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Resource selection and movement of male moose in response to varying levels of off-road vehicle access

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Citation: Brown, C. L., K. Kielland, T. J. Brinkman, S. L. Gilbert, and E. S. Euskirchen. 2018. Resource selection and movement of male moose in response to varying levels of off-road vehicle access. Ecosphere 9(9):e02405. 10.1002/ecs2.2405

Abstract. Many rural communities are increasingly relying on off-road motorized vehicles to access wildlife for both subsistence harvest and recreational hunting. Understanding the effects of trail and road networks on wildlife behavior is crucial to effective management for subsistence opportunities in communities that depend on accessible populations as an ecosystem service. We collared 26 adult male moose (*Alces alces*) in interior Alaska to monitor fine-scale habitat selection and movement patterns before, during, and after the hunting season in relation to trail and habitat characteristics. Moose response varied by region and the associated distribution of regional hunter trails (e.g., trails and secondary roads). Moose that resided in areas with extensive trail access selected habitat closer to trails and vegetative cover. Additionally, moose step length increased as distance to cover increased. Moose in more remote, less accessible regions avoided areas with high trail densities and selected habitat closer to quality forage during the hunting season. Moose step lengths also increased with higher densities of trails. Our research suggests that landscape-level hunter access can affect patterns of male moose movement and habitat selection to avoid risk during the hunting season. Our models provide an innovative approach to examining the spatio-temporal variation of behavioral responses to habitat and landscape features and can serve as a framework for managers to better understand the relationships between human disturbance during the hunting season and wildlife management and conservation.

Key words: all-terrain vehicle; habitat use; hunting; road density.

Received 4 April 2018; revised 28 June 2018; accepted 6 July 2018. Corresponding Editor: Joseph Holbrook.

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Introduction

Rapid social, ecological, and economic changes across high-latitude regions often compel hunters to incorporate more efficient hunting practices, such as using motorized vehicles (e.g., all-terrain vehicles [ATVs], snowmobiles) to access remote areas and difficult terrain (Brinkman et al. 2007, Shanley et al. 2013). In some northern regions, ATVs are the primary means of transportation for subsistence hunting and wild food gathering (Berkes and Jolly 2002). In Alaska, for example, moose are an important food resource for many residents and most hunters use motorized transportation to access remote terrain, as well as for transporting meat long distances. The proliferation of motorized access for the harvest of wildlife resources can create extensive trail networks into otherwise inaccessible areas (Shanley and Pyare 2011), which may create opportunities for hunter access as well as challenges to the management and conservation of wildlife.

Roads can introduce a pervasive disturbance to the landscape that directly impacts the quality of habitat for wildlife populations. Direct impacts include diminishing habitat connectivity (Saunders et al. 2002), an increase in the proportion of edge to core habitat (Forman et al. 2003), exposure to noise and visual disturbance (Stankowich 2008, Brown et al. 2012), and an increase in the anthropogenic footprint past the physical boundary of roads (e.g., road-effect zone; Shanley and Pyare 2011). Additionally, roads, and the vehicles that travel on them, can induce a wide variety of behavioral responses, such as heightened levels of vigilance and increased flight distance (Gavin and Komers 2006, Rumble and Gamo 2011). Wildlife may respond to roads by selecting spatial refugia (e.g., vegetative cover) or areas farther from road corridors (Swenson 1982, Millspaugh et al. 2000, Vieira et al. 2003). Research has found that even narrow (<3 m wide) ATV trails can disrupt the movement and dispersal of wildlife species (Ouren et al. 2007). Additionally, traffic along rural roads and trails is often infrequent, and behavioral response by wildlife is less likely to occur when disturbances are intermittent (Stankowich 2008, Brown et al. 2012).

Behavioral responses are likely to hinge on a variety of landscape characteristics at varying temporal and spatial scales. For example, Beyer et al. (2013) found that rates at which moose (*Alces alces*) cross roads varied both seasonally and as a function of road density. Additionally, moose may select areas with moderate road density at the landscape scale (Bowman et al. 2010), but avoid roads at finer scales (Dussault et al. 2007). Animals may select habitat near rural roads and trails due to their proximity to productive habitat (e.g., low valleys with good drainage). Rural roads can also bisect large patches of relatively undisturbed habitat and may offer accessible trails for wildlife (Whittington et al. 2005). Some predators may preferentially use areas near roads and trails because these linear features can increase speed and ease of travel across their territory (James and Stuart-Smith 2000). Alternatively, risk-sensitive predators might avoid areas with higher probabilities of encountering people and select for low-use roads and trails over high-use roads and trails (Whittington et al. 2004), and by doing so, offer spatial refugia for large herbivores (Muhly et al. 2011).

The amount of exposure to humans (i.e., frequent vs. infrequent) and type of recreation along roads or trails may also affect risk-avoidance strategies (Stankowich 2008). Although previous work (Shanley and Pyare 2011) has shown that moose avoided preferred habitats along ATV trails with increasing levels of traffic, we do not yet know how the degree of exposure or likelihood of encountering humans along ATV trails might affect moose habitat selection and movement patterns. Hunting, in particular, introduces a pulse of humans into areas that may otherwise see little to no recreation activity. Although hunting can be temporally predictable due to set hunting seasons with recurring annual opening and closing dates (Proffitt et al. 2009), varying levels of road access can affect how often ungulates encounter humans during the hunting season. If hunters use roads in the same regions every year, ungulates will likely respond behaviorally to the spatial–temporal predictability of hunting risk (Cromsigt et al. 2013).

Understanding the effects of trail and road networks on wildlife behavior is crucial to effective management for subsistence opportunities in communities that depend on accessible populations as an ecosystem service. The behavioral responses of ungulates to human activity along roads during the hunting season can create challenges for rural hunters that rely on dependable access to local wildlife. If hunter and wildlife distributions do not overlap, there may be a disconnect between wildlife abundance and hunting opportunities, resulting in increased hunter dissatisfaction (Heberlein 2002), especially if wildlife avoid or select habitat away from accessible areas (Fryxell et al. 1988, Brinkman et al. 2007). In such situations, hunting opportunities may decline as hunter activity increases, resulting in negative attitudes toward management. To facilitate effective management, it is thus important to quantify and communicate how spatial and temporal variation of roads in conjunction with varying levels of exposure to anthropogenic activities can affect wildlife habitat selection and movement patterns.

