Time vs. distance: Alternate metrics of animal resource selection provide opposing inference

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Abstract. Quantifying resource use or selection by valued species on a human-altered landscape is important for wise conservation action. Here, we contrast metrics of resource selection based on Global Positioning System (GPS) telemetry, which indexes time spent in various habitats, with tracking in snow, which measures distance travelled. When animals move at different speeds within different habitats, the two methods can produce different results. The study was conducted in winter on endangered mountain caribou (*Rangifer tarandus caribou*) in a landscape fragmented by forestry roads and cutblocks. From 2001 to 2009, 25 caribou were monitored with GPS collars obtaining locations every two to six hours, and compared to 63 caribou trails followed in snow in the same study area and time period. Logistic regression was used to estimate selection for both metrics, with the same definition of use and availability employed. Forest age, tree species, edge distances, and road densities were the covariates of interest. For most covariates, the two metrics produced similar results that agreed with the literature: selection for primary forest stands that represent forage patches. Both metrics indicated selection for habitat edges that potentially enhance foraging. The distance metric (snow trailing) indicated strong selection for forestry roads (42% more than available), whereas GPS locations suggested an avoidance of roads (33% less than available). The GPS analysis was in agreement with the vast majority of work published on woodland caribou, whereas the distance metric suggests some of the first evidence of selection for anthropogenic linear features. Our results highlight a potential bias against detecting selection for habitat features used for movement when using long fix intervals (>2 h) that typify most GPS studies. Avoidance of linear features should be carefully examined and designs considered to asses this bias. Finally, the selection of roads by caribou exacerbates an already desperate situation by creating a potential trap because roads are also preferred by some predators.

Key words: edge effects; Global Positioning System; linear feature; movement; *Rangifer tarandus;* resource selection; road; selection bias; snow trail; woodland caribou.

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INTRODUCTION

Quantifying resource selection by animals has become a major focus of ecological management and research. Much of this work was spurred by the appeal of linking indices of resource use or selection to animal abundance (Boyce and McDonald 1999, Bock and Jones 2004, Street et al. 2017). If such linkages can be established, primary limiting factors can be identified and

options could be developed to preserve or manipulate habitats with the goal of increasing population growth or reducing human impacts.

With this interest, a variety of techniques and ensuing debates have arisen about how to identify resources that are "important" to animals (Garshelis 2000, Keating and Cherry 2004, Johnson et al. 2006, Lele 2009). For most large mammal studies, Global Positioning System (GPS) radio-collar data are used and the currency is the number of locations in different habitats, which index the time spent in each habitat. This approach makes the critical assumption that time within a habitat is linked to a component of fitness that translates to abundance (Boyce and McDonald 1999). However, some resources may not be well indexed by time, particularly those used for movement between foraging or resting areas (Mills et al. 2006, Johnson and Ganskopp 2008, Rowcliffe et al. 2012). Movement corridors for dispersal in particular may limit population abundance or distribution (Paetkau et al. 2009), but are used rarely and thus can be underrepresented in telemetry studies (Rowcliffe et al. 2012). Similarly, linear corridors used to efficiently exploit a home range, such as frozen river beds or game trails (Musiani et al. 1998), may not be well captured by telemetry, which is based on discontinuous sampling.

Roads and trails are often used for animal movement, usually at greater speeds than other landscape features (James 1999, James and Stuart-Smith 2000, Northrup et al. 2012, Dickie et al. 2017). Roads can positively affect the search rate for prey (DeCesare 2012) and consequently the foraging efficiency of some predators (McKenzie et al. 2012), sometimes at considerable expense to their prey (James and Stuart-Smith 2000, Apps et al. 2013). Roads can also provide access to humans leading to direct mortality (McLellan and Shackleton 1988), displace animals from preferred habitat (McLellan and Shackleton 1988), or fragment populations (Proctor et al. 2005).

However, because some animals may use roads and other linear features at greater speeds, inferring their importance on the landscape can be complex. It is possible that the degree of use and thus selection of linear features may be underrepresented in some telemetry-based studies, again because fewer locations would occur on these features due to increased travel speed (Thurfjell et al.

2014). In contrast, the linear distance covered on roads by animals may be high, especially in relation to their availability on the landscape. This logic applies to any feature that may be linear, relatively rare, and facilitates rapid movement. Consequently, the potential exists for inferences to differ based on the alternative metrics of time compared to distance traveled.

