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Evaluating the road-effect zone on wildlife distribution in a rural landscape

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Abstract. The road-effect zone is the area in which ecological effects extend outward from a road. Dispersed off-highway vehicle (OHV; e.g., four-wheelers and snowmachines) activity on rural road networks creates a disturbance that reduces the effective amount of wildlife habitat and therefore has the potential for an extensive road-effect zone. Consequently, land managers must consider the trade-offs between rural road development and the conservation of habitat for species of concern. We conducted a spatially-explicit study of moose, *Alces alces*, occurrence in relation to rural roads and OHV routes in rural Alaska, U.S.A. We used logistic regression and AIC model selection criterion to develop resource selection functions (RSFs) for male and female moose at three spatial scales (250 m, 500 m, and 1000 m) in two seasons (summer and fall). To evaluate an ecological disturbance threshold from increasing route activity on the probability of animal occurrence, the RSFs were plotted against an index of route activity derived from interviews with OHV users, and fit with logarithmic functions. The variable for route activity improved the fit of RSF models for both sexes at all spatial scales and in both seasons. A negative relationship was found between moose occurrence and routes or areas in which routes were in close proximity to primary forage, with the exception of male moose at the 1000-m scale in the fall. Therefore, among the spatial scales of analysis, the road-effect zone for male moose was determined to be between 500 m and 1000 m, and >1000 m for female moose. Furthermore, route activity <0.25 km of vehicle travel/km^2/day was a threshold value at which moose sustained a high probability of occurrence (0.60 to 0.91). The results of our study suggest that the dispersed ecological effect of rural roads and OHV routes should be considered in transportation and land-management planning efforts. Relatively low levels of vehicular activity may create extensive road-effect zones for sensitive species.

Key words: Alaska; *Alces alces*; disturbance; ecological thresholds; habitat selection; moose; off-highway vehicles; resource selection function; road-effect zone; roads; rural landscape; wildlife distribution.

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INTRODUCTION

The growing network of roads in rural landscapes is creating new challenges and opportunities for transportation planning and the conservation of wildlife habitat (Trombulak and Frissell 2000, Forman et al. 2003, Fahrig and Rytwinski 2009). In the last four decades, the use of off-highway vehicles (OHVs; e.g., four-wheelers and snowmachines) on public lands across the U.S. has increased seven-fold (USFS 2004). As a result, illegal OHV use on public lands has been a growing problem across the U.S. (USFS 2004). OHVs have also been used for non-recreational purposes that add another layer of complexity to access management plans in many rural areas. For example, OHVs have been used as the primary means of transportation for subsistence hunting and gathering of wild food resources in many rural communities (Berkes and Jolly 2001, Ford et al. 2006, Brinkman et al. 2007). OHV users have used existing infrastructure, such as old logging roads, in addition to creating an extensive informal network of dispersed routes in the process of searching for game (Mills and Firman 1986, Stedman et al. 2004, Schmidt et al. 2005).

One concept for evaluating the ecological footprint of rural road networks and establishing wildlife conservation measures is the "road-effect zone", which is a measure of the spatial extent of ecological effects that extend beyond the physical edge of roads (Forman et al. 1997). This zone was estimated to average approximately 600 m from roads in urbanized landscapes for a cross-section of ecological components, from altered streams to disrupted ungulate movements (Forman and Deblinger 2000). Extrapolating this impact zone across the 6.2 million-km road system of the U.S. resulted in estimates of ecological effects on 19% of the country, underscoring the large extent of road-affected lands (Forman 2000). Although Forman (2000) suggested this concept can be applied to rural landscapes and even showed the potentially disproportionate impact that vehicle activity on rural areas has (16.7% of the country) as compared to urban areas (2.5%), the 600-m estimate may not typify the road-effect zone in rural landscapes for several reasons. First, road-effects in rural areas may be underestimated due to the low detectability and high dispersion of OHV occurrence on landscapes (Preisler et al. 2006, Seip et al. 2007). Second, habituation to noise and visual disturbances of vehicles is less likely to occur when traffic frequency is lower and thus, OHVs putatively have a greater effect on wildlife in rural landscapes (Creel et al. 2002, Stankowich 2008). Third, whereas vehicular use may be more consistent in urban landscapes, rural use may be highly variable both temporally and spatially (Jaarsma and Willems 2002, Forman et al. 2003); suggesting that road-effect zones in rural areas must account for variability in vehicular frequency. And finally, whereas urban road networks occur in developed corridors that are relatively simple and patchy with respect to natural habitat, rural roads are juxtaposed with relatively undeveloped landscapes; suggesting a greater need to account for environmental covariates (e.g., habitat) when measuring road-effect zones in these areas (Fahrig and Rytwinski 2009).

Although the road-effect zone clearly has relevance, methods of actually estimating this parameter under the complex and dynamic conditions represented by OHVs on rural road networks has received scant attention. Spatially-explicit, multivariate modeling approaches have been applied to a number of animal resource-selection contexts (Johnson et al. 2006) and offer a solution to the problem of estimating the rural road-effect zone. Whereas previous studies on the road-effect zone that have been limited to observational data (Reijnen et al. 1995, Forman and Deblinger 2000, Boarman and Sazaki 2006, Semlitsch et al. 2007, Eigenbrod et al. 2009) and thus likely underestimated the extent of affected habitats, spatially-explicit models can incorporate large, high-frequency, and unbiased animal-tracking datasets to more fully realize impacts (Johnson et al. 2004, Gaines et al. 2005, Farmer et al. 2006, Ciarniello et al. 2007). For example, Sawyer et al. (2006) used three years of collar location-data to quantify the effective area of mule deer (*Odocoileus hemionus*) habitat lost to natural gas development.

In addition, spatially-explicit methods offer a practical benefit for managing OHV distribution: not only do these allow for mapping the maximum extent of a disturbance, e.g., the road-effect zone, but also allow for identification of disturbance thresholds (Huggett 2005, Groffman et al. 2006). An ecological disturbance threshold is a particularly useful and perhaps more ecologically-relevant metric, whereby vehicle activity causes an abrupt nonlinear animal response, rather than a gradual or linear response (Walker and Meyers 2004, Eigenbrod et al. 2009). Mapping portions of roaded landscapes that exceed a disturbance threshold yields an estimate of the effective amount of habitat lost by wildlife populations; a metric that is particularly valuable in situations when more direct evidence of impacts on animal fitness or population trends cannot be ascertained (Andren 1994, Fahrig 2001). Conversely, mapping areas falling below thresholds allows managers to identify potential zones where traditional levels and forms (e.g., subsistence hunting) of OHV use are more compatible with wildlife.

Our study objectives were to derive and evaluate a novel series of methods for evaluating the road-effect zone in rural landscapes. Specifically, we derived estimates of the road-effect zone on moose (*Alces alces*) in a rural landscape using a spatially-explicit, multivariate model approach that incorporated variability in vehicular frequency; conducted a follow-up exploratory analyses to identify ecological disturbance thresholds for OHV management; and finally, compared these estimates to previous estimates in urban areas and other landscapes where alternate analytical methods have been used.

Methods

Study area

Yakutat, Alaska is a rural community of approximately 800 residents located along the coast of southeastern Alaska in the northernmost portion of the Tongass National Forest (Fig. 1), a coastal temperate rainforest. The topography of Yakutat is a relatively flat strip of coastline abutting the Fairweather Range with a mosaic of wetlands, shrub lands, and forests (Shephard 1995). The area is bisected by several large glacial and rain-fed rivers. The forested areas are dominated by Sitka spruce (*Picea sitchensis*) interspersed with western hemlock (*Tsuga heterophylla*) and black cottonwood (*Populus trichocarpa*). The wetlands and shrub lands are composed of graminoids, forbs, and shrubs with several species of willows (Salix spp.) and Sitka alder (*Alnus sinuate*). The geographic bounds of the study area were defined by the availability of fine-scale (5 m) vegetation coverage data derived from remote sensing (SPOT) imagery; an area covering approximately 1000 km^2 (Fig. 1).

