et al., 2016), we anticipated that the effect of management actions (i.e., legal take of wolves outside of the park) would be apparent at a coarse spatial grain but difficult to detect at a fine scale where the influence of physical site characteristics, den site location, and group size were expected to dominate sighting dynamics.

MATERIALS AND METHODS

Study Area

DNPP is a popular wildlife-viewing destination in interior Alaska, with over 400 000 visitors each year (Fix et al., 2012). DNPP management documents define “the possibility of observing free-roaming wildlife at close range in a rugged wilderness setting” as a key feature of the park (NPS, 1995:2) and many visitors come to DNPP specifically for the opportunity to observe wildlife (Manning and Hallo, 2010). The study area encompassed approximately 6350 km^2 of wolf habitat, primarily north of the Alaska Range in and adjacent to DNPP (Fig. 1). This region of DNPP contains patches of boreal forest, high alpine tundra, braided rivers, and willow-lined creeks. The main prey base for wolves in the region are caribou (*Rangifer tarandus*), Dall’s sheep (*Ovis dalli*), and moose (*Alces alces*). The climate is subarctic, with short, cool summers ranging on average from 0˚C to 24˚C (Western Regional Climate Center, 2015). Annual precipitation averages 38 cm with over half occurring during the summer months. The study area is bisected by the Denali Park Road (Fig. 1), which provides visitor access to the region and the majority of wolf viewing opportunities, as well as opportunities to view other wildlife species (caribou, Dall’s sheep, moose, grizzly bear (*Ursus arctos*), small mammals, and birds).

Sighting Data

Data on wildlife sightings along the Denali Park Road were collected during bus and park staff trips from the Savage checkpoint at kilometer 24 to the Eielson Visitor Center at kilometer 106 (Fig. 1). When wildlife was spotted, vehicles would stop to allow passengers to observe the wildlife. During these stops, data on the wildlife sighting were collected following a standardized protocol. Although data on wildlife sightings were collected through various media, the following attributes were consistently collected from 1997 to 2013: 1) observer, 2) trip identification, 3) species, 4) animal group size, 5) date and time, and 6) location of stop (Burson et al., 1999; McKenny et al., 2015). Data were collected by 1) bus drivers as written observations (1995 – 2007) or on electronic panels installed on buses (2007 – 10: Validator V2000, Universal Tracking, Valencia, California; 2011 – 13: Fleet Management System, San Luis Obisbo, California) and 2) park staff and volunteers as written observations (2007 – 09) and on handheld devices (2010 – 13, Trimble, Sunnyvale, California). Prior to 1997, data were sparse and not used in this analysis. In early years (1997 – 2006), the location of sightings was recorded within 1.6 km (1 mile) segments. In the later years (2007 – 12), locations were obtained through GPS units within vehicles (McKenny et al., 2015). Data were included from all trips, including those that saw no wolves.

Population Monitoring and Pack Counts

Wolf population monitoring efforts and the use of radio-telemetry to track and monitor packs began in 1986 (Mech et al., 1998). From 1986 to 2012, 387 individual wolves were instrumented with very high frequency (VHF) collars (Borg and Burch, 2014). From 2003 to 2012, 30 of the VHF collars were additionally equipped with GPS (Telonics, Mesa, California), which provided one or more daily locations (Meier and Burch, 2009). Wolves were immobilized by darting from helicopters and collared following established protocols (Meier and Burch, 2009; Sikes et al., 2011). Wolf project staff used a combination of aerial and ground-monitoring techniques to collect data on wolf locations, pack identification, numbers of pack members, active den site locations and use, and breeding status of individual wolves (Mech et al., 1998; Meier and Burch, 2009).

Den Site Locations

DNPP’s wolf management plan objectives require closing areas around known den sites to hikers for the duration of wolf use of these areas, typically April – August, (Wildlife Team, DNPP, 2007). Thus, den site locations and use were closely monitored for wolf packs in areas along the road corridors. Data on the denning status of packs, as well as den site locations, were gathered by field personnel on foot or during aerial observation and recorded on handheld GPS units (Garmin, Olathe, Kansas). We determined the distance of den sites to the nearest location on the Denali Park Road using the "near" tool in ArcGIS Desktop version 10.2 (Esri, Redlands, California).

Harvest

Wolf harvest management varied throughout the study region and the study period. All areas outside the DNPP boundary were open to hunting and trapping under state regulation, with the exception of an area where hunting and trapping of wolves were prohibited by the AKBOG in some years. Established in 2000, the closed area originally encompassed 49 km^2, was expanded in 2001 and 2002 to 313 km^2 (Fig. 1), and then remained in place until removed by the AKBOG in 2010. Although the closed area was relatively small, it included areas that supported high seasonal densities of caribou and associated wolf activity as well as human habitation and associated hunting and trapping activities (Mech et al., 1998). The wolf hunting season adjacent to the park's boundaries was 10 August to 30 April from regulatory year (1 July – 30 June) 1996 – 97 through 2005 – 06. Starting in 2006 – 07, the season was extended until 31 May. The wolf trapping season spanned 1 November to 30 April. Subsistence and sport hunting and trapping were permitted in the Preserve and 1980 park additions of DNPP, but all hunting and trapping were prohibited in the area of the original Mt. McKinley National Park (Fig. 1). Alaska Department of Fish and Game (ADFG) requires that the hides of all wolves harvested (shot or trapped) are sealed by an ADFG representative within 30 days of take. A seal is affixed to the hide and information on location (Game Management subunit) and date the animal was taken is recorded. We obtained the numbers of wolves harvested from regions adjacent to park boundaries from state harvest records and mortality of collared wolves.

Wolf Proximity

We calculated the proportion of wolf locations near the road in relation to the den site distance from the closest point on the road (*DenDist*), spring pack size recorded during annual surveys in March (*PackSiz*e), breeding status of wolf (*WolfStatus*), denning success (*Recruit*), and the presence or absence of a closure on wolf hunting and trapping (*Closure*; Table 1). We used summer (20 May – 15 September) wolf locations from 2004 to 2012. The maximum recorded distance for a wolf sighting was 500 m, and we therefore used this distance as a cutoff for the wolf being within a distance available for detection. Locations within this distance were classified as *Fixes Near Road* (Table 1). We calculated the proportion of fixes near the road for each wolf-year and averaged across wolf-years. We included only data from wolves in packs with annual territories overlapping or within 1.5 km of the Denali Park Road for this analysis. In addition, we included only GPS-collared wolves with fix acquisition rates above 80%. GPS collars were programmed to collect between 1 and 8 locations daily. To limit autocorrelation, we used the first location per day (collected at 0800 h for all collars) in instances where more than one location per day was collected.

Each wolf's status was classified as "breeder" or "non-breeder" based on observation of leadership behavior, attendance at den sites, observation of nursing pups (for females), or through testes and nipple measurements during collaring (Mech, 1999, 2000; Peterson et al., 2002; Meier and Burch, 2009). When breeding or dominance status was not directly recorded, it was determined after a thorough review of capture, mortality, and aerial tracking information for each pack for all wolves in the dataset (Borg et al., 2015). Recruitment was classified as (1) "successful," based on the presence of pups in fall, (2) "failed," based on early detection of pups that were not seen with the pack in the fall or repeated pack locations around a suspected or known den site with no visual observations of pups during the summer or fall, (3) "no evidence of denning," when there was lack of denning behavior, or (4) "unknown," when there were insufficient data or monitoring to determine recruitment.

We also used generalized linear mixed modeling to evaluate the effect of covariates on the proportion of wolf locations near the road and report detailed methods in the Supplementary file.

Wolf Sighting Model

We used counts of wolf sightings within sections of the Denali Park Road each year from 1997 – 2013 as the response variable for a spatially explicit model to evaluate factors affecting wolf sightings. Every wildlife stop where a wolf was seen was considered one wolf sighting, regardless of the number of wolves seen during the stop. Buses stopped for every wolf sighting, regardless of whether a wolf sighting occurred earlier during the same trip (W. Clark, DNPP, pers. comm. 2013). It was possible that more than one sighting event during the same trip could violate the assumption of independence, given that each sighting was the unit of replication in our analysis, if multiple sightings were recorded for individuals of the same pack displaying correlated movements. To assess the potential lack of independence among sightings, we determined how frequently multiple sightings of wolves occurred during one trip and the average distance between sightings within the same trip. For this assessment, we used data from 1997 to 2007, collected from the same medium (written bus driver observations, see above), to ensure consistency. Because the majority of trips were single sightings (240 of 275 trips, 88%), and when multiple sightings occurred, they were far apart (average distance = 23 km), thus representing sightings of different packs or of individuals displaying independent movement patterns, we considered sightings to be independent in our analyses.