While recent studies have started to examine the effects of hunting on ungulate behavioral responses, few studies have examined how road access can impact the spatial and temporal variation in human-predation risk on the landscape

(Ordiz et al. 2012). Here, we explore this relationship by examining how varying habitat (e.g., distance to quality forage and cover) and infrastructure characteristics (e.g., distance to roads and regional trail densities) affected male moose habitat selection and activity patterns during the hunting season in a highly accessible region compared to a remote region in Alaska. We predicted that moose that reside in areas with high densities of roads and trails would be more likely to exhibit risk-avoidance behaviors (e.g., select for cover habitat, increased movement patterns) and that these responses would be most pronounced during the hunting season.

Methods

Study area

We conducted our research ~40 km southeast of Delta Junction, a rural Alaska community with ~975 residents located 10 km north of the Alaska Range. Our study area was situated in Game Management Unit (GMU) 20D. The Gerstle River naturally divides the study area into two subunits: southwest (SW GMU20D) and southeast (SE GMU20D) regions. Both regions are characterized by a mixture of deciduous and needleleaf canopy forest, and subalpine shrub communities. However, the southwestern region has an extensive network of ATV trails and dirt roads, whereas the southeastern region is relatively inaccessible to ATVs with few roads and trails (Fig. 1). The differing levels of hunter access between these two regions are likely due to a combination of land management decisions, terrain features, and accessibility. The SW GMU20D contains popular public hunting areas managed by the U.S. Army (Gerstle River Training Area) and the Alaska Department of Fish and Game (ADFG; Gerstle Fields). Both agencies have actively used and occasionally maintained ATV roads and trails in the area. This region also has several private properties that permit hunting on their land. Alternatively, SE GMU20D has far

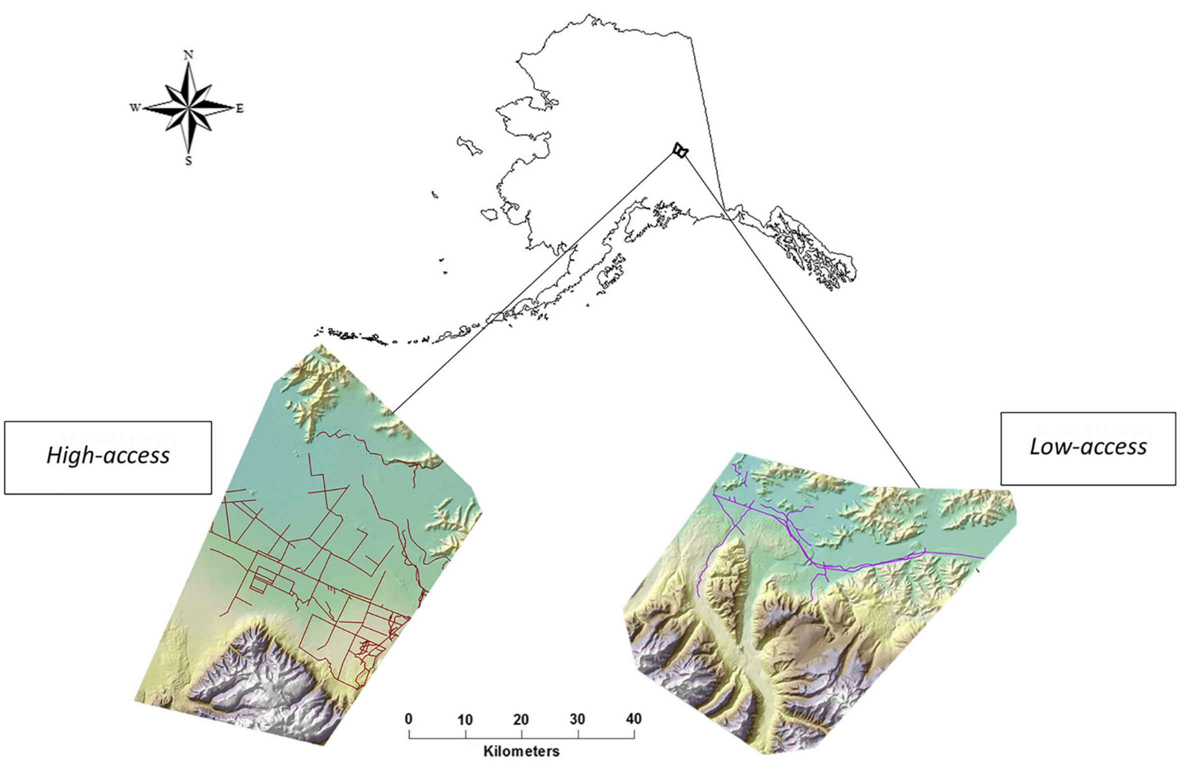

Fig. 1. Map of the high-access and low-access study regions in Game Management Unit 20D. The high-access area has approximately 513 km of all-terrain vehicle (ATV) trails, dirt and paved roads, and a major highway bisecting the landscape, whereas the low-access area has far fewer (139 km) ATV trails and roads.

fewer maintained roads and private properties. The high-elevation terrain in SE GMU20D is generally difficult to access via ATV (see Fig. 1).

Variation in hunter activity

Just as the level of access varies between the two subunits, the number of hunters that were reported accessing SW GMU20D and SE GMU20D during the hunting season differs substantially. Moose hunting in both regions is characterized as a general hunt where hunters purchase licenses, procure moose tags or harvest tickets, and follow the general season dates. General season hunts are available to Alaska residents as well as non-residents. The general season in the study area is from 1 September to 15 September. Each licensed hunter can harvest one bull with 127-cm antlers (50 inch) spread or antlers with four or more brow tines on at least one side.

Between 2005 and 2012, an average of 505 hunters/yr reported hunting in SW GMU20D on their general moose harvest tickets (Bruning 2013). By contrast, during those same years, an average of 70 hunters/yr reported hunting within SE GMU20D (Bruning 2013). Due to the combination of trail densities and hunters accessing those trails, we characterized SW GMU20D as having high access and SE GMU20D as having low access.