Animal location data

We used a three-year dataset of 30,825 locations from 20 GPS-collared moose during November 2002 to March 2005. The dataset was previously used to examine habitat selection and sightability of moose in the region (Oehlers 2007). The collars recorded a GPS location every six hours, an interval sufficient to maintain relative independence between consecutive locations and minimize spatial autocorrelation (Nielson et al. 2002). The dataset was formatted as follows: (1) for a season-specific comparison (Stankowich 2008), locations were separated into discrete five-week analysis periods corresponding to summer or fall (Table 1; Mills and Firman 1986, Franzmann and Schwartz 1997, USFS 2009). (2) To account for the possibility of behavioral differences, male and female moose were separated (Miquelle et al. 1992, Bowyer et al. 2001, Spaeth et al. 2004). (3) To minimize the influence of individual variation on pooled locations for modeling, an equal number of locations were selected from each individual (Thomas and Taylor 2006).

We conducted an analysis on a resulting dataset of 2,374 locations from five female and five male moose. 106 Locations per individual were randomly selected for the summer analysis period and 146 locations for fall (with one male vacating the study area during the fall) to produce individual seasonal home ranges (Girard et al. 2002). A matched use-availability design was employed to compare animal locations to random locations within seasonal home ranges (Design II; Manly et al. 2002, Johnson et al. 2006). Kernel home ranges (99.9%) were created for each individual with the Home Range Extension (Rodgers et al. 2007) in ArcGIS 9.2 (ESRI, Redlands, CA). The smallest whole kernel was found by lowering the h*ref* (smoothing parameter) in 0.1 increments until the home range polygon split or a hole formed inside the polygon. The individual home ranges were then pooled for different sexes and seasons to investigate third-order (Johnson 1980), sex-specific and season specific resource selection. To conservatively define available locations (Aebischer et al. 1993, Keating and Cherry 2004), lakes, rivers, and coastlines were also removed from these four combined home ranges before the available locations were randomly selected for analysis.

Route mapping and classification

The majority of existing route information was digitized from IKONOS remote sensing imagery in 2004 by the U.S. Forest Service Yakutat Ranger District. This information was supplemented and verified with ground-based GPS delineation of routes used by OHVs and by aerial survey from a

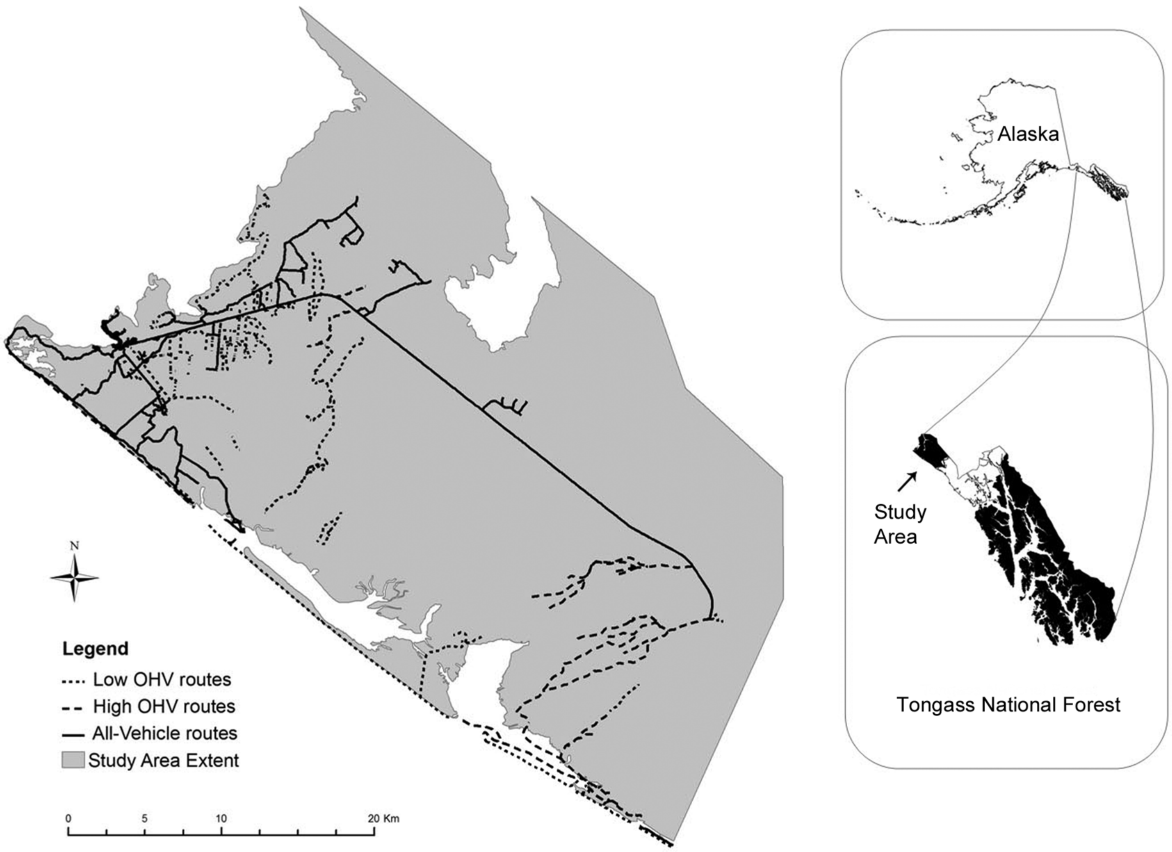

Fig. 1. The extent of remote sensing imagery covering the study area of Yakutat, Alaska, located on the northernmost coast of the Tongass National Forest, USA.

Table 1. Biological and anthropogenic factors used to justify the classification of GPS-collar data into seasonal analysis periods to evaluate a rural road-effect on moose in Yakutat, Alaska.

Season	Biological factors	Anthropogenic factors	Approx. time frame	Five-week analysis period
Summer	Summer forage/ Post-calving	Low terrestrial subsistence/ low OHV traffic	June 1–Sept. 15	July 1–Aug. 7
Late Fall	Fall forage/Post-rut	High terrestrial subsistence/ high OHV traffic	Oct. 8–Nov. 30	Oct. 8–Nov. 15

helicopter (Fig. 2). We then held a series of meetings with the land managers in 2006 to update and refine existing route information. Land managers did the following: (1) visually verified new routes observed on 2005 SPOT5 remote sensing imagery; (2) identified which routes were actively used over the study period; (3) categorized routes in three categories (Low OHV, High OHV, and All-Vehicles) according to perceived level of use as well as the visible wear and soil types (Table 2); and (4) selected three representative routes in each category to sample for route-use frequency in subsequent interviews with OHV users.

A total of 523 km of routes were mapped across the study area. The routes were composed of 184 km of Low OHV, 118 km High OHV, and 221 km of All-Vehicle routes. A random sample of approximately one-third (n = 25) of federally registered subsistence moose hunters were inter-