TABLE 1. Proportion of summer (20 May – 15 September) locations of collared wolves within 0.5 km of the Denali Park Road from 2004 to 2012 in Denali National Park and Preserve, Alaska, USA, summarized by a number of potential explanatory factors. Proportion of fixes near road were calculated for each wolf-year and averaged across wolf-years. SE is the standard error of sample proportion; sample size is wolf-years. The summary of den distance includes the categories of near (< 1.0 km from the road) and far (> 1.0 km from the road). Den distance summary excludes cases of unknown denning status or no evidence of denning.

Covariates	Fixes near road	Total fixes	Average proportion across wolf-years	SE	Wolf years (n)	Collared wolves
Breeding status:						
Breeder	285	2567	0.10	0.143	24	12
Non-breeder	19	894	0.02	0.036	9	6
Den distance:						
Near	277	1698	0.16	0.009	16	9
Far	24	1244	0.02	0.021	12	8
Recruitment:						
Successful	292	2648	0.10	0.161	25	14
Failed	9	274	0.03	0.046	3	3
No evidence of denning	0	439	0.00	0.000	4	4
Unknown	3	100	0.03	NA	1	1
Closure:						
Yes	269	2097	0.13	0.021	19	11
No	35	1364	0.03	0.004	14	9

TABLE 2. Brief description of covariates used in the spatially explicit model of wolf sightings along the Denali Park Road in Denali National Park and Preserve, Alaska, USA, from 1997 to 2013.

Covariates	Description
Physical (PHYS):	
Vis	Measure of visibility of surrounding terrain from road
Mask	Measure of vegetation tall enough to mask a wolf in the surrounding terrain (m)
Biological (BIO):	
DenDist	Den distance of nearest pack (km)
PackSize	Pack size of nearest pack
DenStat	Den status (denning: success, failed, or unknown)
Harvest (HARV):	
WHarv	Number of wolves harvested in season prior
BHarv	Harvest of a breeder from the near pack in the season prior (yes or no)
Closure	Presence or absence of closure on hunting and trapping
Included in all models:	
OFF	Number of trips collecting data that passed through each section
CT	Collection Type (bus driver, NPS staff)

We developed eight covariates to represent key processes that we hypothesized would influence wolf sightings and classified these covariates into 3 categories representing physical (PHYS), biological (BIO), and harvest (HARV) characteristics (Table 2). We considered 4 different road section lengths (1.6, 3.2, 8.0, and 16.1 km) to investigate the importance of spatial grain size on the annual number of sightings per road section. Our section lengths were created to reflect the level of precision (1.6 km) of the early (1997 – 2006) wolf sighting data and 2, 5, and 10-fold increases in section length. The covariates were calculated for each road section length. Although it was far finer than the scale of wolf home range movements, we used the resolution of wolf sighting data as our finest-scale analysis, as we hypothesized that factors affecting wolf sightings can vary substantially at this scale.

Two physical (PHYS) covariates were calculated to represent an index of the amount of visible area along each road section: (*Vis*) and the likelihood that vegetation would mask (*Mask*) the visibility of wolf-sized animals (Fig. 2). We analyzed physical covariates within a 0.5 km strip on either side of the road. We used the Viewshed Analysis tool in ArcGIS 9.0 (Esri) to create a raster with 60 by 60 m resolution where each raster cell value represented a measure of how visible a cell was from the Denali Park Road. Height of vegetative cover can greatly impact visibility by blocking line of sight. We combined average height of vegetation cover and digital elevation models (DEM) to create a raster of visible landscape for use in the visibility analysis. Our analysis assumes no vegetation within 7 m of the centerline of the Denali Park Road, accounting for the roadbed and low vegetation resulting from park brushing operations. We used the Feature Vertices to Points tool in the ArcGIS 9.0 (Esri) to generate a dataset of 5171 points at vertices along the Denali Park Road and the Viewshed Analysis tool to conduct the visibility analysis. We averaged the values of the visibility raster within each section of road to create the visibility index (*Vis*). High values of Vis indicate a section of road with highly visible terrain such as wide river bars and open expanses, and low values indicate less visible terrain such as areas where the road corridor was in a valley bottom limiting expansive views.

FIG. 2. Wolves traveling (A) along the Denali Park Road and (B) in short vegetation are easy to see, but (C) a wolf in the surrounding vegetation could be easily obscured, Denali National Park and Preserve, Alaska. NPS photos.

We used data from a land cover classification map (Boggs et al., 2001) to develop a measure of masking vegetation (*Mask*) along the road that could hide the presence of a wolf (Fig. 2). Vegetation height higher than 1 m (the average height of a wolf is approximately 0.8 m) was given a value of 1, and vegetation below 1 m was given a value of 0. We averaged the values of the masking raster within each buffered section of road to create *Mask*. Although some changes in vegetation height might have occurred during the course of our study, major changes in vegetation types were not common during the timescale of the study (Brodie et al., 2019).

Biological covariates (BIO) included den distance (*DenDist*), pack size (*PackSize*), and denning status (*DenStat*). For the wolf sighting model, the variables *PackSize* and *DenDist* were similar to the variables for the wolf proximity analysis but were calculated for each segment of the road: *PackSize* was the size of packs recorded during annual surveys in March for packs with the closest den site, and *DenDis*t was the distance of the nearest active den to the closest point on the road for each segment of road in year *t*. We log-transformed *DenDist* to improve parameter estimation with maximum likelihood methods because values of *DenDist* spanned three orders of magnitude (range = 74 – 12 342 m). Denning status (*DenStat)* was classified as "successful" or "failed" using the same criteria described for the wolf proximity analysis. We included another classification for cases of packs that denned, as indicated by pups present in the fall, but with uncertain den locations. In these cases, "unknown" indicated that the suspected location of the den site or alternate activity center, as determined by GPS locations of collared wolves, was used to estimate the pack den site location. We included known or estimated den sites for packs with denning information only. Although the number of pups is another potential factor that could have influenced wolf movements, we lacked reliable pup counts for each pack.

Harvest covariates (HARV) included three metrics describing harvest levels of wolves adjacent to DNPP in the season prior to the observation year (*t*). *Closure* was the presence or absence of a closure on wolf hunting and trapping adjacent to DNPP in the northeast (Fig. 1) and was a yearly covariate (absent: 1997 – 99 and 2011 – 13, present: 2000 – 10). *WolfHarv* was the number of wolves harvested adjacent to the study region in the regulatory year prior to the sighting year (July year *t*−1 to June year *t*) and was also a yearly covariate. Harvest data were assigned to specific geographic areas designated as Uniform Coding Units (UCUs) by the ADFG. We included all recorded wolf harvest within UCUs 605 and 607 in analyses because these UCUs were within DNPP, the harvest closure, or immediately adjacent to DNPP (Fig. 1). UCU 502 extended north beyond DNPP and we therefore attempted to include only instances of wolves harvested in this UCU that were within DNPP or the former harvest closure based on ancillary information provided by the hunter or trapper on the location of harvest. *BHarv* was a factor describing if a breeder was harvested in the season prior (yes or no) from the pack near the road segment and was the only spatially explicit harvest covariate.

We developed a candidate model set to represent combinations of the three classes of covariates hypothesized a priori to influence sightings. In addition, as count data often have an exposure variable, indicating sampling effort, we included the number of trips through a section as the exposure variable using the "offset" option in the model formulation. We also included method of data collection (*Collection Type*, *CT*) to account for potential effects of different methods. We developed a global model that included all terms and evaluated additional models that included reasonable and biologically relevant combinations of covariates (Table S1).

We used an information-theoretic approach to find the most parsimonious set of independent variables to estimate the annual number (or rate) of wolf sightings per road section (wolf sighting model). We evaluated multicollinearity among covariates using a variance inflation factor statistic (VIF). All covariates included in the models had a VIF less than 10 (Kutner et al., 2004). For the wolf sighting model, a large number of "zero" counts of wolf sightings per 1.6-km road section resulted in overdispersed count data. We modeled the overdispersed count data with a negative binomial regression model, using the glm.nb function and log link function in the "pscl" library in program R (Zeileis et al., 2008) to develop count based regression models of wolf sightings as a function of covariates described above (n = 29 models).