We installed 15 infrared trail cameras (Reconyx HyperFire 5.0) on trails within the study area to monitor how hunter activity fluctuated before (15 August–30 August), during (31 August–16 September), and after (17 September–15 October) the 2013–2014 hunting seasons. We added a one-day buffer to the hunting season before and after the general hunt to account for activity associated with movement in and out of hunting camps. Cameras were placed 1 m above the ground within 3 m of ATV trails and roads in known hunter use areas in close proximity to the Gerstle River. Cameras were operational 24 h/d and were set to take three pictures per detection. For each picture, we recorded the entity (e.g., human activity type), location, date, and time. We followed techniques from Carter et al. (2012) to define entity detections. A detection was either (a) consecutive pictures of *different* individuals, (b) consecutive pictures of the same individual >30 min apart, or (c) nonconsecutive pictures of the same individuals. We then summed the number of entity detections at every camera trap location. Human activity included all ATV, automobile, 4 × 4 trucks, and dirt bikes.

Predictive landscape variables

Moose habitat characteristics were identified using the Alaska Natural Heritage Program's Interior Vegetation Map (ANHP 2016) and the Salcha-Delta Soil and Water Conservation District's map (S-DSandW 2014) of the Gerstle River Training Area. Both maps included a variation of Viereck et al.'s (1992) Alaska Vegetation Classification III and IV coding definitions. We reclassified the 74 vegetation classes (Appendix S1) according to three categories (high, medium, and low) for both browse quality and vegetation cover (Kellie 2005, Brinkman and Kellie 2014). At each individual location, we calculated the minimum distance (km) to high-quality forage as well as cover type.

To assess the relationship between moose and hunter access, we used a statewide road layer to identify all major highways, paved roads, and secondary roads. Additionally, we digitized ATV trails in ArcGIS 10.1 (ESRI, Redlands, California, USA) using the Salcha-Delta Soil and Water Conservation District Map trail guide, aerial imagery, and handheld GPS units. We also included major rivers (e.g., Tanana River, Gerstle River) that could be navigated by boat. All trails, roads, and navigable rivers were defined as hunter trails. Trails were checked for accuracy by local wildlife managers. The minimum distance (km) to hunter trails was calculated for each location, and we used the Line Density tool in ArcGIS to calculate the density of hunter trails. This tool calculates the density of linear features in the neighborhood of each output raster cell in length per unit area (km^2).

Moose activity and habitat selection

In October 2012, 26 adult male moose (antlers 30–40″ wide) were captured by darting from helicopter. We fitted captured moose with GPS radio collars (TDW-4780; Telonics, Mesa, Arizona, USA) equipped with ARGOS connectivity. Collars were programmed to collect one location every hour from 15 August to 15 October 2014 and every two hours throughout the rest of the year. We obtained 75,900 locations of the 26 moose, with an overall fix rate of 90%, and removed locations with obvious location errors. Individuals with locations in SW GMU20D were designated as high-access moose, and moose with locations in

SE GMU20D were designated as low-access moose. We further defined study-region boundaries by mapping the summer/fall locations from GPS-collared moose over two hunting seasons (2013–2014) creating minimum convex polygons from seasonal locations for each region (Fig. 1; high-access, 1570 km^2; low-access, 1592 km^2). Four animals died during the 2012–2013 winter and were excluded from the analyses.

To examine the effects of hunting season on moose movement patterns, we used step length as an indicator of moose movement rates relative to time periods before and after the hunting season. A step is a line segment between two consecutive GPS locations taken at regular intervals (Turchin 1998). Step lengths have been used to characterize animal behaviors, where longer steps generally indicate increased travel or displacement (Franke et al. 2006) and shorter step lengths imply longer residency time in a given habitat patch (Turchin 1998). Moose step lengths were calculated between consistent fix intervals of one hour. We used length-weighted means to analyze the habitat and trail characteristics along each step. Length-weighted means were calculated by dividing each step into segments that pass through single raster cells. The length of each segment is multiplied by the value of the raster cell, and then, segment values are summed across the step and divided by the total step length to derive a mean step value for each variable of interest.

We used generalized additive mixed models (GAMMs) to examine moose step length as a function of habitat characteristics with individual moose as a random factor to account for within-individual dependency among the observations. Time periods before, during, and after the hunting season were modeled separately for both regions. A $\log_{10}$ transformation was used to normalize the distribution of step lengths. Our candidate models (Appendix S2) included all combinations of habitat variables (distance to high-quality forage and cover) and trail variables (trail density and distance to trail). We reported model weights and Akaike information criterion (AIC) differences, measuring the information loss between models given the data, to compare model ranking. This approach allowed us to verify whether moose had different movement rates during the hunting season vs. before/after the onset of hunting. Using GAMMs also allowed us to flexibly model step length through time (Julian date) by fitting smoothing splines.

Step selection functions (SSFs) were used to identify habitat, landscape, and anthropogenic variables that influenced moose movement (Fortin et al. 2005). Steps can be characterized by the line segments between locations, the average continuous habitat variables along the step, the proportion of habitat along each step, or by the environmental characteristics at the endpoint of each step (Thurfjell et al. 2014). In total, we analyzed 36,505 steps for moose in the high-access area (n = 12) and 29,850 steps for moose in the low-access area (n = 10). We analyzed the used and available locations at step endpoints. Matched sets of used and available steps are compared using conditional logistic regression, taking the same generalized exponential form as a resource selection function with a log-link function. Five available steps were generated for each used point by randomly drawing step length and turn angles from two distributions established from observations of monitored individuals. Separate step length and turn angle distributions were generated for each time period (pre-hunting, hunting, post-hunting). Because step length and turning angle may not be independent (Morales et al. 2004) and high fix rates increase the correlation between step length and turning angle (Thurfjell et al. 2014), we used linear regressions to test for differences between distributions.

Next, we used a two-stage modeling approach that fits models separately for each individual animal and then averages regression parameters across individuals to quantify population-level patterns for both regions (Fieberg et al. 2010). We fit conditional logistic regression models for each individual moose separately resulting in AIC values and weights (Burnham and Anderson 2002). We then calculated an average AIC value and weight (wt) for each model across individuals. To obtain population-level coefficient estimates, we then averaged coefficient values from the best model across all moose for each region (Fieberg et al. 2010). We evaluated the same set of candidate models for moose in both regions (high-access and low-access). We found no highly correlated variables ($|r| > 0.7$). The 15 candidate models (Appendix S3) included combinations of five habitat and landscape predictor variables (distance to high-quality cover, distance to high-quality forage, trail density, and distance to trail). The predictive performance of SSF models was validated using a fivefold cross-validation based on "individual" blocking (Roberts et al. 2017). Here, we split data by randomly selecting individuals, in which each moose contributed all GPS fixes to a single fold.