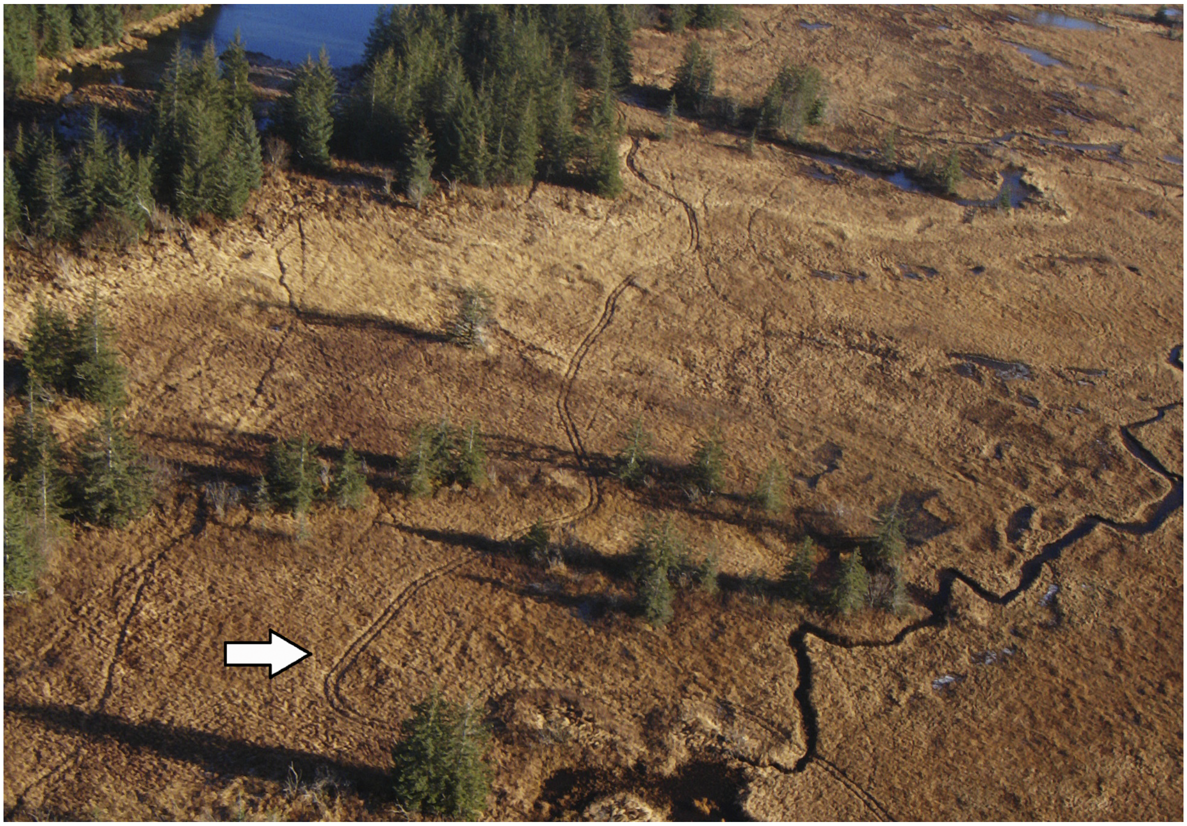

Fig. 2. A low-elevation aerial photograph showing a parallel wheel-track (indicated with an arrow) that typifies a dispersed off-highway vehicle (OHV) route through the mosaic of wetlands, shrub lands, and forests that compose the rural landscape of Yakutat, Alaska. Photo credit: U.S. Forest Service.

Table 2. The classification of vehicle routes based on vegetation displacement and soil types in Yakutat, Alaska.

Route type	Criteria
Low OHV	(a) Silt and clay soils: lack of incised ruts, wheel track is generally vegetated, one wheel track predominates, few parallel wheel tracks for short distances only (b) Beach and sand/gravel proximal outwash soils: not connected to the road system directly and not connected to high use trails through other soil types
High OHV	(a) Silt and clay soils: incised ruts, displaced soil, track denuded of vegetation, many parallel tracks, often in marginally passable areas (b) Beach or sand/gravel proximal outwash soils: connected to the road system directly or connected to high use trails through other soil types
All-Vehicles	Any route known to be driven by standard motor vehicles at any point in time that may also have OHV traffic

viewed in December 2007 to determine the frequency of route-use. Hunters were presented a 1.5 m × 1 m aerial photograph of the region with mapped roads and OHV routes. Without disclosing the preconceived route-use categories to hunters, hunters provided estimates of the number of one-way trips they traveled on the nine representative routes in each seasonal analysis period. Data were pooled for each of the three route categories, resulting in 75 route-use estimates for each category in each of the two seasonal analysis periods. Differences in the frequency of use among route-use categories were statistically significant (ANOVA; $p < 0.05$), so the average number of one-way trips observed in each route category was used as a weight in subsequent road-effect modeling (Table 3).

Table 3. The total length of digitized routes as well as the results of a one-way ANOVA used to test for differences in the frequency of use among route-use categories.

Route type	Total (km)	Average ± SE	p
Summer			
Low OHV	184	0.03 ± 0.04	0.0116
High OHV	118	0.50 ± 0.26	<0.0001
All-Vehicles	221	14.1 ± 2.83	<0.0001
Fall			
Low OHV	184	0.75 ± 0.31	0.0126
High OHV	118	2.04 ± 0.66	<0.0001
All-Vehicles	221	13.1 ± 2.42	<0.0001

Road-effect modeling

We used an information-theoretic approach with multiple working hypotheses (Burnham and Anderson 2002) to investigate a road-effect on moose. We developed 10 a priori models to evaluate resource selection based on the following. First, we eliminated commonly employed habitat variables (e.g., elevation, slope, and aspect) due to the relatively flat terrain over the study area. Second, we were interested in evaluating specifically the effect of route activity on animal distribution so we developed models with and without a route activity variable. And third, we hypothesized that the primary predictors of moose occurrence in our study area during the snow-free summer and fall would be the proximity to high-quality forage, cover from predators, and riparian areas (Van Ballenberghe and Ballard 1998, Kunkel and Pletscher 2000, Dussault et al. 2005).

Table 4. Independent variables calculated for each used and random location at three spatial scales.

Variable	Description
Willow	Percent willow was created by adding the total area of cells the remote sensing imagery identified as willow, divided by the area of each scale buffer.
Edge	Edge density was created with the spatial statistics software FRAGSTATS (McGarigal and Marks 1995). The cells remote sensing imagery identified as trees were combined to create a tree canopy cover for the software to determine the average canopy edge density at each scale buffer.
Streams	Stream density was created by adding the total length of streams in each scale buffer, divided by the number of hectares in each scale buffer.
Routes	A measure of route activity was created from the average number of one-way trips in each route category. The total length of routes in each category were added within each scale buffer, and then multiplied by the average number of one-way trips for each category. These results for each scale buffer were combined across categories to represent the total vehicle travel in each scale buffer.

We produced three GIS raster datasets at a 20 m × 20 m cell resolution for spatial data consistency: (1) percent willow, (2) edge density (McGarigal and Marks 1995), and (3) stream density (Table 4). Select combinations of these variables were tested with and without a route variable and an interaction term for routes with willow to determine if inclusion of routes improved model fit (Table 4). Each variable was calculated at three spatial scales (250 m, 500 m, and 1000 m around each used and random point location) for each sex and for the two seasonal analysis periods. Spatial scales were chosen to represent a gradient in multi-scale habitat selection (Kie et al. 2002). Before variables were used in modeling, a Pearson's pair-wise correlation analysis was conducted at each scale to identify multi-collinearities among variables that were excluded from the analysis (Hosmer and Lemeshow 1989).

We then used logistic regression in SAS 9.1 (SAS, Cary, NC) on the 10 a priori models. Akaike's Information Criterion (AIC) was used for model selection, and the lowest ΔAIC scores and highest Akaike weights were used to select the most parsimonious best-fit models (Anderson 2008). We evaluated the predictive performance of the model with an area-corrected *k*-fold cross validation procedure (Boyce et al. 2002). This technique involved dividing animal locations into five datasets, applying the resource selection function (RSF) of the final model to one dataset, and evaluating model performance with the remaining four datasets. The range of logistic regression probability scores resulting from each dataset was divided into 10 equal-interval probability bins. The bins were area-corrected by dividing the middle probability score by the mapped area of the probability range occurring on the landscape. The average score across the 10 area-corrected probability bins was ranked, and Spearman rank analysis (r_s) was used to analyze the correlation between the ordinal rank and observed rank of probability bins.

The best-fit RSFs were used in an exploratory analysis to identify an ecological disturbance threshold of vehicle activity on the probability of animal occurrence. We chose the 500-m scale because RSFs at this scale exhibited consistent patterns across sex and season for moose. A space and time-explicit metric of route activity was calculated in the GIS with the following formula, Eq.1, which converted the route-use area (km^2) of the 500-m buffer, and incorporated the sample size and the sampling period:

$$\left\{\left[(\text{Total km of vehicle travel in 500 m buffer}) \times \left(\frac{1.27\,\text{km}^2}{500\,\text{m buffer}}\right) \times (3\,\text{user samples in population})\right] \div (35\,\text{day sampling period})\right\} = \text{Total km of vehicle travel/km}^2\text{/day}. \qquad (1)$$

Point locations (n = 1000) were randomly sampled from portions of the landscape with 0.01 km to 2 km vehicle travel/km^2/day to represent a gradient of areas with route activity. Route-activity values at sample locations were plotted against the corresponding probability of use derived from the RSF; and fit with a logarithmic function. This was performed for both sexes and both seasons.