We used the Akaike information criterion to rank models (Burnham and Anderson, 2002). Confidence intervals for parameter estimates were evaluated for significance in models within ≤ 2 ΔAICc units and differing by only one parameter from the top model, as their increase in AICc values could be due to the addition of an uninformative parameter (Burnham and Anderson, 2002; Arnold, 2010; Leroux, 2019). Parameter estimates were considered significant if 95% confidence intervals did not overlap zero. For ease of interpretation of parameter estimates, we back-transformed parameter estimates (β) such that the transformed parameter estimates were equal to e^β. The back-transformed parameter estimates are interpreted as incidence rate ratios for the wolf sighting model.

To account for model selection uncertainty in the wolf sighting model, we used model averaging to calculate unconditional parameter estimates and variances for models with model weight, w_i greater than 0.05. We used the MuMIn package in R (Bartoń, 2014) for model selection and to calculate model-averaged parameter estimates and unconditional standard errors.

Den Distance and Closure

Previous analyses combined wolf pack size and den proximity to the road into an annual metric to analyze the effects of these factors on an annual scale along the entire road corridor (Borg et al., 2016). The combined index (Pack Near Road Index) was higher during the period when a harvest closure was in place, potentially confounding the relative effects of the closure and den location on wolf sightings (Borg et al., 2016). To further elucidate the relationship between the effects of den site distance and harvest management, we fit two-way ANOVA tests of wolf proximity to the road and annual wolf sightings each as a function of den distance (*DenDist*), harvest management (*Closure*), and the interaction between den distance and harvest management. The annual wolf sightings response variable was calculated as the proportion of bus trips where at least one wolf was seen. Average den distance by year was calculated using den site distance from the park road for all packs with territories overlapping the park road. In cases where there was more than one den or rendezvous site used by a single pack, we used the mean of the distances of multiple den or rendezvous sites as the value for that pack.

RESULTS

Wolf Proximity

Our dataset consisted of locations from 18 wolves that were collared for one to four summers from 2004 to 2012 and had fix acquisition rates of 80% or higher. Of the 18 wolves, 12 wolves were breeders and six were non-breeders. Data from each wolf in a year constituted a "wolf-year," yielding a sample size of 33 wolf-years composed of 24 breeder wolf-years and nine non-breeder wolf-years prior to censoring (Table 1). Five samples (three breeder and two non-breeder wolf-years) lacked den site information and were censored from both the generalized linear model for wolf presence and the summary of proportion of wolf locations near the road with den distance. In four of the five censored cases, there were no locations near the road (≤ 0.5 km); in one case, the proportion of locations near the road was 0.03. After censoring these wolf-years, our data set consisted of 21 breeder wolf-years, seven non-breeder wolf-years, 25 cases of successful recruitment, and three cases of failed recruitment.

The proportion of locations near the road (≤ 0.5 km) per wolf-year ranged from 0 to 0.52 (mean 0.08 ± 0.14 SE). The proportion of wolf locations near the park road was greater for breeder than non-breeder wolves, when dens were located near the road, during the presence of a closure on trapping and hunting, and when recruitment of pups was successful for the wolf's pack (Table 1). Sample sizes were low for several categories and these differences were not tested for statistical significance (Table 1). Results from generalized linear mixed modeling indicated that the proportion of locations near the road decreased with increasing distance of the den site from the road (*DenDist*: β = −0.51 ± 0.094 SE) and wolves were more likely to be near the road during the presence of a closure on trapping and hunting adjacent to the park than during its absence (*Closure*: Present: β = 1.32 ± 0.255 SE; Table S2).

Wolf Sighting Model

A total of 589 wolf sightings were recorded along the Denali Park Road from 1997 to 2013. Pack size ranged from 2 to 16 wolves (7.8 ± 4.29 SE). During the study period, there were 20 cases of wolves or wolf packs monitored in the study region that did not contribute to the wolf sighting model because they apparently did not den or we had no denning information available. The number of wolves harvested from the region each year ranged from 0 to 11 (for details, see Borg et al., 2016). Values in the viewshed raster, which corresponded to the number of locations along the park road from which a cell was visible, ranged from 0 to 2863 (Fig. 3). At all grains (1.6, 3.2, 8.0, and 16.2 km), the top ranked models for wolf sightings included *Mask*, *PackSize*, *DenDist*, and *Closure* (Table 3).

Physical (PHYS) Covariates: As anticipated, sightings were negatively associated with the amount of masking vegetation within a given road section (range of incidence ratios for *Mask*: −0.80 – 0.90; Fig. 2, Table 4). The effect of masking vegetation showed no apparent trend with increasing spatial grain. Model-averaged parameter estimates for the visibility index overlapped zero at all grains (Table 4).

Biological (BIO) Covariates: The incidence of wolf sightings decreased by 0.58% for a 1% increase in den site

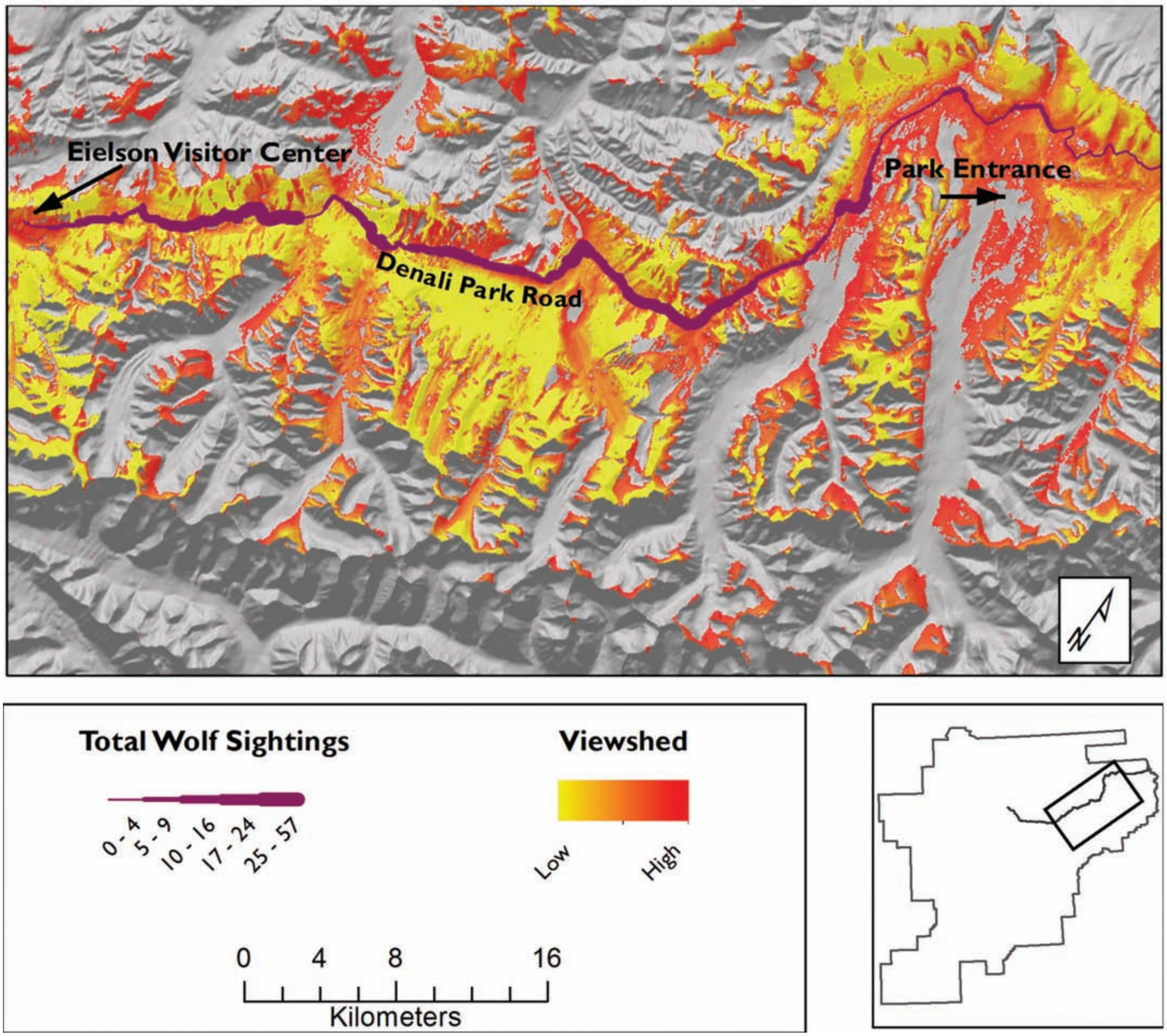

FIG. 3. Viewshed raster output from analysis of a set of 5171 points and total wolf sightings along the Denali Park Road in Denali National Park and Preserve, Alaska. The highest viewshed cell values occur in cells that are visible from the most locations along the Denali Park Road.