Woodland caribou (*Rangifer tarandus caribou*), a subspecies that is in danger of extinction in some areas (Serrouya and Wittmer 2010, Wittmer et al. 2010, Festa-Bianchet et al. 2011, Hervieux et al. 2013), are often found to avoid roads and other linear disturbances such as trails and seismic lines (James and Stuart-Smith 2000, DeCesare 2012). This pattern is presumably caused by increased predation risk or disturbance from humans (Apps et al. 2013). The mountain ecotype (Serrouya et al. 2012; hereafter mountain caribou) is a particularly small and vulnerable ecotype of woodland caribou, with <1600 animals that are fragmented into 18 subpopulations (Wittmer et al. 2005), at least two of which have recently gone extinct. This ecotype has been recommended by the Committee on the Status of Endangered Wildlife in Canada for listing as endangered under the Species at Risk Act. Therefore, considerable research effort has been directed at measuring limiting factors through telemetry studies by estimating resource selection (Terry et al. 2000, Apps et al. 2001, Johnson et al. 2004, 2015, Serrouya et al. 2007, Wittmer et al. 2007).

In our study, we compared two methods of estimating resource selection, one based on GPS radio telemetry and the second based on tracking animals in snow. Our primary objective was to determine whether the method of data collection affected inferences of resource selection. The telemetry indexed time spent in different habitats, whereas snow trailing measured a continuous path through the landscape. Our study area, scale of investigation, and analytical approach were the same in both cases. Our motivation was prompted by the observation that our telemetry-based studies, and those in the literature from other woodland caribou ecotypes (James and Stuart-Smith 2000, Latham et al. 2011, DeCesare 2012, DeCesare et al. 2012), almost universally found an avoidance of human-caused linear features. Yet, while trailing caribou in the snow, we

noticed considerable use of roads. We hypothesized that this difference was due to the method of data collection and that this difference would affect inferences of animal resource selection.

METHODS

Study area

We studied caribou in southeastern British Columbia (BC), Canada, from south of Valemount (52°40′–119°19′) to south of Revelstoke (50°46′–118°14′). This area is steep and rugged, with some high-elevation plateaus. Elevations range from 450 to 3500 m. The area receives >2000 mm of precipitation each year, most falling as snow (Meidinger and Pojar 1991). Average snowfall is 396 cm/yr ($n = 100$ yr, standard deviation [SD] = 120) in valleys and 1427 cm/yr ($n = 39$ yr, SD = 263, Parks Canada files) at 1875 m (where caribou live during late winter; Apps et al. 2001). Lower elevations (<1400 m) are in the Interior Cedar-Hemlock biogeoclimatic zone (Meidinger and Pojar 1991) and are dominated by climax stands of western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*), most of which are hundreds of years old. Mid- and upper slopes (1400–1900 m) are in the Engelmann Spruce–Subalpine Fir (ESSF) zone. These forests consist of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Above about 1900 m, subalpine fir grows in clumps forming mostly open subalpine parkland and alpine, rock, and glaciers are extensive features at higher elevations. The forests are highly fragmented by natural and anthropogenic influences. Due to high snowfall and steep terrain, avalanche paths are common and young forests replanted after logging are widespread, with most of the cutblocks <30 yr old. Extensive networks of gravel roads exist in harvested areas; however, most roads receive little traffic and are not plowed in winter.

Mountain caribou use low-elevation ecosystems in early winter (late October to early January), but move to higher ecosystems in late winter (January to mid-April; Apps et al. 2001). Diet differs between these habitats—in low-elevation forests caribou forage on arboreal lichen (*Bryoria* spp. and *Alectoria sarmentosa*) on standing or windthrown trees, lichen litterfall, and occasionally on shrubs and herbs in areas where snow has yet to accumulate (Serrouya et al. 2007). At higher elevations, caribou forage on arboreal lichen on standing or windthrown trees, or on lichen litterfall.

Study design

We worked with two data sets: GPS data from radio-collared caribou and trailing data from following caribou tracks in snow during winter (November 1 to April 15; Apps et al. 2001). Location data were obtained from 25 caribou (23 females and two males) fitted with GPS collars captured across the study area. Caribou were captured using a net-gun fired from a helicopter during late winter in parkland habitat when >85% of the population was easily observed (Wittmer et al. 2005). Captures were conducted in accordance with provincial animal care protocols for endangered species (e.g., permit no. VI08-49757). Caribou were collared with GPS collars (models included ATS GPS2000, Lotek 2200 and 4400, Televilt C900 and Televilt Prosrec) and fix rates of 2, 3, 4, or 6 h, as with many other studies that used variable fix rates (Appendix S1). Between one and 19 caribou were monitored each year from 2001 to 2009, with individual caribou monitored for one to three years. Caribou were from the Wells Gray, Groundhog, Columbia North, Columbia South, and Frisby-Boulder subpopulations (Wittmer et al. 2005).