Results

All the RSF models with the Route variable yielded the lowest ΔAIC score and highest Akaike weights (Table 5). This trend suggests that rural roads and OHVs influence moose distribution. The most frequently selected best-fit model for both sexes and both seasons included all four main variables: Willow + Edge + Streams + Routes. In two cases, comparable models resulted with a ΔAIC ≤ 2, which indicated these models had approximately equivalent explanatory power. The most parsimonious models were selected for each scale, sex, and season (Anderson 2008).

For female moose, Route coefficients in the best-fit models were consistently negative in the summer and fall at all three spatial scales. This pattern suggests that female moose avoided rural roads and OHV routes at multiple spatial scales (Table 6). Route coefficients were also statistically significant in all models, except in the summer at the 250-m scale. The non-significant Route variable at the 250-m scale in the summer suggests that a larger spatial scale of analysis was more appropriate to evaluate a road-effect on female moose in the summer. The four main variables were included as the best-fit for most female models, with the exception of the 250-m scale in the summer and fall. At the 250-m scale in summer, the four main and Willow × Routes interaction variables had the best-fit, although the interaction term was not statistically significant. The non-significant interaction term also suggests that a larger spatial scale of analysis was more appropriate to evaluate a road-effect on female moose in the summer. At the 250-m scale in the fall, Willow + Streams + Routes had the best-fit, suggesting edge density was of less importance to females at the 250-m scale in the fall or, again, that a larger spatial scale of analysis was more appropriate to evaluate a road-effect on female moose in the summer.

For male moose, Route coefficients or the interaction term Willow × Routes, were negative in best-fit models, with the exception of the 1000-m scale in the fall (Table 6). These results suggest male moose avoid rural roads and OHV routes or areas with willow in close proximity to routes. The positive relationship between males and routes at the 1000-m scale also suggests male moose may be less sensitive to routes than female moose at larger spatial scales. All the Route coefficients were statistically significant, with the exception of the 250-m scale in the summer. The exceptions to the inclusion of the main four variables as the best-fit model were in the summer at the 1000-scale and in the fall at the 250-m and 500-m scales. In the summer at the 1000-m scale, the best-fit model included the interaction term for Willow × Routes with a negative coefficient. In the fall at the 250-m and 500-m scale, the best-fit models were Willow + Edge + Routes + Willow × Routes. The lack of selection for stream density suggested riparian areas were of less importance at finer spatial scales for male moose in the fall.

Table 5. Differences in AIC scores (ΔAIC), weights (*w*), and number of model parameters (*k*) used to evaluate rural roads and OHV routes effect on moose habitat selection with resource selection functions; male and female moose were evaluated separately during the summer and fall at three spatial scales.

Model	*k*	250 m ΔAIC	250 m AIC*w*	500 m ΔAIC	500 m AIC*w*	1000 m ΔAIC	1000 m AIC*w*
Summer Female							
Willow	1	43.1	0.000	35.2	0.000	36.8	0.000
Willow + Edge	2	44.0	0.000	36.1	0.000	37.2	0.000
Willow + Edge + Routes	3	26.1	0.000	23.3	0.000	23.2	0.000
Willow + Edge + Routes + Willow × Routes	4	22.1	0.000	24.9	0.000	25.0	0.000
Willow + Streams	2	19.3	0.000	12.2	0.001	14.6	0.000
Willow + Streams + Routes	3	9.0	0.009	8.1	0.011	12.4	0.001
Willow + Streams + Routes + Willow × Routes	4	4.3	0.095	9.2	0.006	14.4	0.000
Willow + Edge + Streams	3	17.5	0.000	7.2	0.018	6.1	0.031
Willow + Edge + Streams + Routes	4	4.4	0.088	0.0	0.642	0.0	0.649
Willow + Edge + Streams + Routes + Willow × Routes	5	0.0	0.808	1.4	0.321	1.4	0.318
Summer Male							
Willow	1	62.4	0.000	68.3	0.000	68.8	0.000
Willow + Edge	2	50.4	0.000	62.1	0.000	66.3	0.000
Willow + Edge + Routes	3	16.5	0.000	9.1	0.007	18.1	0.000
Willow + Edge + Routes + Willow × Routes	4	17.9	0.000	10.4	0.004	6.9	0.031
Willow + Streams	2	40.2	0.000	50.1	0.000	51.3	0.000
Willow + Streams + Routes	3	19.2	0.000	16.0	0.000	22.6	0.000
Willow + Streams + Routes + Willow × Routes	4	21.0	0.000	17.6	0.000	12.3	0.002
Willow + Edge + Streams	3	26.3	0.000	39.8	0.000	43.7	0.000
Willow + Edge + Streams + Routes	4	0.0	0.693	0.0	0.703	8.7	0.012
Willow + Edge + Streams + Routes + Willow × Routes	5	1.6	0.307	1.8	0.286	0.0	0.954
Fall Female							
Willow	1	51.7	0.000	63.9	0.000	111.5	0.000
Willow + Edge	2	48.5	0.000	53.1	0.000	101.4	0.000
Willow + Edge + Routes	3	32.0	0.000	19.9	0.000	11.8	0.002
Willow + Edge + Routes + Willow × Routes	4	33.9	0.000	20.8	0.000	8.6	0.008
Willow + Streams	2	5.2	0.032	21.7	0.000	59.1	0.000
Willow + Streams + Routes	3	0.0	0.425	3.5	0.098	10.6	0.003
Willow + Streams + Routes + Willow × Routes	4	2.0	0.157	3.9	0.080	10.9	0.003
Willow + Edge + Streams	3	12.1	0.001	20.1	0.000	57.4	0.000
Willow + Edge + Streams + Routes	4	0.8	0.281	0.0	0.561	1.0	0.372
Willow + Edge + Streams + Routes + Willow × Routes	5	2.8	0.104	1.5	0.261	0.0	0.613
Fall Male							
Willow	1	24.2	0.000	33.0	0.000	54.7	0.000
Willow + Edge	2	7.3	0.017	17.5	0.000	25.3	0.000
Willow + Edge + Routes	3	5.2	0.050	6.0	0.026	2.5	0.159
Willow + Edge + Routes + Willow × Routes	4	0.0	0.663	0.7	0.372	4.0	0.075
Willow + Streams	2	26.0	0.000	32.4	0.000	51.9	0.000
Willow + Streams + Routes	3	24.9	0.000	27.5	0.000	38.7	0.000
Willow + Streams + Routes + Willow × Routes	4	20.5	0.000	23.6	0.000	38.2	0.000
Willow + Edge + Streams	3	9.2	0.007	11.8	0.001	15.2	0.000
Willow + Edge + Streams + Routes	4	7.2	0.018	3.9	0.075	0.0	0.555
Willow + Edge + Streams + Routes + Willow × Routes	5	2.0	0.245	0.0	0.526	1.9	0.210

Model validation suggested that best-fit models had a high level of predictive power (Table 7). The highest Spearman rank correlation model for females in the summer was the same at the 250-m and 1000-m scales. In the fall, the female model with the highest correlation was at the 250-m scale. For male moose in the summer and fall, the model with the highest Spearman rank correlation was at the 250-m scale.

The mapped RSFs show a reduced probability of use by moose in areas of increasing route-use and route density, with the exception of male moose in the fall (Fig. 3). This disturbance pattern was accentuated for female moose in the fall season when route-use in Low OHV and High OHV categories increased. These data also exhibit a nonlinear relationship between moose occurrence and route activity (Fig. 4). Based on logarithmic fitting to this relationship, a high probability of moose occurrence (0.60 to 0.91)

Table 6. Coefficients (β) and 95% confidence intervals of the most parsimonious RSF models used to evaluate rural roads and OHV routes effect on moose habitat selection; male and female moose were evaluated separately during the summer and fall at three spatial scales.