distance, and sightings increased 6%–8% for an increase in pack size of one wolf (Fig. 4). Confidence intervals for *DenDist* and *PackSize* did not overlap zero at any spatial grain (range of parameter estimates for *DenDist*: −0.41 to −0.58, *PackSize*: 0.06–0.08, Table 4). Successful recruitment at the closest den location increased the incidence of wolf sightings 2.05–2.86-fold compared to denning failure (Table 4). Denning success likewise suggested an increase in wolf sightings compared to denning failure, but considerable uncertainty surrounded these estimates and their confidence intervals overlapped zero (Table 4). The parameter estimates for den distance and denning success decreased in strength with increasing section length whereas parameter estimates for pack size were similar across all grains of analysis.

Harvest (HARV) Covariates: Covariates describing harvest were included in the top models at all analysis grains (Table 3). The presence of the closure on trapping and hunting was associated with increased sightings in road segments at every grain (range of incidence ratios for *Closure*: present 1.45–2.08; Table 4) and was significant at every scale except 16.2 km sections. Contrary to expectations, the effect of the closure was greater at finer grains of analysis (small section lengths). The harvest of a breeder was negatively associated with sightings at all scales (range of parameter estimates for *BHarv*: –0.20 to −0.32), and the number of wolves harvested was negatively associated with sightings at all but the 16.2 km sections (range of parameter estimates for *WHarv*: 0.004 to –0.03; Table 4), but the confidence intervals for both parameter estimates overlapped zero.

TABLE 3. Top models and model selection criteria evaluating covariates affecting the spatially explicit probability of wolf sightings along the Denali Park Road in Denali National Park and Preserve, Alaska, USA, from 1997 to 2013. Collection Type and Offset were included in all models and are not explicitly listed in the covariate set below. Only models with model weight w_i more than 0.05 are shown. The covariates used in the models are described in Table 2.

Scale and models	Log likelihood	AIC	Δ Log likelihood	ΔAIC	df	AIC weight
1.6 km segments:						
Mask +PackSize +DenDist +Closure	−857.40	1726.90	71.00	0.00	6	0.60
Vis +Mask+PackSize+DenDist+DenStat+Closure	−855.10	1728.20	73.30	1.30	9	0.31
3.2 km segments:						
Vis+Mask+PackSize+DenDist+DenStat+Closure	−617.00	1256.00	64.40	0.00	11	0.55
Mask+PackSize+DenDist+Closure	−620.60	1257.20	60.80	1.20	8	0.30
Vis+Mask+PackSize+DenDist+DenStat+Wharv +Closure+Bharv	−616.40	1258.80	65.00	2.80	13	0.14
8.0 km segments:						
Mask+PackSize+DenDist+Closure	−371.70	759.40	34.10	0.00	8	0.53
Vis+Mask+PackSize+DenDist+DenStat+Closure	−369.30	760.60	36.50	1.30	11	0.28
Vis+Mask+PackSize+DenDist+DenStat+Wharv+Closure+Bharv	−368.80	763.60	37.00	4.30	13	0.06
16.2 km segments:						
Mask+PackSize+DenDist+Closure	−234.20	484.40	28.00	0.00	8	0.30
Mask+PackSize+DenDist	−235.30	484.60	26.90	0.20	7	0.28
Mask+PackSize+DenDist+BHarv	−234.90	485.90	27.30	1.50	8	0.15
Mask+PackSize+DenDist+Wharv	−235.30	486.50	27.00	2.10	8	0.10
Vis+Mask+PackSize+DenDist+DenStat	−233.90	487.90	28.30	3.50	10	0.05
Vis+Mask+PackSize+DenDist+DenStat+Closure	−233.00	487.90	29.30	3.60	11	0.05

TABLE 4. Model-averaged parameter estimates for models evaluating the effect of spatially explicit covariates on the probability of wolf sightings along the Denali Park Road in Denali National Park and Preserve, Alaska, USA, from 1997 to 2013. Collection Type and Offset were included in all models and are not explicitly listed in the covariate set below. β and incidence ratio estimates for DenStat are relative to denning failure (failure to recruit pups). β and incidence ratio (IR) estimates for Closure are relative to absence of the harvest closure. Confidence intervals for estimates in italics overlap zero. Light grey text indicates that parameters were not included in top models ranked by AIC. The covariates used in the models are described in Table 2.

Parameter	1.6 km sections		3.2 km sections		8.0 km sections		16.2 km sections	
	β ± SE	IR	β ± SE	IR	β ± SE	IR	β ± SE	IR
PHYS:								
Vis	*0.02 ± 0.04*	*1.02*	*0.01 ± 0.04*	1.01	*0.05 ± 0.06*	1.05	*−0.01 ± 0.12*	0.99
Mask	−0.21 ± 0.03	0.81	−0.22 ± 0.04	0.80	−0.10 ± 0.04	0.90	−0.17 ± 0.05	0.84
BIO:								
DenDist	−0.58 ± 0.07	0.56	−0.58 ± 0.08	0.56	−0.41 ± 0.07	0.66	−0.41 ± 0.07	0.66
PackSize	0.07 ± 0.02	1.07	0.06 ± 0.02	1.06	0.07 ± 0.02	1.07	0.08 ± 0.03	1.08
DenStat: success	1.05 ± 0.35	2.86	0.92 ± 0.38	2.51	0.92 ± 0.45	2.51	*0.72 ± 0.46*	*2.05*
DenStat: unknown	*0.50 ± 0.66*	*1.65*	*0.34 ± 0.65*	1.40	*0.88 ± 0.78*	2.41	*0.90 ± 0.76*	*2.46*
HARV:								
WHarv	*−0.03 ± 0.03*	*0.97*	*−0.02 ± 0.03*	0.98	*−0.01 ± 0.05*	0.99	*0.004 ± 0.04*	*1.00*
BHarv	*−0.23 ± 0.40*	*0.79*	*−0.30 ± 0.21*	0.74	*0.20 ± 0.42*	0.82	*0.32 ± 0.42*	*0.73*
Closure: present	0.73 ± 0.18	2.08	0.70 ± 0.19	2.01	0.64 ± 0.22	1.90	0.37 ± 0.25	1.45

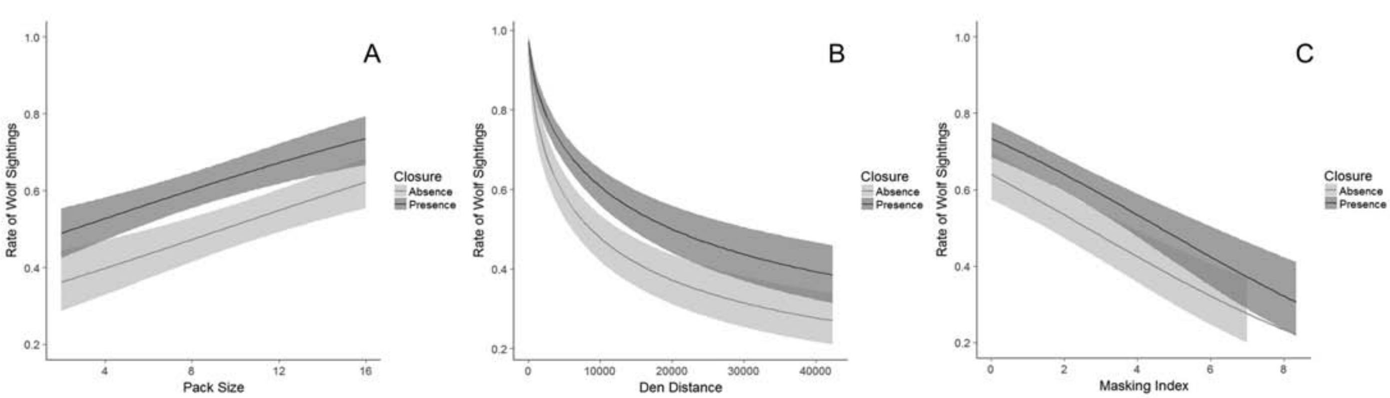

FIG. 4. Effect of (A) pack size, (B) distance to the nearest den, and (C) masking vegetation (i.e., masking index) on the rate of wolf sightings along the Denali Park Road in Denali National Park, Alaska, 1997–2013. Shaded areas show 95% confidence intervals around predicted probabilities using parameter estimates from the 1.6 km segment length model with lowest AIC value (Masking Index + Den Distance + Pack Size + Closure).