Results

Overall, the high-access area had three times the road/trail density of the low-access area, with 513 km (0.3 km/km^2) of ATV trails and dirt and paved roads bisecting the landscape compared to 140 km (0.1 km/km^2) trails and roads. Over the course of two years, we identified 3622 camera trap detections of automobiles, ATVs, and dirt bikes at camera trap stations along hunter travel corridors. The mean (± SE) number of daily hunter detections varied, with highest activity during the hunting season (2013 = 296 ± 15, 2014 = 123 ± 13), as opposed to before (2013 = 13 ± 1, 2014 = 8 ± 0.6) and after (2013 = 12 ± 2, 2014 = 15 ± 1.5) the hunting season (Fig. 2).

Pre-hunting movement and resource selection

Prior to the hunting season, moose hourly step lengths were significantly longer in the high-access region (177.8 m ± 2.7 m) compared to the low-access region (149.5 m ± 2.9 m; $P < 0.0005$, Fig. 3). The top model from GAMMs predicting step length for high-access moose included the full model set. Moose step lengths increased in areas with more trails (i.e., higher trail densities), and when distance from forage, cover, and trails increased (Table 1). For low-access moose, step lengths likewise increased in areas with more trails, but were shorter in areas farther from forage (Table 1). The top-ranked model predicting high-access (wt = 0.28 and low-access (wt = 0.21) moose habitat selection included distance to high-quality forage and cover where individuals selected areas closer to high-quality forage and avoided habitat closer to cover (Table 2).

Hunting movement and resource selection

Moose in the high-access region had significantly longer hourly step lengths (174 m ± 3.6 m) than low-access moose (136 m ± 3.4 m; $P < 0.005$; Fig. 3). The top models predicting step length

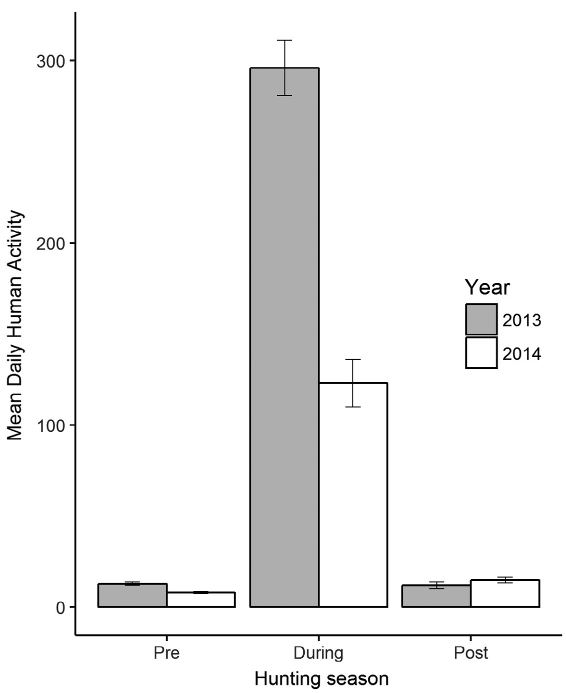

Fig. 2. Mean ± SE number of daily hunter detections (2013–2014) from the Gerstle camera trap grid.

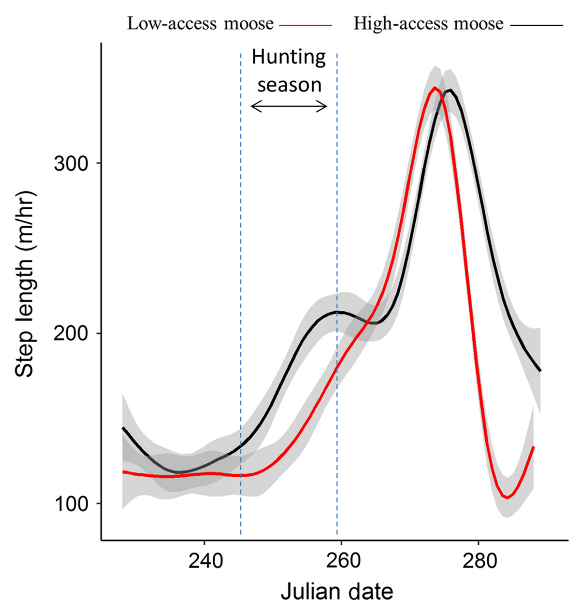

Fig. 3. Moose step lengths over the hunting (30 August–16 September) season. Peak step lengths for both regions were 1 October–7 October and are likely associated with the annual rut.

Table 1. Coefficients, 95% confidence limits, and model weights estimated by the top-ranked general additive mixed model predicting step length for moose in high-access and low-access areas.

	High-access	Low-access
Pre-hunting season	β (upper/lower CL)	β (upper/lower CL)
Distance to cover	0.06 (0.04/0.08)	NA
Distance to forage	0.05 (0.03/0.07)	−0.005 (−0.06/0.05)
Trail density	5.4 (4.9/6.0)	4.6 (3.9/5.3)
Distance to trail	0.01 (0.002/0.02)	NA
Model weight, wt	**0.24***	**0.36**
Hunting season		
Distance to cover	0.10 (0.08/0.2)	NA
Distance to forage	NA	0.08 (0.002/0.2)
Trail density	−8.2 (−13/−2.9)	2.7 (1.9/3.5)
Distance to trail	NA	NA
Model weight, wt	**0.41**	**0.28**
Post-hunting season		
Distance to cover	0.04 (0.02/0.06)	0.01 (0.006/0.01)
Distance to forage	0.03 (−0.009/0.07)	0.4 (0.3/0.5)
Trail density	−1.5 (−1.9/−0.9)	−0.6 (−1.2/−0.05)
Distance to trail	−0.06 (−0.4/0.3)	NA
Model weight, wt	**0.45**	**0.63**

Notes: Trail distance represents distance to all hunter travel corridors (trails, roads, navigable rivers). Trail density represents the number of trails/km^2 in a given area. Models results are across three time periods: pre-hunting season (15 August–29 August), hunting season (30 August–16 September), and post-hunting season (17 September–15 October).