	250 m		500 m		1000 m	
Variable	β	95% CI	β	95% CI	β	95% CI
Summer Female						
Willow	0.019*	0.011, 0.026	0.022*	0.013, 0.032	0.019*	0.007, 0.031
Edge	0.004*	0.001, 0.008	0.008*	0.003, 0.012	0.013*	0.006, 0.019
Streams	0.01*	0.006, 0.014	0.013*	0.008, 0.018	0.016*	0.01, 0.022
Routes	−0.001	−0.003, 0.0003	−0.00004*	−0.0001, −0.00001	−0.00001*	−0.00002, −0.000002
Willow × Routes	0.00004	−0.00001, 0.0001				
Summer Male						
Willow	0.021*	0.014, 0.028	0.026*	0.016, 0.035	0.039*	0.027, 0.052
Edge	0.007*	0.004, 0.01	0.009*	0.005, 0.014	0.012*	0.006, 0.018
Streams	0.009*	0.005, 0.013	0.008*	0.003, 0.013	0.009*	0.003, 0.015
Routes	−0.0001	−0.002, 0.001	−0.0002*	−0.0003, −0.0001	0.00003	−0.00001, 0.0001
Willow × Routes					−0.00001*	−0.00001, −0.000001
Fall Female						
Willow	0.016*	0.01, 0.022	0.008	−0.001, 0.017	−0.006	−0.017, 0.005
Edge			−0.004*	−0.008, −0.001	−0.009*	−0.014, −0.004
Streams	0.011*	0.007, 0.015	0.011*	0.006, 0.016	0.01*	0.004, 0.016
Routes	−0.001*	−0.001, −0.0002	−0.0002*	−0.0003, −0.0001	−0.0002*	−0.0002, −0.0001
Willow × Routes						
Fall Male						
Willow	0.02*	0.012, 0.027	0.026*	0.016, 0.035	0.042*	0.029, 0.055
Edge	−0.007*	−0.01, −0.004	−0.011*	−0.015, −0.006	−0.022*	−0.029, −0.015
Streams					−0.007*	−0.013, −0.0004
Routes	0.001*	0.0003, 0.001	−0.0001*	−0.0002, −0.0001	0.00004*	0.00002, 0.0001
Willow × Routes	−0.00002*	−0.00004, −0.00001	0.00001*	0.00001, 0.000002		

Note: *Coefficients (β) significant at 5%

Table 7. Spearman rank correlations (r_s) of cross validated and area-corrected RSF-bin ranks for male and female moose during the summer and fall at three spatial scales.

	Summer		Fall	
Scale (m)	r_s	p	r_s	p
Female				
250	0.988	<0.0001	0.952	<0.0001
500	0.976	<0.0001	0.794	0.0061
1000	0.988	<0.0001	0.879	0.0008
Male				
250	0.988	<0.0001	0.988	<0.0001
500	0.912	0.0002	0.733	0.0158
1000	0.891	0.0005	0.903	0.0003

was observed where route frequency was less than approximately 0.25 km of vehicle travel/km^2/day (Table 8).

Discussion

The results of our analysis suggest rural roads and OHV traffic created an ecological road-effect zone that displaced moose and altered use of potential habitat near roads. The size of the road-effect zone was different for male and female moose. Among the spatial scales of our analyses, male moose were found to be negatively impacted to at least a 500-m distance from rural roads and OHV routes, whereas for female moose, the road-effect zone may extend >1000 m. These results suggest rural roads and OHV routes have a greater impact on wildlife in rural landscapes

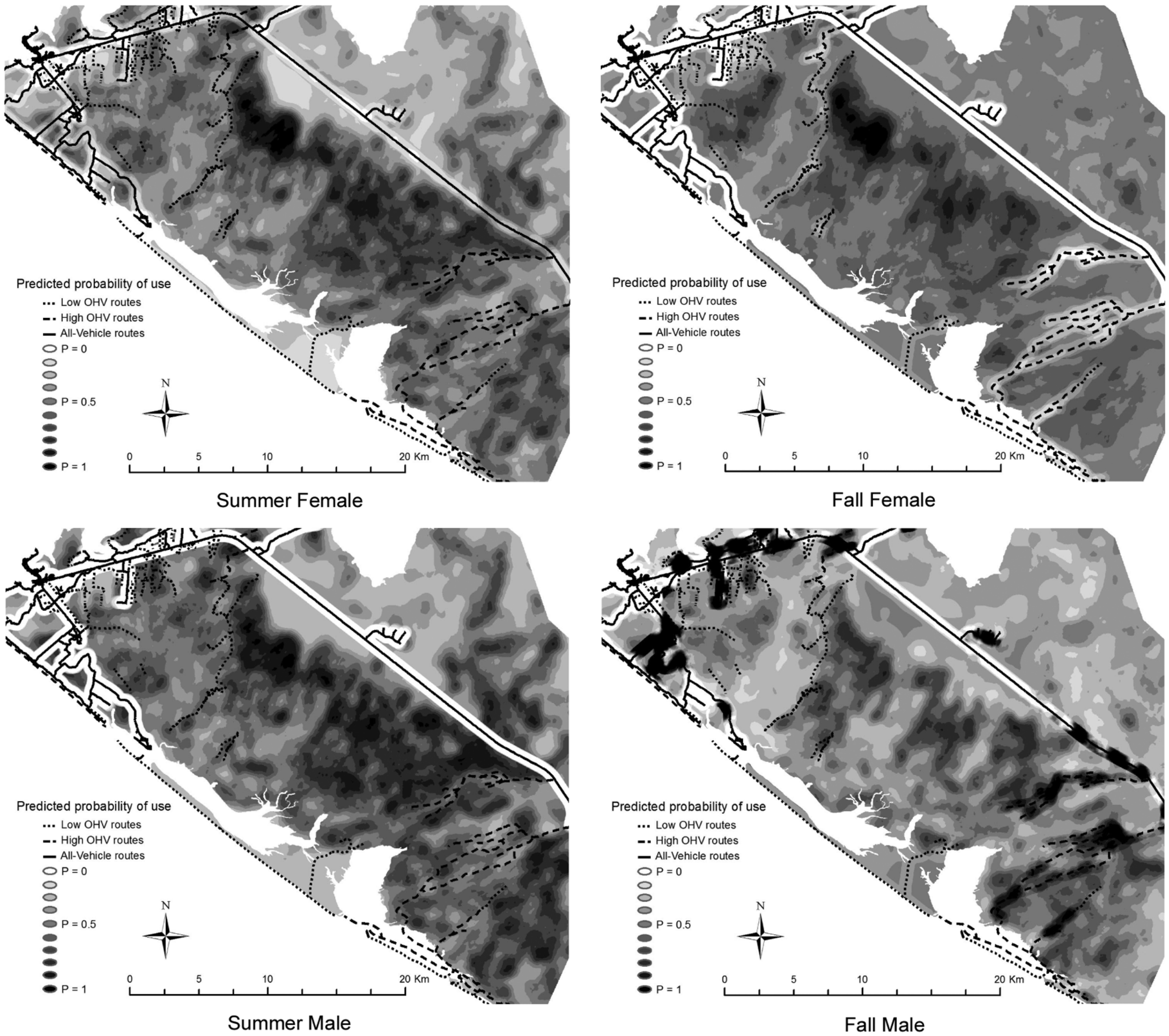

Fig. 3. Resource selection functions for male and female moose at the 500-m scale in the summer and fall; illustrating the road-effect zone created by rural roads and OHV routes in Yakutat, Alaska.

than the 600 m extent that Forman and Deblinger (2000) observed from urban roads. In addition, route activity less than 0.25 km of vehicle travel/km^2/day is an approximate space and time-explicit metric that land managers could use to reduce the probability of moose disturbance in our study area, when and where OHV access is necessary (e.g., subsistence hunting). We calculated that 13.2% of the study area in the summer and 23.5% in the fall exceeded this disturbance threshold, suggesting a substantial loss of effective wildlife habitat. Should future vehicle activity double on the current road network, >15% of the study area in the summer and >30% of the study area in the fall would exceed the disturbance threshold (Table 9).