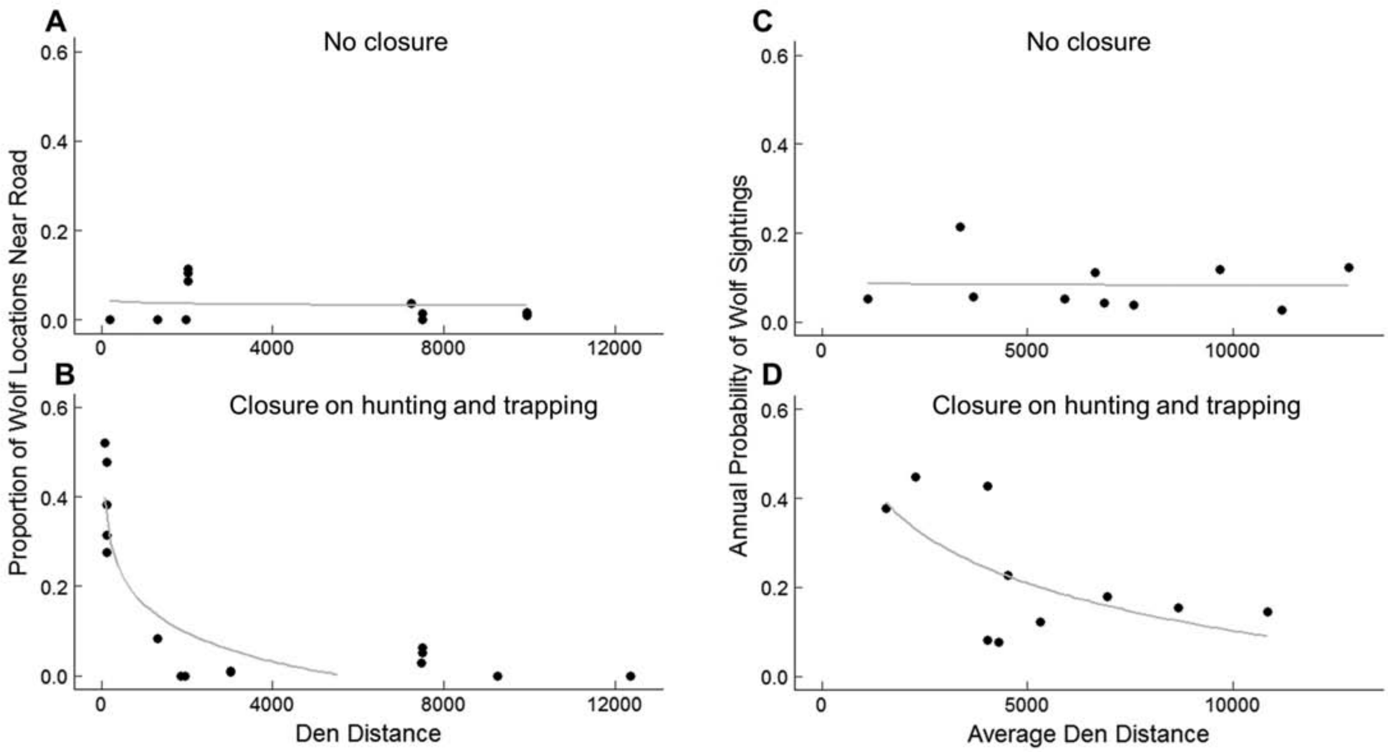

FIG. 5. Proportion of GPS-collared wolf locations within 0.5 km of the park road in relation den site distance in (A) years with no harvest closure and (B) years with a harvest closure adjacent to Denali National Park, and annual probability of wolf sightings in relation to average den distance of wolves in (C) years with no harvest closure and (D) years with a harvest closure adjacent to Denali National Park and Preserve, Alaska.

Den Distance and Closure

Generalized linear regression models showed that the effect of den distance on wolf proximity to the road and annual wolf sightings depended on harvest management (Fig. 5). The proportion of wolf locations near the road increased with den proximity to the park road when the closure of trapping and hunting was in place but had no effect on den proximity to the road in years when the closure of trapping and hunting was absent (*DenDis*t × *Closure* interaction $F_{1,24} = 16.87$, $p < 0.001$; Fig. 5A, B). Similarly, the annual probability of sightings increased with den proximity to the park road when the closure on trapping and hunting was in place but had no relationship with den site proximity to the road in years when the closure on trapping and hunting was absent (*DenDist* × *Closure* interaction $F_{1,16} = 4.94$, $p = 0.04$; Fig. 5C, D). The effect of den proximity to the road on wolf locations and sightings appeared to level off at distances over 0.4 km (Fig. 5).

DISCUSSION

Refuges play a vital role in preserving wildlife populations around the globe (Brashares et al., 2001) and provide some of the world's most sought-after opportunities for viewing increasingly threatened species, such as large carnivores (Duffield et al., 2008; Skibins et al., 2012; Ripple et al., 2014). However, these wide-ranging species are sensitive to human impacts outside and even within these protected areas (Woodroffe and Ginsberg, 1998). As visitation to protected areas increases (Eagles et al., 2002; U.S. Census Bureau, 2011), improving our understanding of the dynamics that influence sightings can help managers better understand how to protect this valuable experience. Our results highlight the importance of activity centers (such as den sites), the physical landscape, and vegetative cover to explain variation in wildlife sightings while also showing potential for management activities occurring outside the boundaries of protected areas to influence viewing opportunities within reserves.

We found that den site proximity to the road corridor in DNPP increased the probability of a wolf being near the road, and in conjunction with successful recruitment and larger pack size, these factors increased wolf sighting rates. Denning adult wolves are central place foragers, and activity patterns during the pup-rearing season are centered around homesites as wolves leave to pursue prey and return at intervals (as reviewed in Mech and Boitani, 2003). Previous analyses found that a metric combining den distance and pack size was important in describing variation in the annual probability of wolf sightings in both Denali and Yellowstone National Parks (Borg et al., 2016). Our spatially explicit model partitioned variation in sightings due to den site location and pack size along the Denali Park Road to provide a quantitative measure of the relative impact of these factors. For other species with predictable activity centers determined by breeding, rearing young, or location of specific resources (e.g., mineral licks), distance to activity centers and group size estimates could be used to develop quantitative models of wildlife sighting probabilities.

We expected that breeder attendance at den sites would decrease their proximity to the road compared to non-breeding wolves. While breeders were more likely to occur near the road compared to non-breeding wolves (Table 1), we did not find evidence that breeding status influenced proximity to the park road in our wolf presence model (See Supplementary file). Instead, much of the variation in proximity to the road was due to variation in individual behaviors, as indicated by the large amount of variation explained by the random effect (Table S3). Rates of den site attendance can be highly variable for breeders (Thurston, 2002; Potvin et al., 2004) and breeding status may not indicate increased attendance at a den site. Although breeding wolves are typically older and more experienced (Haber, 1977; Mech, 1999), these factors may not increase wariness or avoidance of the Denali Park Road.