* Model weights are denoted in bold type.

Table 2. Coefficients, 95% confidence limits, and model weights estimated by the top-ranked population-level model predicting resource selection for moose in high-access and low-access areas.

	High-access	Low-access
Pre-hunting season	β (lower/upper CL)	β (lower/upper CL)
Distance to cover	0.06 (0.04/0.08)	0.08 (0.002/0.2)
Distance to forage	−0.05 (−0.1/0.03)	−0.11 (−0.1/−0.07)
Trail density	NA	NA
Distance to trail	NA	NA
Model weight, wt	**0.28***	**0.21**
Hunting season		
Distance to cover	−0.07 (−0.1/−0.03)	NA
Distance to forage	0.1 (0.04/0.2)	−0.08 (−0.2/−0.002)
Trail density	NA	−0.2 (−0.3/−0.06)
Distance to trail	−0.02 (−0.3/0.2)	NA
Model weight, wt	**0.15**	**0.29**
Post-hunting season		
Distance to cover	0.12 (0.002/0.2)	0.2 (−0.3/−0.07)
Distance to forage	−0.10 (−0.2/−0.002)	−0.1 (−0.2/−0.05)
Trail density	0.02 (0.0004/0.04)	NA
Distance to trail	−0.32 (−0.7/0.07)	NA
Model weight, wt	**0.27**	**0.38**

Notes: Trail distance represents distance to all hunter travel corridors (trails, roads, navigable rivers). Trail density represents the number of trails/km^2 in a given area. Models results are across three time periods: pre-hunting season (15 August–29 August), hunting season (30 August–16 September), and post-hunting season (17 September–15 October).

* Model weights are denoted in bold type.

during the hunting season included trail density for high-access and low-access moose. For moose in the high-access region, step lengths decreased in areas with more trails (Table 1). Step lengths increased in areas with more trails for low-access moose (Fig. 4). During the hunting season, moose step length increased in low-access areas as distance to forage increased. For moose in high-access areas, step length increased as distance to cover increased. During the hunting season, high-access moose selected areas closer to cover and areas closer to trails (wt = 0.15), but the trail association was weakly positive (Table 2), whereas low-access moose selected areas closer to high-quality forage while avoiding areas with more trails (wt = 0.29; Table 2).

Post-hunting movement and resource selection

Following hunting season, moose hourly step lengths were significantly different between the high-access (250.8 m ± 3.5 m) and low-access (218.9 m ± 3.8 m; $P < 0.0005$) areas. In both areas, moose step lengths decreased in areas with more trails in both regions (Table 1).

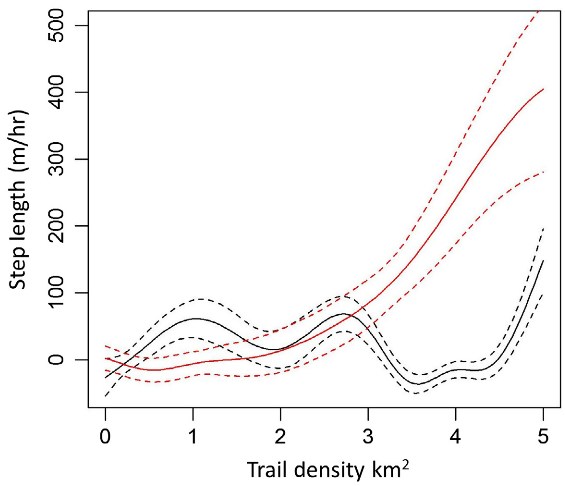

Fig. 4. Moose step lengths during the hunting season in relation to trail density (km2). Stippled lines indicate 95% CI; black lines represent "high-access"; and red lines represent "low-access."

Additionally, moose step lengths increased as distance to forage and cover increased. After hunting season, moose in high-access areas selected habitat with more trails and closer to trails (wt = 0.27; Table 2). Moose in both regions selected areas closer to high-quality forage and avoided habitat closer to cover (Table 2).

Our results indicated that SSF models, on average, accurately predicted habitat use patterns of moose across seasons in both high- and low-access areas (Table 3). Spearman rank correlations for individuals in the high-access region, averaged across folds, were as follows: pre-hunting: $r_s = 0.90$; hunting: $r_s = 0.98$; and post-hunting: $r_s = 0.92$. Spearman rank correlations for individuals in the low-access region, averaged across folds, were as follows: pre-hunting: $r_s = 0.94$; hunting: $r_s = 0.98$; and post-hunting: $r_s = 0.97$.

Discussion

Moose exhibited different movement and habitat selection strategies to avoid risk during the hunting season depending on the level of hunter access. Moose in the study area characterized by an extensive and accessible network of trails and roads had significantly longer step lengths during the hunting season than moose in the more remote, inaccessible study region. Correspondingly, moose movement patterns responded to the effect of trail density differentially between the two regions. In the high-access area, moose step lengths were shorter as trail densities increased, whereas step lengths were longer as trail densities increased in the low-access region, indicating that high-access but not low-access moose were moving less when encountering areas with more trails, presumably because trails were more used by hunters in the high-access region. This suggests that male moose tried to

Table 3. Individual block cross-validation results describing the predictive performance of Step selection function (SSF) models.

Season	Fold 1	Fold 2	Fold 3	Fold 4	Fold 5	Average
High-access						
Pre- hunting	$r_s = 0.83$ ($P = 0.08$)	$r_s = 0.98$ ($P = 0.006$)	$r_s = 0.92$ ($P = 0.05$)	$r_s = 0.88$ ($P = 0.06$)	$r_s = 0.90$ ($P = 0.03$)	$r_s = 0.90$
Hunting	$r_s = 0.98$ ($P = 0.005$)	$r_s = 0.97$ ($P = 0.006$)	$r_s = 0.99$ ($P = <0.001$)	$r_s = 0.99$ ($P = <0.001$)	$r_s = 0.97$ ($P = 0.03$)	$r_s = 0.98$
Post-hunting	$r_s = 0.94$ ($P = 0.05$)	$r_s = 0.98$ ($P = 0.003$)	$r_s = 0.81$ ($P = 0.10$)	$r_s = 0.95$ ($P = 0.05$)	$r_s = 0.91$ ($P = 0.08$)	$r_s = 0.92$
Low-access						
Pre-hunting	$r_s = 0.99$ ($P = <0.001$)	$r_s = 0.83$ ($P = 0.05$)	$r_s = 0.96$ ($P = 0.02$)	$r_s = 0.99$ ($P = <0.001$)	$r_s = 0.93$ ($P = 0.04$)	$r_s = 0.94$
Hunting	$r_s = 0.99$ ($P = <0.001$)	$r_s = 0.99$ ($P = <0.001$)	$r_s = 0.95$ ($P = 0.02$)	$r_s = 0.99$ ($P = <0.001$)	$r_s = 0.98$ ($P = 0.003$)	$r_s = 0.98$
Post-hunting	$r_s = 0.95$ ($P = 0.04$)	$r_s = 0.99$ ($P = <0.001$)	$r_s = 0.98$ ($P = 0.003$)	$r_s = 0.99$ ($P = <0.001$)	$r_s = 0.96$ ($P = <0.01$)	$r_s = 0.97$