Typically land management agencies lack long-term wildlife demographic data to evaluate disturbance effects on population trends or persistence (Jaeger et al. 2005). The change in effective habitat as a result of disturbance, however, is a type of ecological indicator that provides a sound alternative basis for establishing habitat conservation measures (Andren 1994, Fahrig 2001). For example, road avoidance and resulting habitat loss was attributed to a four-fold decrease in grizzly bear (*Ursus arctos*) density using spatially-explicit modeling inde-

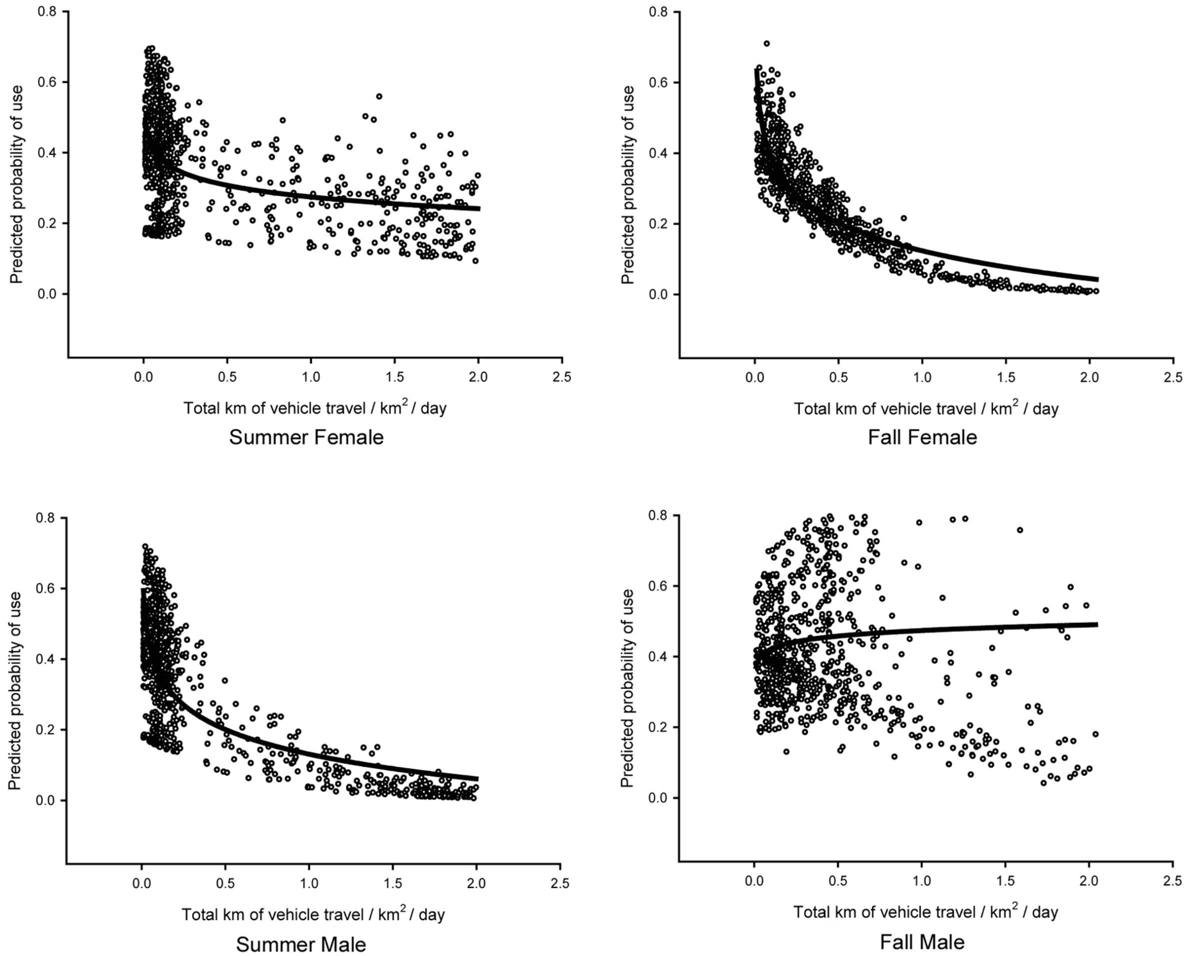

Fig. 4. Scatter plots with logarithmic regressions showing the probability of moose occurrence (500-m scale RSF) relative to the total km of vehicle travel/km^2/day in Yakutat, Alaska: Female, Summer $y = -0.0478\text{Ln}(x) + 0.2741$ ($R^2 = 0.2171$, $p < 0.0001$); Female, Fall $y = -0.1134\text{Ln}(x) + 0.1235$ ($R^2 = .7524$, $p < 0.0001$); Male, Summer $y = -0.101\text{Ln}(x) + 0.1306$ ($R^2 = 0.5378$, $p < 0.0001$); Male, Fall $y = 0.0229\text{Ln}(x) + 0.474$ ($R^2 = 0.0133$, $p = 0.0003$).

Table 8. Range of vehicle travel/km^2/day and resulting probability scores for male and female moose derived from logarithmic regressions.

Total km of vehicle travel/km^2/day	Probability of moose occurrence		
	Summer Female	Fall Female	Summer Male
0.001	0.60	0.91	0.83
0.25	0.34	0.28	0.27
0.50	0.31	0.20	0.20
0.75	0.29	0.16	0.16
1.00	0.27	0.12	0.13
1.25	0.26	0.10	0.11
1.50	0.25	0.08	0.09
1.75	0.25	0.06	0.07
2.00	0.24	0.04	0.06

Table 9. Percent increase in vehicle activity effect on the percent of the landscape with a low probability of moose occurrence (i.e., exceeding the disturbance threshold).

Percent increase in vehicular activity	Percent of landscape with low probability of use	
	Summer	Fall
10	13.3	24.1
20	13.6	24.7
30	13.9	25.2
40	14.3	25.8
50	14.6	26.6
60	15.0	28.6
70	15.3	29.9
80	15.5	30.8
90	15.8	31.5
100	16.1	32.2

pendently verified with DNA-based mark-recapture techniques (Ciarniello et al. 2007). We estimated habitat loss >20% in the fall, a critical period during which moose are typically building overwinter fat reserves (Van Ballenberghe and Ballard 1998). Displacement and loss of effective habitat in this small and isolated population of moose (Schmidt et al. 2008) therefore may have important consequences for animal fitness and demographics, suggesting a need for proactive access management (Seip et al. 2007).

The impact of roads and OHV routes on moose habitat selection was clearly evident from the consistently lowest ΔAIC scores for models with Routes and predominantly negative coefficients for the Route variable or the interaction term for Willow × Routes. The only exception to a negative association with Routes or the interaction for Willow × Routes, males at the 1000-m scale in the fall, could be explained by the fact that many OHV routes were specifically created by hunters to access concentrations of male moose for the fall hunting season (Mills and Firman 1986, USFS 2009). This pattern could also explain the positive association observed in models of male habitat selection at the fall 500-m scale for Willow × Routes and Routes at the summer 1000-m and fall 250-m scale. Or, perhaps, male moose are less sensitive to disturbance than female moose at broader spatial scales. In general, female moose appeared to be more sensitive to disturbance, with no statistically significant positive associations with Routes or Willow × Routes. This could be explained possibly by a female's higher levels of vigilance necessary for protecting calves (Bowyer et al. 1998, Stankowich 2008).

Our model-validation process suggested a high level of model accuracy at multiple spatial scales. This illustrates the importance of a multi-scale approach in wildlife habitat studies because disturbance effects may be exhibited at multiple spatial scales and be undetectable at other spatial scales (Johnson 1980, Bowyer and Kie 2006, Boyce 2006). All models at the 500-m scale had a statistically significant negative coefficient for specifically the Route variable, whereas the Route variable and statistical significance in models at other scales were inconsistent across male and female moose. In the subsequent exploratory analysis of an ecological disturbance threshold at the 500-m scale, the only exception to an avoidance pattern beyond approximately 0.25 km of vehicle travel/km^2/day was for male moose in the fall. This was likely due to the positive association seen with the interaction term for Willow × Routes in the 500-m scale model. The strong nonlinear negative response observed in the probability of female moose occurrence to increasing vehicle traffic in the summer and fall suggests a low avoidance-threshold within the range of vehicular frequency that occurred in Yakutat. A low avoidance threshold suggests that managers would be warranted to keep OHV traffic at lower levels than has traditionally occurred on this landscape; but because enforcement of such low OHV levels on a remote landscape could also be a challenge (Karasin 2003, Buckley 2004), restricting OHV access entirely could, in some instances, be defensible.