Although breeding status may not substantially affect the proximity of individuals to the road, breeding status may indirectly affect wildlife sightings via impacts on recruitment rates. A breeder's role is vital in ensuring reproduction and increases recruitment (Brainerd et al., 2008; Stahler et al., 2013; Borg et al., 2015). We found that successful recruitment increased incidence of wolf sightings compared to cases where packs failed to recruit pups (Table 4). In turn, harvest of breeding wolves may disproportionately influence wolf sightings if breeder mortality decreases the probability of recruitment. We found some evidence that the harvest of a breeder might decrease the incidence of wolf sightings, but the uncertainty in these estimates was high (Table 4) and therefore these estimates were not significant. Our ability to document harvest of breeders from packs was limited to the sample of collared breeders and was most likely an underrepresentation. Current harvest records are not sufficient to determine breeding status or pack affiliation for wolves harvested in areas adjacent to DNPP. Recording breeding status and tracking pack affiliation of wolves harvested adjacent to park boundaries would improve our understanding of how harvest of these wolves may influence wolf sightings.

Terrain and masking vegetation have been highlighted as important factors affecting detectability of wildlife during surveys (Kellner and Swihart, 2014), and our findings indicate that these factors strongly affect wildlife sighting opportunities for the public. Both physical landscape factors (the amount of masking vegetation and the visibility of the surrounding landscape) were included in the top-ranked models, but only the masking covariate was statistically significant (Table 4). Thus, the effect of masking vegetation along the road had a stronger effect on wolf sightings than the measure of visible terrain. This highlights the importance of the type and height of vegetation in the surrounding area for influencing sightings (Fig. 2). Shrub cover is increasing with climate change, especially in the Arctic (Sturm et al., 2001; Tape et al., 2006). Our results indicate this climate change impact could substantially reduce opportunities to view wildlife. Land managers tasked with managing for wildlife viewing opportunities may consider the impacts of vegetation change and habitat management to enhance the viewing opportunities of the species they manage. Specific recommendations for improving wildlife viewing opportunities may include vegetation alteration such as roadside and viewpoint brushing and controlled burns.

Although prey abundance and distribution likely influence wolf distribution and therefore sighting probability, the abundance of ungulate prey in the DNPP study area was relatively stable during the years of this study (Adams and Roffler, 2009; Owen and Meier, 2009; Schmidt and Rattenbury, 2013). We assumed that local prey distribution shifts were reflected in our delineation of road sections because our road sections captured broadscale patterns of local variation in habitat. Additionally, although levels of human activity are known to impact wolves' use of habitat (Whittington et al., 2005; Hebblewhite and Merrill, 2008; Musiani et al., 2010), public access along the Denali Park Road was regulated during the study period and subject to the same annual limit and daily traffic levels (NPS, 1986).

The harvest of wide-ranging carnivores adjacent to protected areas could reduce sightings within protected areas through numerical impacts of removing individuals or through behavioral changes of individuals that survive negative encounters with people. Although both wolf presence and the annual wolf sightings increased predictably with den site proximity to the road in years with a harvest closure, wolf proximity and sightings were uniformly low during years with no harvest closure (Fig. 5). Even after accounting for fine-scale variation in wolf sightings due to the physical landscape and the characteristics of packs denning near the road in the spatially explicit model, a negative effect of the harvest closure on sightings remained. The effect of the closure on sightings was consistent across multiple scales (Table 4) and further supports a previous finding indicating that the harvest of wolves near park boundaries decreased sightings in both Denali and Yellowstone National Parks when measured on an annual basis (Borg et al., 2016).

This finding may indicate a behavioral avoidance of the road following years of exposure to harvest, although this direct link warrants further investigation (Borg et. al., 2016). Wolves selectively use human-made linear travel corridors (James and Stuart-Smith, 2000) when traffic and human activity is low (Thurber et al., 1994; Whittington et al., 2005). Through repeated exposure to non-lethal human activity such as vehicle and human traffic along the Denali Park Road, wolves may become habituated to human activity (Schultz and Bailey, 1978; Whittaker and Knight, 1998) and use the road corridor as a preferred travel route when they den in close proximity to the road. However, most trapping mortality in our study area occurs along linear travel corridors (winter trails). Increases in human persecution can alter animal activity patterns (Kitchen et al., 2000) and may result in a reduction of wolf use near the park road, in turn influencing wolf sightings.

There were few instances of den sites near the road in years with no harvest closure (Fig. 5). While this may indicate a causal link where wolves select breeding sites in response to human-related risk (Sazatornil et al., 2016), we caution that the relationships of wolf sightings and the proportion of wolf locations near the road with a harvest closure are highly dependent on a few data points. The issue warrants further monitoring of wolf proximity and sightings in years with and without the presence of a harvest closure to strengthen our understanding of this relationship. Although managers have little control over the locations wolves choose for denning, maintaining harvest closures adjacent to parks might increase sightings. Reinstatement of the closure on wolf hunting and trapping adjacent to DNPP would provide a strong test of the causal relationship between harvest adjacent to DNPP and reduced wolf sightings suggested by our findings. This relationship has important implications for managing wildlife harvest and viewing opportunities around the world (Borg et al., 2016). However, any proposed harvest closure creates a trade-off by decreasing trapping and hunting opportunities that may be highly valued. Hunting and trapping are important activities of Alaskan culture, and there is a desire to maintain the culture and knowledge related to trapping specifically (Alaska Trappers Association, 2015). However, typically only one to three individuals record harvesting wolves in the harvest closure areas adjacent to Denali in a given year (ADFG, 2013). While the lifestyle or livelihood of these individuals may be impacted, this cost should be weighed against the substantial benefits that would be gained in understanding the impacts of harvest on sightings by temporarily reinstating the closure.

Both the State of Alaska and the National Park Service (NPS) have mandates, regulations, and policies directing the management of wildlife, including wolves. While managing to protect wildlife sightings is rooted in NPS policy to maintain visitor enjoyment and Alaska state mandates to provide for non-consumptive use, there are no explicitly stated quantitative objectives. Without understanding the source of variability in sightings, these objectives are difficult to define. Here, we used a spatially explicit model that accounted for terrain and vegetation along the road corridor, and den site proximity to sections of the road. Our spatially explicit model of wolf sightings provides a framework for modeling the effects of physical, biological, and anthropogenic factors on visitor sightings of terrestrial wildlife, which may assist managers in developing quantitative objectives. Our results in the wolf sighting model showed consistency across multiple spatial scales, indicating that the coarse scale of 16.2 km segments was sufficient for understanding spatially explicit determinates of wolf sightings in our study system. This spatial scale appears appropriate to capture home-range level variation in movements influencing wolf sightings. We found strong effects of masking vegetation, denning behavior, pack size, and harvest management in areas surrounding DNPP on wolf sightings, providing managers with a quantitative model that can be used to evaluate how alternative management actions might affect sighting probabilities.

Although we used a unique dataset to identify key factors that influence wildlife sightings, this approach also could be applied to systems in which sighting data were collected less systematically if effort could be accounted for. Our physical covariates could be applied across a broad range of taxa, and the species-specific covariates could be developed and incorporated into a model to improve our understanding of factors that influence the sightings of other key species. As demonstrated here, these analyses can be powerful tools to inform management efforts and maintain wildlife viewing opportunities in the face of rapid global change.

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REFERENCES

Adams, L.G., and Roffler, G.H. 2009. Dynamics of the Denali caribou herd, Denali National Park, Alaska: Progress report (October 2007–September 2008). Anchorage: USGS Alaska Science Center. 18 p.

ADFG (Alaska Department of Fish and Game). 2010. Alaska Board of Game Meeting Information: Unit 20 wolf closure proposals. Proposal 152. Fairbanks: ADFG. http://www.adfg.alaska.gov/index.cfm?adfg=gameboard.meetinginfo&date=02-26-2010&meeting=fairbanks

———. 2013. Hunting and trapping data. Fairbanks: ADFG.

Alaska Trappers Association. 2015. Alaska's trapping heritage. Fairbanks: Alaska Trappers Association. http://www.alaskatrappers.org/trapperhert.html

Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's information criterion. Journal of Wildlife Management 74(6):1175–1178.
https://doi.org/10.2193/2009-367

Ballard, W.B., Ayres, L.A., Gardner, C.L., and Foster, W.J. 1991. Den site activity patterns of gray wolves, *Canis lupus*, in southcentral Alaska. Canadian Field-Naturalist 105(4):497–504.

Bartoń, K. 2014. MuMIn: Multi-model inference. R package version 1.12.1.
http://cran.r-project.org/package=MuMIn

Beale, C.M. 2007. The behavioral ecology of disturbance responses. International Journal of Comparative Psychology 20(2):111–120.