Caribou were trailed in snow from November to February. Because we were interested in caribou movements in landscapes with a history of forest harvesting, we limited our data collection to areas where forest harvesting or road networks existed. To reduce potential bias with the starting points for snow trailing, locations of radio-collared caribou or tracks sighted from an airplane while homing in on collared caribou during telemetry flights were used to locate caribou snow trails. To obtain a representative sample of trails, we attempted to systematically cycle through each collared caribou, rather than to focus on just a few collared caribou to trail. Weather and logistics occasionally forced us to miss certain individuals, but we ensured they were sampled with snow trails after subsequent telemetry flights. It was not possible to compare each snow trail to individually collared caribou because some caribou were collared with very high-frequency (VHF) collars (which were suitable to locate trailing sites and for

demographic analyses), but VHF collars could not be used for detailed road analyses as we did with the GPS collars. Sites were accessed on snowmobile or, for four remote trails, by helicopter. Once caribou tracks were located, we recorded the location of the snow trail with a handheld GPS (Garmin GPS76 and GPS V; positional accuracy typically <10 m) and tracked backward along the path to ensure animals were not approached. Along the caribou snow trail, we recorded habitat transitions between primary forest, young forest, and roads. Although analyses were conducted using geographic information system (GIS) basemaps, field notes of habitat types provided continual verification and here we define habitat types as broad associations of vegetation or seral stage, described in Table 1.

Caribou snow-trailing data were imported into ArcView 3.3 (ESRI, Redlands, California, USA) using DNR Garmin 5.1.1 software (Minnesota Department of Natural Resources, Minnesota, USA). We chose to investigate habitats selected by caribou at the temporal scales of hours and days. Because GPS data showed caribou moved approximately 100 m/h in winter, but took approximately 3 d to travel 1000 m away from a starting location, we used these spatial scales to investigate habitat selection. In a GIS, we buffered both caribou snow trails and GPS locations with concentric polygons (circles for GPS data) for analysis. We described "used" habitat around snow trails at two scales. At the finer scale, we generated a 10-m buffer around the trail to incorporate the measurement error associated using a handheld GPS device. At the larger scale, we used a 100-m buffer to represent habitat potentially used by caribou within an hour's movement. We used the same metric to define "used" habitat for the GPS data, generating 100-m buffers around individual GPS locations. To define what was "available" to the animal in the landscape for both trails and GPS locations, we generated 1000-m buffers. We present the comparison of used (100-m buffer) to available (1000-m buffer) habitats for both the GPS and snow-trailing data to ensure the same scales were compared between the two methods, even though the snow-trailing data could provide finer resolution (i.e., 10-m accuracy). Yet, we also present the 10-m use buffers compared to the 1000-m available buffers for the snow-trailing data in Appendix S2.

Table 1. Variables extracted within each used and available buffer.

Variables	Detail (units)
Road density	(km/km^2)
Age	Projected forest cover age (years)
Elevation	Elevation (m)
Slope	**Slope (%)**
Spruce	Any spruce (%)
Fir	Subalpine fir (%)
Cedar	Western redcedar (%)
Hemlock	Any hemlock (%)
Other Tree	Other tree species (%)
Open	No tree cover (%)
Habitat type	
Primary forest	**Forests >100 yr (%)**
Secondary forest	**Forests 21–100 yr (%)**
Young clearcut forest	**Clearcut logged, ≤20 yr old (%)**
Young natural forest	**Forests ≤20 yr old, often avalanche paths or parkland forest (%)**
Alpine	**(%)**
Distance into:	
Primary forest	(m)
Secondary forest	(m)
Young clearcut forest	(m)
Young natural forest	(m)
Alpine	(m)
Distance to edge	**Distance into the dominant habitat (m)**

Notes: All variables are area-weighted averages or average distance measures from all pixels in the buffer (see text for explanations of buffers). Variables in bold font were included in logistic regression models.

Variables considered to explain caribou habitat use are listed in Table 1. Data on stand age, crown closure, tree species, and harvested blocks were obtained from the updated digital forest cover database. To ensure current coverage, manual identification of newly logged areas was done with 30-m resolution satellite imagery. Road density was derived from BC Ministry of Forests data, using the total length of road in the buffer divided by the area of the buffer. Average elevation, slope (%), and aspect of each buffer were derived from a 20-m resolution digital elevation model. Forest cover polygons were combined into five main stand age and disturbance classes, which we have called habitat types: young cut forest (0–20 yr old), naturally disturbed young forest (0–20 yr old), secondary forest (older cutting units or older naturally disturbed forest; 21–100 yr old), primary forest (>100 yr old), and alpine. Age class, satellite images, and field notes were used to

identify these habitat types. Each habitat type was rasterized to a 10-m resolution. To quantify "use" and "availability" for each variable, we calculated the area-based weighted average within each buffer. Note that this approach samples the entirety of each buffer at the pixel scale. The shortest distance to edge was calculated for each raster point within a given habitat type in a buffer, and the average value from all the points used as the average distance to edge. For univariate analyses, this averaging was done for each habitat type within a used or available buffer. For analyses with multiple covariates (logistic regression), we used a single distance to edge measure to avoid missing values associated with rarely used habitat types. We calculated the average distance to the edge of the predominant habitat type of the buffer (snow trail data) or the habitat type that the actual location was in (GPS data).