Previous studies on the indirect effect of roads on moose distribution have demonstrated mixed results relative to our study and may not be comparable due to differences in the resolution of data and the scale of analysis. For instance, coarser scale analyses have shown a positive association between moose and roads while finer scale analyses have shown a negative association between moose and roads. Schneider and Wasel (2000) suggested that while access is generally assumed to have a negative effect on moose locally, the regional density of moose was positively associated with roads in northern Alberta, Canada. Likewise, Remm and Luud (2003) found that the density of moose was positively associated with roads at a regional scale in Estonia. In contrast, the number of moose observed within 100 m of roads in Denali National Park, Alaska declined by >50% when visitor use increased eight-fold (Burson et al. 2000). Yost and Wright (2001) also found that moose sightings were less than expected up to 1200 m from a road in Denali, but the spatial configuration of habitats was not considered. For example, the availability of preferred moose habitat occurred closer to roads in Sweden, suggesting that an analysis that does take into account the spatial pattern of habitats could produce misleading results (Ball and Dahlgren 2002, Seiler 2005). The conflicting results of these studies indicate that the spatial configuration of habitats must be taken into consideration to more accurately investigate the potential effect of roads on wildlife distribution. Roads may interact with habitat to influence the observed distribution of wildlife (Maier et al. 2005). The value of incorporating habitat information has been demonstrated in previous road-impact studies involving grizzly bears (*Ursus arctos*) (Mace et al. 1996, Ciarniello et al. 2007, Roever et al. 2008), mule deer (*Odocoileus hemionus*) (Sawyer et al. 2006), and elk (*Cervus elaphus*) (Sawyer et al. 2007). These studies collectively illustrate that animals avoided preferred habitats with increasing levels of traffic, with potential repercussions on forage availability, individual fitness, and ultimately population productivity.

We suspect that the road-effect detected in moose is at least partially due to noise produced by vehicular traffic, as well as the perceived risk to hunting that is observed among many ungulates (Stankowich 2008). Ungulates in rural landscapes that experience low-levels of disturbance are less likely to habituate and therefore have a stronger tendency to show disturbance effects (Stankowich 2008). Noise could also inhibit predator detection by ungulates in rural landscapes, in contrast to ungulates in urban landscapes where primary predators (i.e., grizzly bears and wolves) are rare (Forman and Alexander 1998).

These findings should be treated within the context of assumptions made in our analyses. The limited sample size of moose individuals could have increased the chance that atypical disturbance behavior influenced resource selection patterns (Thomas and Taylor 2006). To help reduce this possibility, however, we used an equal number of locations from each animal. Furthermore, our reliance on social interviews to derive route activity levels could have influenced modeling results; and the use of infrared or magnetic trail-counters (e.g., Shephard and Whittington 2006) would have potentially provided a less biased measurement of route use. However, these data were not attainable at the time of the study. Nonetheless, we believed our approach was better than simply treating all route types equally with respect to levels of activity when clearly, the width and soil wear of routes indicated different levels of use.

Conclusion

The results of our study suggest that even dispersed vehicular activity on rural road networks significantly affects moose distribution. Therefore, rural road networks should be incorporated into transportation planning scenarios to most accurately estimate the road-effect zone on target species. Road-effect zones with extents like that observed in this study (>1000 m) could have a substantial impact on the effective amount of habitat available for target species on landscapes. Furthermore, our exploratory analysis to determine an ecological disturbance threshold suggests that moose exhibit a relatively low threshold to such dispersed activity. Although it may be difficult to limit vehicular activity below such a threshold on well established road networks, land managers should carefully consider the trade-offs between new rural road development and the conservation of wildlife habitat: even new rural routes with infrequent use can measurably displace sensitive species.

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Literature Cited

Aebischer, N. J., P. A. Robertson, and R. E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74:1313–1325.

Anderson, D. R. 2008. Model Based Inference in the Life Sciences: A Primer on Evidence. Springer, New York, New York, USA.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366.

Ball, J. P., and J. Dahlgren. 2002. Browsing damage on pine (*Pinus sylvestris* and *P-contorta*) by a migrating moose (*Alces alces*) population in winter: relation to habitat composition and road barriers. Scandinavian Journal of Forest Research 17:427–435.

Berkes, F., and D. Jolly. 2001. Adapting to climate change: social-ecological resilience in a Canadian western arctic community. Conservation Ecology 5:18.

Boarman, W. I., and M. Sazaki. 2006. A highway's road-effect zone for desert tortoises. Journal of Arid Environments 65:94–101.

Bowyer, R. T., and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. Diversity and Distributions 12:244–257.

Bowyer, R. T., B. M. Pierce, L. K. Duffy, and D. A. Haggstrom. 2001. Sexual segregation in moose: effects of habitat manipulation. Alces 37:109–122.

Bowyer, R. T., V. Van Ballenberghe, and J. G. Kie. 1998. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. Journal of Mammalogy 79:1332–1344.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269–276.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

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 11:1–6.

Buckley, R. 2004. Environmental impacts of motorized off-highway vehicles. Pages 83–97 *in* R. Buckley, editor. Environmental Impacts of Ecotourism. CABI Publishing.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York, New York, USA.

Burson, S. L., J. L. Belant, K. A. Fortier, and W. C. Tomkiewicz. 2000. The effect of vehicle traffic on wildlife in Denali National Park. Arctic 53:146–151.

Ciarniello, L. M., M. S. Boyce, D. C. Heard, and D. R. Seip. 2007. Components of Grizzly Bear habitat selection: density, habitats, roads, mortality risk. Journal of Wildlife Management 71:1446–1457.

Creel, S., J. E. Fox, A. Hardy, J. Sands, B. Garrott, and R. O. Peterson. 2002. Snowmobile activity and glucocorticoid stress responses in wolves and elk. Conservation Biology 16:809–814.

Dussault, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, and H. Jolicoeur. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–628.

Eigenbrod, F., S. J. Hecnar, and L. Fahrig. 2009. Quantifying the road-effect zone: threshold effects of a motorway on anuran populations in Ontario, Canada. Ecology and Society 14:24.

Fahrig, L. 2001. How much habitat is enough? Biological Conservation 100:65–74.

Fahrig, L., and T. Rytwinski. 2009. Effects of roads on animal abundance: an empirical review and synthesis. Ecology and Society 14:21.

Farmer, C. J., D. K. Person, and R. T. Bowyer. 2006. Risk factors and mortality of Black-Tailed Deer in a managed forest landscape. Journal of Wildlife Management 70:1403–1415.

Ford, J. D., B. Smit, and J. Wandel. 2006. Vulnerability to climate change in the Arctic: a case study from Arctic Bay, Canada. Global Environmental Change 16:145–160.

Forman, R. T. T. 2000. Estimate of the area affected ecologically by the road system in the United States. Conservation Biology 14:31–35.

Forman, R. T. T., D. Sperling, J. A. Bissonette, A. P. Clevenger, C. D. Cutshall, V. H. Dale, L. Fahrig, R. France, C. R. Goldman, K. Heanue, J. A. Jones, F. J. Swanson, T. Turrentine, and C. Winter. 2003. Road ecology: science and solutions. Island Press, Washington, D.C., USA.

Forman, R. T. T., and L. E. Alexander. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207–231.

Forman, R. T. T., and R. D. Deblinger. 2000. The ecological road-effect zone of a Massachusetts (USA) suburban highway. Conservation Biology 14:36–46.

Forman, R. T. T., D. S. Friedman, D. Fitzhenry, J. D. Martin, A. S. Chen, and L. E. Alexander. 1997. Ecological effects of roads: toward three summary indices and an overview for North America. Pages 40–54 *in* K. Canters, editor. Habitat Fragmentation and Infrastructure. Ministry of Transport, Public Works and Water Management, Delft, Netherlands.