Boggs, K., Garibaldi, A., Stevens, J., Grunblatt, J., and Helt, T. 2001. Denali National Park and Preserve Landcover Mapping Project, Vol. 2: Landcover classes and plant associations. Natural Resource Technical Report NPS/DENA/NRTR-2001/002. National Park Service.

Borg, B.L., and Burch, J. 2014. Vital signs monitoring of wolf (*Canis lupus*) distribution and abundance in Denali National Park and Preserve, Central Alaska Network: Biological year 2012 report. Natural Resource Data Series NPS/CAKN/NRDS—2014/738. Fort Collins, Colorado: Natural Resource Stewardship and Science, National Park Service.
https://irma.nps.gov/DataStore/DownloadFile/522688

Borg, B.L., and Taylor, L. 2018. Denali wolf territories.
www.nps.gov/gis/storymaps/mapseries/v2/index.html?appid=64c2271845e049058aeb59828b0a0187#

Borg, B.L., Brainerd, S.M., Meier, T.J., and Prugh, L.R. 2015. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. Journal of Animal Ecology 84(1):177–187.
https://doi.org/10.1111/1365-2656.12256

Borg, B.L., Arthur, S.M., Bromen, N.A., Cassidy, K.A., McIntyre, R., Smith, D.W., and Prugh, L.R. 2016. Implications of harvest on the boundaries of protected areas for large carnivore viewing opportunities. PLoS ONE 11(4): e0153808.
https://doi.org/10.1371/journal.pone.0153808

Brainerd, S.M., Andrén, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W., Iliopoulos, Y., et al. 2008. The effects of breeder loss on wolves. Journal of Wildlife Management 72(1):89–98.
https://doi.org/10.2193/2006-305

Brashares, J.S., Arcese, P., and Sam, M.K. 2001. Human demography and reserve size predict wildlife extinction in West Africa. Proceedings of the Royal Society B: Biological Sciences 268:2473–2478.
https://doi.org/10.1098/rspb.2001.1815

Brodie, J.F., Roland, C.A., Stehn, S.E., and Smirnova, E. 2019. Variability in the expansion of trees and shrubs in boreal Alaska. Ecology 100(5): e02660.
https://doi.org/10.1002/ecy.2660

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: A practical information-theoretic approach, 2nd ed. New York: Springer Verlag.

Burson, S., III, Belant, J.L., Fortier, K.A., and Tomkiewicz, W.C., III. 1999. The suitability of bus drivers for monitoring large mammal abundance. In: Harmon, D., ed. On the Frontiers of Conservation: Proceedings of the Tenth Conference of Research and Resource Management in Parks and on Public Lands. Hancock, Michigan: George Wright Society. 102–106.

———. 2000. The effect of vehicle traffic on wildlife in Denali National Park. Arctic 53(2):146–151.
https://doi.org/10.14430/arctic844

Duffield, J.W., Neher, C.J., and Patterson, D.A. 2008. Wolf recovery in Yellowstone: Park visitor attitudes, expenditures, and economic impacts. Yellowstone Science 16(1):20–25.
https://www.nps.gov/yell/learn/upload/YS_16_1_sm.pdf

Duffus, D.A., and Dearden, P. 1990. Non-consumptive wildlife-oriented recreation: A conceptual framework. Biological Conservation 53(3):213–231.
https://doi.org/10.1016/0006-3207(90)90087-6

Eagles, P.F.J., McCool, S.F., and Haynes, C.D. 2002. Sustainable tourism in protected areas: Guidelines for planning and management. Best Practice Protected Area Guidelines Series No. 8. IUCN Gland, Switzerland: IUCN; Cambridge, United Kingdom: U.N. Environment Programme and the World Tourism Organization.
https://portals.iucn.org/library/sites/library/files/documents/PAG-008.pdf

Fix, P.J., Ackerman, A.J., and Fay, G. 2012. Estimating visits to Denali National Park and Preserve: Spring/summer 2011. Natural Resource Technical Report NPS/AKR/NRTR—2012/641. Fort Collins, Colorado: National Park Service.

Gill, J.A., Sutherland, W.J., and Watkinson, A.R. 1996. A method to quantify the effects of human disturbance on animal populations. Journal of Applied Ecology 33(4):786–792.
https://doi.org/10.2307/2404948

Haber, G.C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. PhD thesis, University of British Columbia, Vancouver.

Hebblewhite, M., and Merrill, E. 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. Journal of Applied Ecology 45(3):834–844.
https://doi.org/10.1111/j.1365-2664.2008.01466.x

Higginbottom, K., ed. 2004. Wildlife tourism: Impacts, management and planning. Champaign, Illinois: Common Ground Publishing.
https://sustain.pata.org/wp-content/uploads/2014/12/WildlifeTourism-impacts.pdf

James, A.R.C., and Stuart-Smith, A.K. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management 64(1):154–159.
https://doi.org/10.2307/3802985

Keller, R. 2019. Backcountry visitor experience survey report briefs. Wildlife Viewing Brief. Denali Park, Alaska: National Park Service
https://irma.nps.gov/DataStore/Reference/Profile/2266424

Kellner, K.F., and Swihart, R.K. 2014. Accounting for imperfect detection in ecology: A quantitative teview. PLoS ONE 9(10): e111436.
https://doi.org/10.1371/journal.pone.0111436

Kitchen, A.M., Gese, E.M., and Schauster, E.R. 2000. Changes in coyote activity patterns due to reduced exposure to human persecution. Canadian Journal of Zoology 78(5):853 – 857. https://doi.org/10.1139/z00-003

Knight, J. 2009. Making wildlife viewable: Habituation and attraction. Society & Animals 17(2):167 – 184. https://doi.org/10.1163/156853009X418091

Kutner, M.H., Nachtsheim, C.J., and Neter, J. 2004. Applied linear regression models, 4th ed. New York: McGraw-Hill Irwin.

Leroux, S.J. 2019. On the prevalence of uninformative parameters in statistical models applying model selection in applied ecology. PLoS ONE 14(2): e0206711. https://doi.org/10.1371/journal.pone.0206711

Levin, S.A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. Ecology 73(6):1943 – 1967. https://doi.org/10.2307/1941447

Manfredo, M.J., ed. 2002. Wildlife viewing: A management handbook. Corvallis: Oregon State University Press.

Manning, R.E., and Hallo, J.C. 2010. The Denali park road experience: Indicators and standards of quality. Park Science 27:33 – 41.

McKenny, H.C., Clark, W.C., Toubman, J.S., and Borg, B.L. 2015. Standards in the Denali Park Road vehicle management plan — how current conditions measure up: A summary report 2014. Natural Resources Technical Report NPS/DNP/NRR – 2015/905. Fort Collins, Colorado: National Park Service. https://irma.nps.gov/DataStore/DownloadFile/503432

Mech, L.D. 1999. Alpha status, dominance, and division of labor in wolf packs. Canadian Journal of Zoology 77:1196 – 1203. https://doi.org/10.1139/z99-099

———. 2000. Leadership in wolf (*Canis lupus*) packs. Canadian Field-Naturalist 114(2):259 – 263.

Mech, L.D., and Boitani, L., eds. 2003. Wolves: Behavior, ecology, and conservation. Chicago, Illinois: University of Chicago Press. https://doi.org/10.7208/chicago/9780226516981.001.0001

Mech, L.D., Adams, L.G., Meier, T.J., Burch, J.W., and Dale, B.W. 1998. The wolves of Denali. Minneapolis: University of Minnesota Press.

Meier, T.J., and Burch, J.W. 2009. Wolf monitoring protocol for Denali National Park and Preserve, Yukon-Charley Rivers National Preserve and Wrangell-St. Elias National Park and Preserve. Natural Resources Report NPS/CAMN/NRR-2009/168. Fort Collins, Colorado: National Park Service.