Note: Spearman rank correlations between SSF bin ranks and area-adjusted frequencies, along with the average across all folds for each season.

reduce the risk of being detected in areas that were more likely to be used by hunters. This relationship was especially pronounced for moose in areas with >4 km/km^2 of trails. Additionally, as distance to cover increased, so did moose step lengths, indicating faster movements (e.g., displacement) when cover opportunities decreased.

Results from SSF models further support our findings that the distribution of off-road vehicle access can influence habitat use patterns. We found that high-access moose selected habitats closer to trails but also areas in close proximity to high-quality cover. Although this relationship may seem counterintuitive, moose that reside in the high-access region are more likely to encounter humans along ATV trails and may be selecting areas with more vegetative cover as a behavioral response to perceived predation by humans. Other studies have found that ungulates utilize habitat that provides cover opportunities, such as closed-canopy forests, during the hunting season (Bjørneraas et al. 2011, Bonnot et al. 2013). Since moose are selecting for high-quality cover over forage during the hunting season, this indicates a trade-off between time spent on antipredator behavior and foraging behavior. As long as moose maintain close proximity to vegetative cover, this strategy may also be more energetically effective than long-distance movements away from human disturbance. Although we had expected to find moose further away from trails in the high-access area due to human disturbance, we found moose were more likely to select areas closer to trails and roads in high-access areas. Moose in high-access areas may be less sensitive to human disturbance along trails, or they may be utilizing rural roads and trails as travel corridors into relatively undisturbed habitat or productive habitat (e.g., low valleys with good drainage) or responding to the physical disturbance of ATV trails on the landscape, which can facilitate growth of highly desirable forage (e.g., willows; Child 1998). In contrast, we found that low-access moose avoided areas with high trail densities and selected habitat closer to quality forage. This would suggest that moose with less exposure to trails and roads are particularly sensitive to road densities and are adjusting their use patterns to avoid these areas.

Our results indicate that moose are responding to temporal changes in human activity and environmental conditions throughout the season. Before hunting season, moose step lengths in both regions were longer in areas with high trail densities, indicating that trails enhanced movement rates for both high- and low-access moose. However, after hunting season, this relationship was reversed, and moose step lengths decreased in areas with high trail densities. Animal step lengths have been applied to examine whether behaviors vary in response to anthropogenic features such as roads (Roever et al. 2010, Chen and Koprowski 2016, Kite et al. 2016), trails (Whittington et al. 2004), and surface mining (Cristescu et al. 2016). We hypothesized that moose have longer step lengths (i.e., displacement or movement away from disturbance) during the hunting season in areas with more trails. Contrary to our predictions, moose step lengths decreased in areas with more trails, which could suggest that moose were moving less to reduce the likelihood of encountering hunters. Previous research has found that highly mobile ungulates from hunted populations were detected more often by hunters (Cleveland et al. 2012, Little et al. 2014). The decrease in movement in relation to areas with more trails post-hunting season could be a behavioral effect carried over from hunting season, with restricted movement rates persisting even after the disturbance abates. Finally, moose step lengths increased gradually from mid-August to mid-October. We speculate that the increase in moose step length following the start of hunting season is associated with the spike in hunter activity. However, the peak in moose step lengths for both regions was 1 October–7 October and is likely associated with the annual rut (late September–early October; Miquelle 1990).

We found that high-quality forage was an important predictor in habitat selection before and after hunting season for high-access moose, but this relationship was not evident during the hunting season. Although reduced forage intake by males typically coincides with the beginning of rut, moose appear to avoid areas with high-quality forage during the hunting season, which is before the rut, likely to avoid potential risk from hunters. The effects of human activity on optimal habitat selection could impact the acquisition of food resources and assimilation of energetic reserves. Future research should investigate how the energetic costs of human disturbance during the hunting season can translate to effects on reproduction and survival. During the post-hunting season, which corresponds with the rut, forage availability is less important for male moose, but males are likely occupying areas with high-quality forage because females in estrous have an opportunity to recover energetic losses associated with parturition during the late summer and early fall when forage quality is still relatively high (Miquelle et al. 1992).

Our analysis indicates that moose with less exposure to humans (i.e., low-access region) move away from areas with elevated human activity during the hunting season, whereas moose with more exposure to humans (i.e., high-access region) move more overall, and seek habitat with high-quality cover during the hunting season. We suggest that managers carefully communicate our findings to moose hunters to illustrate how hunting opportunities may decline in accessible areas, despite relatively high moose densities in the GMU. It will be important to consider that if hunters focus their effort on habitats with good access (e.g., close to roads or areas with high visibility), moose may adjust their movement and habitat selection patterns to avoid risk, resulting in lower hunter success rates in high-access areas and enhanced chances of encountering moose in low-access areas, especially if hunters are willing to travel off-trail. In rural communities, hunting opportunity is often determined by access to wildlife populations (Berman and Kofinas 2004, Kofinas et al. 2010, Brinkman et al. 2014, Johnson et al. 2016). There are several socio-economic variables (e.g., hunter income, available transportation, cost of fuel) that can influence hunter access (Brinkman et al. 2013, Hansen et al. 2013). Additionally, the concentration of ATV activity will depend on the quality of the trail, an area's topographic and landscape features (e.g., terrain ruggedness, slope, and hydrology), and the proximity to towns and major roads. Based on this, future studies may want to examine the effects of trail conditions on hunting effort and subsequent habitat use patterns. Understanding how the distribution of trails on the landscape can influence movement behavior and hunter access can provide managers with useful information to help inform future management decisions.