Franzmann, A. W., and C. C. Schwartz. 1997. Ecology and management of the North American moose. Smithsonian Institution Press, Washington, D.C., USA.

Gaines, W. L., A. L. Lyons, J. F. Lehmkuhl, and K. J. Raedeke. 2005. Landscape evaluation of female black bear habitat effectiveness and capability in the Northern Cascades, Washington. Biological Conservation 125:411–425.

Girard, I., J. P. Ouellet, R. Courtois, C. Dussault, and L. Breton. 2002. Effects of sampling effort based on GPS telemetry on home-range size estimations. Journal of Wildlife Management 66:1290–1300.

Groffman, P., J. Baron, T. Blett, A. Gold, I. Goodman, L. Gunderson, B. Levinson, M. Palmer, H. Paerl, G. Peterson, N. Poff, D. Rejeski, J. Reynolds, M. Turner, K. Weathers, and J. Wiens. 2006. Ecological thresholds: The key to successful environmental management or an important concept with no practical application? Ecosystems 9:1–13.

Hosmer, D. W., and S. Lemeshow. 1989. Applied Logistic Regression. John Wiley and Sons, New York, New York, USA.
Huggett, A. J. 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. Biological Conservation 124:301–310.
Jaarsma, C. F., and G. P. A. Willems. 2002. Reducing habitat fragmentation by minor rural roads through traffic calming. Landscape and Urban Planning 58:125–135.
Jaeger, J. A. G., J. Bowman, J. Brennan, L. Fahrig, D. Bert, J. Bouchard, N. Charbonneau, K. Frank, B. Gruber, and K. T. von Toschanowitz. 2005. Predicting when animal populations are at risk from roads: an interactive model of road avoidance behavior. Ecological Modelling 185:329–348.
Johnson, C. J., S. E. Nielsen, E. H. Merrill, L. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.
Johnson, C. J., D. R. Seip, and M. S. Boyce. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology 41:238–251.
Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.
Karasin, L. N. 2003. All-Terrain Vehicles in the Adirondacks: Issues and Options. Wildlife Conservation Society, Working Paper No. 21.
Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 68:774–789.
Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83:530–544.
Kunkel, K. E., and D. H. Pletscher. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. Canadian Journal of Zoology 78:150–157.
Mace, R. D., J. S. Waller, T. L. Manley, L. Jack Lyon, and H. Zuuring. 1996. Relationships among grizzly bears, roads, and habitat in the Swan Mountains, Montana. Journal of Applied Ecology 33:1395–1404.
Maier, J. A. K., J. M. Ver Hoef, A. D. McGuire, R. T. Bowyer, L. Saperstein, and H. A. Maier. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. Canadian Journal of Forest Research 35:2233–2243.
Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Kluwer Academic Publishers, The Netherlands.
McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure. Gen. Tech. Report PNW-GTR-351. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA.
Mills, D. D., and A. S. Firman. 1986. Fish and Wildlife Use Patterns in Yakutat, Alaska: Contemporary Patterns and Changes. Alaska Department of Fish and Game, Division of Subsistence, Douglas, Alaska, USA.
Miquelle, D. G., J. M. Peek, and V. Vanballenberghe. 1992. Sexual segregation in Alaskan moose. Wildlife Monographs 122:1–57.
Nielson, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead Ecosystem of Alberta: taking autocorrelation seriously. Ursus 13:45–56.
Oehlers, S. A. 2007. Habitat Selection and Sightability of Moose in Southeast Alaska. MS Thesis. University of Alaska Fairbanks, Fairbanks, Alaska, USA.
Preisler, H. K., A. A. Ager, and M. J. Wisdom. 2006. Statistical methods for analyzing responses of wildlife to human disturbance. Journal of Applied Ecology 43:164–172.
Reijnen, R., R. Foppen, C. ter Braak, and J. Thissen. 1995. The effects of car traffic on breeding bird populations in woodland. III. Reduction of density in relation to the proximity of main roads. Journal of Applied Ecology 32:187–202.
Remm, K., and A. Luud. 2003. Regression and point pattern models of moose distribution in relation to habitat distribution and human influence in Ida-Viru County, Estonia. Journal for Nature Conservation 11:197–211.
Rodgers, A. R., A. P. Carr, H. L. Beyer, L. Smith, and J. G. Kie. 2007. HRT: Home Range Tools for ArcGIS. Ontario Ministry of Natural Resources, Center for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.
Roever, C. L., M. S. Boyce, and G. B. Stenhouse. 2008. Grizzly bears and forestry I: road vegetation and placement as an attractant to grizzly bears. Forest Ecology and Management 256:1253–1261.
Sawyer, H., R. M. Nielson, F. Lindzey, and L. L. McDonald. 2006. Winter habitat selection of mule deer before and during development of a natural gas field. Journal of Wildlife Management 70:396–403.
Sawyer, H., R. M. Nielson, F. G. Lindzey, L. Keith, J. H. Powell, and A. Abraham. 2007. Habitat selection of Rocky Mountain Elk in a nonforested environment. Journal of Wildlife Management 71:868–874.
Schmidt, J. I., J. M. V. Hoef, J. A. K. Maier, and R. T. Bowyer. 2005. Catch per unit effort for moose: a new approach using weibull regression. Journal of

Wildlife Management 69:1112–1124.
Schmidt, J. I., K. J. Hundertmark, R. T. Bowyer, and K. G. McCracken. 2008. Population structure and genetic diversity of moose in Alaska. Journal of Heredity 100:170–180.
Schneider, R. R., and S. Wasel. 2000. The effect of human settlement on the density of moose in northern Alberta. Journal of Wildlife Management 64:513–520.
Seiler, A. 2005. Predicting locations of moose-vehicle collisions in Sweden. Journal of Applied Ecology 42:371–382.
Seip, D. R., C. J. Johnson, and G. S. Watts. 2007. Displacement of Mountain Caribou from winter habitat by snowmobiles. Journal of Wildlife Management 71:1539–1544.
Semlitsch, R. D., T. J. Ryan, K. Hamed, M. Chatfield, B. Drehman, N. Pekarek, M. Spath, and A. Watland. 2007. Salamander abundance along road edges and within abandoned logging roads in Appalachian forests. Conservation Biology 21:159–167.
Shephard, M. E. 1995. Plant Community Ecology and Classification of the Yakutat Foreland, Alaska. R10-TP-56 USDA Forest Service, Alaska Region, Juneau, Alaska, USA.
Shephard, B., and J. Whittington. 2006. Response of wolves to corridor restoration and human use management. Ecology and Society 11:1.
Spaeth, D. F., R. T. Bowyer, T. R. Stephenson, and P. S. Barboza. 2004. Sexual segregation in moose *Alces alces*: an experimental manipulation of foraging behaviour. Wildlife Biology 10:59–72.
Stankowich, T. 2008. Ungulate flight responses to human disturbance: a review and meta-analysis. Biological Conservation 141:2159–2173.
Stedman, R., D. R. Diefenbach, C. B. Swope, J. C. Finley, A. E. Luloff, H. C. Zinn. G. J. San Julian, and G. A. Wang. 2004. Integrating wildlife and human-dimensions research methods to study hunters. Journal of Wildlife Management 68:762–773.
Thomas, D. L., and E. J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70:324–336.
Trombulak, S. C., and C. A. Frissell. 2000. Review of the ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14:18–30.
USFS. 2004. Managing the National Forest System: Great Issues and Great Divisions. USDA Forest Service, Washington, D.C., USA.
USFS. 2009. Yakutat Access Travel Management Plan. USDA Forest Service, Yakutat, Alaska, USA.
Van Ballenberghe, V., and W. B. Ballard. 1998. *Population dynamics*. Pages 223–245 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, D.C., USA.
Walker, B. and J. Meyers. 2004. Thresholds in ecological and social-ecological systems: a developing database. Ecology and Society 9:3.
Yost, A. C., and R. G. Wright. 2001. Moose, caribou, and grizzly bear distribution in relation to road traffic in Denali National Park, Alaska. Arctic 54:41–48.