Montag, J.M., Patterson, M.E., and Freimund, W.A. 2005. The wolf viewing experience in the Lamar Valley of Yellowstone National Park. Human Dimensions of Wildlife 10(4):273 – 284. https://doi.org/10.1080/10871200500292843

Musiani, M., Morshed Anwar, S., McDermid, G.J., Hebblewhite, M., and Marceau, D.J. 2010. How humans shape wolf behavior in Banff and Kootenay National Parks, Canada. Ecological Modelling 221(19):2374 – 2387. https://doi.org/10.1016/j.ecolmodel.2010.06.019

Nakagawa, S., and Schielzeth, H. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4(2):133 – 142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

NPS (National Park Service). 1986. General management plan, land protection plan wilderness suitability review, Denali National Park and Preserve, Alaska. Anchorage: National Park Service, Department of the Interior. 231 p. https://www.nps.gov/dena/learn/management/generalmanagementplan.htm

———. 1995. Statement for management: Park purpose and significance. Denali Park: National Park Service, U.S. Department of the Interior. https://irma.nps.gov/DataStore/Reference/Profile/2284303

Orams, M.B. 1996. A conceptual model of tourist-wildlife interaction: The case for education as a management strategy. Australian Geographer 27(1):39 – 51. https://doi.org/10.1080/00049189608703156

Owen, P.A., and Meier, T.J. 2009. 2008 Aerial moose survey, Denali National Park and Preserve. Denali Park: National Park Service.

Packard, J.M. 2003. Wolf behavior: Reproductive, social and intelligent. In: Mech, L.D., and Boitani, L., eds. Wolves: Behavior, ecology and conservation. Chicago, Illinois: University of Chicago Press. 35 – 65.

Peterson, R.O., Jacobs, A.K., Drummer, T.D., Mech, L.D., and Smith, D.W. 2002. Leadership behavior in relation to dominance and reproductive status in gray wolves, *Canis lupus*. Canadian Journal of Zoology 80:1405 – 1412. https://doi.org/10.1139/z02-124

Potvin, M.J., Peterson, R.O., and Vucetich, J.A. 2004. Wolf homesite attendance patterns. Canadian Journal of Zoology 82:1512 – 1518. https://doi.org/10.1139/z04-121

R Core Team. 2014. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. http://www.r-project.org/

Radeloff, V.C., Stewart, S.I., Hawbaker, T.J., Gimmi, U., Pidgeon, A.M., Flather, C.H., Hammer, R.B., and Helmers, D.P. 2010. Housing growth in and near United States protected areas limits their conservation value. Proceedings of the National Academy of Sciences 107(2):940 – 945. https://doi.org/10.1073/pnas.0911131107

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., et al. 2014. Status and ecological effects of the world's largest carnivores. Science 343(6167):151 – 162. https://doi.org/10.1126/science.1241484

Ruprecht, J.S., Ausband, D.E., Mitchell, M.S., Garton, E.O., and Zager, P. 2012. Homesite attendance based on sex, breeding status, and number of helpers in gray wolf packs. Journal of Mammalogy 93(4):1001 – 1005. https://doi.org/10.1644/11-MAMM-A-330.1

Sazatornil, V., Rodríguez, A., Klaczek, M., Ahmadi, M., Álvares, F., Arthur, S., Blanco, J.C., et al. 2016. The role of human-related risk in breeding site selection by wolves. Biological Conservation 201:103–110.
https://doi.org/10.1016/j.biocon.2016.06.022

Schmidt, J.H., and Rattenbury, K.L. 2013. Reducing effort while improving inference: Estimating Dall's sheep abundance and composition in small areas. Journal of Wildlife Management 77(5):1048–1058.
https://doi.org/10.1002/jwmg.557

Schultz, R.D., and Bailey, J.A. 1978. Responses of national park elk to human activity. Journal of Wildlife Management 42(1):91–100.
https://doi.org/10.2307/3800694

Sikes, R.S., Gannon, W.L., and The Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92(1):235–253.
https://doi.org/10.1644/10-MAMM-F-355.1

Singer, F.J., and Beattie, J.B. 1986. The controlled traffic system and associated wildlife responses in Denali National Park. Arctic 39(3):195–203.
https://doi.org/10.14430/arctic2074

Skibins, J.C., Hallo, J.C., Sharp, J.L., and Manning, R.E. 2012. Quantifying the role of viewing the Denali "Big 5" in visitor satisfaction and awareness: Conservation implications for flagship recognition and resource management. Human Dimensions of Wildlife 17(2):112–128.
https://doi.org/10.1080/10871209.2012.627531

Stahler, D.R., MacNulty, D.R., Wayne, R.K., vonHoldt, B., and Smith, D.W. 2013. The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. Journal of Animal Ecology 82(1):222–234.
https://doi.org/10.1111/j.1365-2656.2012.02039.x

Stander, P.E. 2008. Tourism and the conservation of desert lions in Namibia. Desert Lion Research Report. Skeleton Coast, Namibia: Desert Lion Conservation Trust.
https://lionrangers.org/wp-content/uploads/2020/08/Stander2008ConservationTourismDesertAdapted.pdf

Stankowich, T. 2008. Ungulate flight responses to human disturbance: A review and meta-analysis. Biological Conservation 141(9):2159–2173.
https://doi.org/10.1016/j.biocon.2008.06.026

Steyaert, S.M., Leclerc, M., Pelletier, F., Kindberg, J., Brunberg, S., Swenson, J.E., and Zedrosser, A. 2016. Human shields mediate sexual conflict in a top predator. Proceedings of the Royal Society B: Biological Sciences 283: 20160906.
https://doi.org/10.1098/rspb.2016.0906

Sturm, M., Racine, C., and Tape, K. 2001. Increasing shrub abundance in the Arctic. Nature 411:546–547.
https://doi.org/10.1038/35079180

Tape, K., Sturm, M., and Racine, C. 2006. The evidence for shrub expansion in northern Alaska and the Pan-Arctic. Global Change Biology 12(4):686–702.
https://doi.org/10.1111/j.1365-2486.2006.01128.x

Theuerkauf, J., Jędrzejewski, W., Schmidt, K., and Gula, R. 2003. Spatiotemporal segregation of wolves from humans in the Białowieża Forest (Poland). Journal of Wildlife Management 67(4):706–716.
https://doi.org/10.2307/3802677

Thomas, C.C., and Koontz, L. 2020. 2019 national park visitor spending effects: Economic contributions to local communities, states, and the nation. Natural Resource Report NPS/NRSS/EQD/NRR—2020/2110. Fort Collins, Colorado: National Park Service.
https://www.nps.gov/subjects/socialscience/vse.htm

Thurber, J.M., Peterson, R.O., Drummer, T.D., and Thomasma, S.A. 1994. Gray wolf response to refuge boundaries and roads in Alaska. Wildlife Society Bulletin 22(1):61–68.

Thurston, L.M. 2002. Homesite attendance as a measure of alloparental and parental care by gray wolves (*Canis lupus*) in northern Yellowstone National Park. M.S. thesis, Texas A&M University, College Station, Texas.

Tsunoda, H., Gula, R., Theuerkauf, J., Rouys, S., Radler, S., Pirga, B., Eggermann, J., and Brzezowska, B. 2009. How does parental role influence the activity and movements of breeding wolves? Journal of Ethology 27: 185.
https://doi.org/10.1007/s10164-008-0106-z

U.S. Census Bureau. 2011. National survey of fishing, hunting, & wildlife-associated recreation 2011.
https://www.census.gov/data/datasets/2011/demo/fhwar/2011.html

Western Regional Climate Center. 2015. Cooperative climatological data summaries.
https://wrcc.dri.edu/Climate/west_coop_summaries.php

Whittaker, D., and Knight, R.L. 1998. Understanding wildlife responses to humans. Wildlife Society Bulletin 26(2):312–317.

Whittington, J., St. Clair, C.C., and Mercer, G. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications 15(2):543–553.
https://doi.org/10.1890/03-5317

Wiens, J.A. 1989. Spatial scaling in ecology. Functional Ecology 3(4):385–397.
https://doi.org/10.2307/2389612

Wildlife Team, DNPP. 2007. Wolf-human conflict management plan, Denali National Park and Preserve. Denali Park: National Park Service.
https://irma.nps.gov/DataStore/Reference/Profile/2275692

Woodroffe, R., and Ginsberg, J.R. 1998. Edge effects and the extinction of populations inside protected areas. Science 280(5372):2126–2128.
https://doi.org/10.1126/science.280.5372.2126

Zeileis, A., Kleiber, C., and Jackman, S. 2008. Regression models for count data in R. Journal of Statistical Software 27(8):1–25.
https://doi.org/10.18637/jss.v027.i08