Acknowledgments

All captures were carried out with approval from the ADFG Institutional Animal Care Use and Committee (#2012-033). Our research was supported by National Science Foundation grant "Integrative Graduate Education and Research Traineeship: Global-Local Interactions: Resilience and Adaption of Social-Ecological Systems in a Rapidly Changing North" (Grant #0654441). Moose collaring efforts were supported by the U.S. Army Garrison, Fort Wainwright Alaska, and the Alaska Department of Fish and Game (W912CZ-08-D-0012). Additional funding to support this research was provided by grants from the Joint Fire Science Program Graduate Research Innovation Award and the American Association of University Women "American Fellowship." We gratefully acknowledge the Alaska Department of Fish and Game, specifically the Delta Junction Area Office, for providing valuable assistance in the field with data collection. We thank J. Haddix, K. Kellie, S. Brainerd, T. Paragi, and K. Zellers for consultation and advice on the project. We thank D. Bruning J. Staker, D. Feierabend, and B. Schmidt for field assistance. Finally, we thank the Bonanza Creek LTER for collaborative support throughout this project.

Literature Cited

Alaska Natural Heritage Program (ANHP), Interior Alaska Vegetation Map and Classification. 2016. [1: 1:63,360]. http://accs.uaa.alaska.edu/vegetation-ecology/vegetation-map-northern-western-and-interior- alaska/

Berkes, F., and D. Jolly. 2002. Adapting to climate change: social-ecological resilience in a Canadian western Arctic community. Conservation Ecology 5:18.

Berman, M., and G. Kofinas. 2004. Hunting for models: grounded and rational choice approaches to analyzing climate effects on subsistence hunting in an Arctic community. Ecological Economics 49:31–46.

Beyer, H. L., R. Ung, D. L. Murray, and M. J. Fortin. 2013. Functional responses, seasonal variation and thresholds in behavioural responses of moose to road density. Journal of Applied Ecology 50:286–294.

Bjørneraas, K., E. J. Solberg, I. Herfindal, B. V. Moorter, C. M. Rolandsen, J.-P. Tremblay, C. Skarpe, B.-E. Sæther, R. Eriksen, and R. Astrup. 2011. Moose *Alces alces* habitat use at multiple temporal scales in a human-altered landscape. Wildlife Biology 17:44–54.

Bonnot, N., N. Morellet, H. Verheyden, B. Cargnelutti, B. Lourtet, F. Klein, and A. M. Hewison. 2013.

Habitat use under predation risk: Hunting, roads and human dwellings influence the spatial behaviour of roe deer. European Journal of Wildlife Research 59:85–193.

Bowman, J., J. C. Ray, A. J. Magoun, D. S. Johnson, and F. N. Dawson. 2010. Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. Canadian Journal of Zoology 88:454–467.

Brinkman, T. J., and K. A. Kellie. 2014. Tanana flats training area moose calving site study final report. U.S. Army, Fairbanks, Alaska, USA.

Brinkman, T. J., G. P. Kofinas, F. S. Chapin III, and D. K. Person. 2007. Influence of hunter adaptability on resilience of subsistence hunting systems. Journal of Ecological Anthropology 11:58.

Brinkman, T., G. Kofinas, W. Hansen, F. S. Chapin III, and S. Rupp. 2013. A new framework to manage hunting. Wildlife Professional 7:38–43.

Brinkman, T., K. T. B. Maracle, J. Kelly, M. Vandyke, A. Firmin, and A. Springsteen. 2014. Impact of fuel costs on high-latitude subsistence activities. Ecology and Society 19:18.

Brown, C. L., A. R. Hardy, J. R. Barber, K. M. Fristrup, K. R. Crooks, and L. M. Angeloni. 2012. The effect of human activities and their associated noise on ungulate behavior. PLoS ONE 7:e40505.

Bruning, D. 2013. Unit 20D moose. Chapter 25, Pages 1–25 *in* P. Harper and L. McCarthy, editors. Moose management report of survey and inventory activities 1 July 2011–30 June 2013. Alaska Department of Fish and Game, Division of Wildlife Conservation, Federal Aid in Wildlife Restoration Project 1.0, Juneau, Alaska, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer Science and Business Media, New York, New York, USA.

Carter, N. H., B. K. Shrestha, J. B. Karki, N. M. B. Pradhan, and J. Liu. 2012. Coexistence between wildlife and humans at fine spatial scales. Proceedings of the National Academy of Sciences of the United States of America 109:15360–15365.

Chen, H. L., and J. L. Koprowski. 2016. Differential effects of roads and traffic on space use and movements of native forest-dependent and introduced edge-tolerant species. PLoS ONE 11: e0148121.

Child, K. 1998. Incidental mortality. Pages 275–301 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and management of the North American Moose. Smithsonian Institution, Washington, D.C., USA.

Cleveland, S. M., M. Hebbelwhite, M. Thompson, and R. Henderson. 2012. Linking elk movement and resource selection to hunting pressure in a heterogeneous landscape. Wildlife Society Bulletin 36:658–668.

Cristescu, B., G. B. Stenhouse, and M. S. Boyce. 2016. Large omnivore movements in response to surface mining and mine reclamation. Scientific Reports 6:19177.

Cromsigt, J. P., D. P. Kuijper, M. Adam, R. L. Beschta, M. Churski, A. Eycott, G. I. Kerley, A. Mysterud, K. Schmidt, and K. West. 2013. Hunting for fear: innovating management of human–wildlife conflicts. Journal of Applied Ecology 50:544–549.

Dussault, C., J. P. Ouellet, C. Laurian, R. Courtois, M. Poulin, and L. Breton. 2007. Moose movement rates along highways and crossing probability models. Journal of Wildlife Management 71: 2338–2345.

Fieberg, J., J. Matthiopoulos, M. Hebblewhite, M. S. Boyce, and J. L. Frair. 2010. Correlation and studies of habitat selection: Problem, red herring or opportunity? Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:2233–2244.

Forman, R., D. Sperling, J. Bissonette, A. Clevenger, C. Cutshall, V. Dale, L. Fahrig, R. France, C. Goldman, and K. Heanue. 2003. Road ecology: science and solutions. Island Press, Washington, D. C., USA.

Fortin, D., H. L. Beyer, M. S. Boyce, D. 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.

Franke, A., T. Caelli, G. Kuzyk, and R. J. Hudson. 2006. Prediction of wolf (*Canis lupus*) kill-sites using hidden Markov models. Ecological Modelling 197:237–246.

Fryxell, J. M., J. Greever, and A. Sinclair. 1988. Why are migratory ungulates so abundant? American Naturalist 131:781–798.

Gavin, S. D., and P. Komers. 2006. Do pronghorn (*Antilocapra americana*) perceive roads as a predation risk? Canadian Journal of Zoology 84:1775–1780.

Hansen, W. D., T. J. Brinkman, M. Leonawicz, F. S. Chapin III, and G. P. Kofinas. 2013. Changing daily wind speeds on Alaska's north slope: implications for rural hunting opportunities. Arctic 66: 448–458.

Heberlein, T. A. 2002. Peer-reviewed articles too many hunters or not enough deer? Human and biological determinants of hunter satisfaction and quality. Human Dimensions of Wildlife 7:229–250.

James, A. R. C., and A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. Journal of Wildlife Management 64:154–159.

Johnson, I., T. Brinkman, K. Britton, J. Kelly, K. Hundertmark, B. Lake, and D. Verbyla. 2016. Quantifying rural hunter access in Alaska. Human Dimensions of Wildlife 21:1–14.

Kellie, K. A. 2005. Summer movements of female moose at high density. Thesis. University of Alaska Fairbanks, Fairbanks, Alaska, USA.

Kite, R., T. Nelson, G. Stenhouse, and C. Darimont. 2016. A movement-driven approach to quantifying grizzly bear (*Ursus arctos*) near-road movement patterns in west-central Alberta, Canada. Biological Conservation 195:24–32.

Kofinas, G. P., F. S. Chapin III, S. BurnSilver, J. I. Schmidt, N. L. Fresco, K. Kielland, S. Martin, A. Springsteen, and T. S. Rupp. 2010. Resilience of Athabascan subsistence systems to interior Alaska's changing climate. Canadian Journal of Forest Research 40:1347–1359.

Little, A. R., S. Demarais, K. L. Gee, S. L. Webb, S. K. Riffell, J. A. Gaskamp, and J. L. Belant. 2014. Does human predation risk affect harvest susceptibility of white-tailed deer during hunting season? Wildlife Society Bulletin 38:797–805.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen, and K. J. Raedeke. 2000. Elk and hunter space-use sharing in South Dakota. Journal of Wildlife Management 64:994–1003.

Miquelle, D. G. 1990. Why don't bull moose eat during the rut? Behavioral Ecology and Sociobiology 27:145–151.

Miquelle, D. G., J. M. Peek, and V. Van Ballenberghe. 1992. Sexual segregation in Alaskan moose. Wildlife Monographs 122:3–57.

Morales, J. M., D. T. Haydon, J. Frair, K. E. Holsinger, and J. M. Fryxell. 2004. Extracting more out of relocation data: building movement models as mixtures of random walks. Ecology 85: 2436–2445.

Muhly, T. B., C. Semeniuk, A. Massolo, L. Hickman, and M. Musiani. 2011. Human activity helps prey win the predator-prey space race. PLoS ONE 6: e17050.

Ordiz, A., O. G. Støen, S. Sæbø, J. Kindberg, M. Delibes, and J. E. Swenson. 2012. Do bears know they are being hunted? Biological Conservation 152:21–28.

Ouren, D. S., C. Haas, C. P. Melcher, S. C. Stewart, P. D. Ponds, N. R. Sexton, L. Burris, T. Fancher, and Z. H. Bowen. 2007. Environmental effects of off-highway vehicles on Bureau of Land Management lands: a literature synthesis, annotated bibliographies, extensive bibliographies, and internet resources. US Department of the Interior, US Geological Survey, Reston, Virginia, USA.

Proffitt, K. M., J. L. Grigg, K. L. Hamlin, and R. A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. Journal of Wildlife Management 73:345–356.

Roberts, D. R., et al. 2017. Cross-validation strategies for data with temporal, spatial, hierarchical or phylogenetic structure. Ecography 40:913–929.

Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2010. Grizzly bear movements relative to roads: application of step selection functions. Ecography 33:1113–1122.

Rumble, M. A., and R. S. Gamo. 2011. Habitat use by elk (*Cervus elaphus*) within structural stages of a managed forest of the northcentral United States. Forest Ecology and Management 261: 958–964.

Salcha-Delta Soil and Water Conservation District (S-DSandW), Gerstle River Training Area Vegetation Map. 2014. [1:50,000]. https://www.salchadeltaswcd.org

Saunders, S. C., M. R. Mislivets, J. Chen, and D. T. Cleland. 2002. Effects of roads on landscape structure within nested ecological units of the Northern Great Lakes Region, USA. Biological Conservation 103:209–225.

Shanley, C. S., G. P. Kofinas, and S. Pyare. 2013. Balancing the conservation of wildlife habitat with subsistence hunting access: a geospatial-scenario planning framework. Landscape and Urban Planning 115:10–17.

Shanley, C. S., and S. Pyare. 2011. Evaluating the road-effect zone on wildlife distribution in a rural landscape. Ecosphere 2:1–16.

Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation 141:2159–2173.

Swenson, J. E. 1982. Effects of hunting on habitat use by mule deer on mixed-grass prairie in Montana. Wildlife Society Bulletin 10:115–120.

Thurfjell, H., S. Ciuti, and M. S. Boyce. 2014. Applications of step-selection functions in ecology and conservation. Movement Ecology 2:4.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, UK.

Vieira, M. E., M. M. Conner, G. C. White, and D. J. Freddy. 2003. Effects of archery hunter numbers and opening dates on elk movement. Journal of Wildlife Management 67:717–728.

Viereck, L. A., C. Dyrness, A. Batten, and K. Wenzlick. 1992. The Alaska vegetation classification. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
Whittington, J., C. C. St.Clair, and G. Mercer. 2004. Path tortuosity and the permeability of roads and trails to wolf movement. Ecology and Society 9:4.
Whittington, J., C. C. St.Clair, and G. Mercer. 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecological Applications 15: 543–553.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2405/full