Analysis

We focused only on caribou when in human-altered landscapes by constraining our analyses to collared caribou and snow trails with roads or clearcuts within their available buffers. Caribou that did not have roads or clearcuts within the available buffer were excluded from analyses to ensure that both metrics were collected in similar landscapes. Data were examined for outliers and collinearity (Zuur et al. 2010). When variables were highly correlated (Pearson's $r > 0.7$), we retained those thought to have more direct relevance to caribou ecology. We evaluated the differences between used and available habitats using multiple metrics. At a univariate level, we estimated the mean percent difference (PD) between used and associated available buffers, calculating PD as: (use − available)/available × 100. We also used paired t tests to compare used and associated available buffers. For analyses with multiple covariates, we standardized all predictor variables (($x - \bar{x}$)/SD) and used logistic regression to predict caribou selection. Four candidate models were defined a priori, based on information from the literature and our univariate analyses. The full model included habitat type, slope, distance to edge, and road density. The next model excluded habitat type, and final models excluded habitat type and distance from edge, or excluded habitat type and slope. We used Akaike's Information Criteria (AIC) to rank the models (Burnham and

Anderson 2002), and considered model averaging if models were within 2 AIC units of the top model. For the GPS data, we used mixed-effects logistic regression, allowing random effects for individual caribou. We specified road density and slope (%) as random slopes (and intercepts) to explicitly maintain individual caribou as the sampling unit for these variables and thus derive appropriate variance estimates, which produces the most conservative type of inference (Schielzeth and Forstmeier 2009). For the snow-trailing data, each snow trail provided one sample and all snow trails were used to estimate a logistic regression model. To highlight individual variation among caribou, we summarized the proportion of individuals (GPS data) or snow trails with a positive coefficient for a given variable. For mixed-effects models of the GPS data, this was achieved by summing the coefficient of the fixed effect with the coefficient of the random slope, by caribou. For snow trails, we calculated the ratio of used to available for each trail, with ratios >1 indicating positive selection. Model fit was assessed by calculating Nagelkerke's (1991) modified R^2 for logistic regression, and using Johnson's (2014) modification for mixed models.

Differences in habitat availability are known to potentially affect inferences on habitat selection (i.e., functional responses in selection; Mysterud and Ims 1998, Beyer et al. 2010). We used two methods to assess for this potential confound. First, we used bootstrapping methods to estimate 95% confidence intervals (CIs) for the mean PDs. This approach allows the magnitude of potential availability effects to vary across each bootstrap sample. Second, for the road density variable, we assessed for a functional response in selection by evaluating the strength of correlation between the individual selection coefficients (for individual caribou and individual snow trail) and availability. We considered a linear or quadratic relationship with an R-value >0.30 to be indicative of a functional response.

All statistical analyses were done in R version 3.1.1 (R Development Core Team 2014), using packages boot (Canty and Ripley 2014) and lme4 (Bates et al. 2014). Geographic information system images of all snow trails are available in Appendix S3 so readers can easily view these trails in Google Earth (however, the date of the orthophoto image will differ from the date of trailing).

Results

During the winters of 2004 through 2007, we conducted 63 different snow-trailing sessions, averaging 3.9 km (standard error = 0.4; range 0.4–19.2). From 2001 to 2009, there were 25 caribou fitted with GPS collars (7407 fixes total recorded during winter, mean of 296 fixes per caribou, range 32–1063; Tables 2, 3). For both the trailing and GPS data sets, the full model contained the lowest AIC score, by at least 16.8 AIC units (Appendix S4). For this reason, comparisons between the two metrics are based on the full models in both cases (Tables 4, 5), though each of the candidate models (parameter estimates and precision, AIC values) is presented in Appendix S4.

Habitat use

In human-altered landscapes, both GPS and snow-trailing methods resulted in caribou consistently selecting areas with a high proportion of older, primary forest although they also used other habitat types on occasion (Tables 2–5). Mean tree age was 17 yr older in use buffers for the GPS analysis and 13 yr older in use buffers of the trailing data, compared to their respective availability buffers (Tables 2, 3). Most GPS locations were in primary forest (80%), but some were in young natural forest (8%), young cut forest (5%), secondary forest (4%), or alpine (3%). Regardless of what habitat they were in, caribou showed neutral or negative selection for the distance to the edge of habitat patches (meaning animals were found closer to edges than expected), for both methods and both univariate and logistic regression analyses (Tables 2–5). For both metrics, the direction of parameter estimates was identical in logistic regression models, with the notable exception of road density (Tables 4, 5).

Roads

Global Positioning System locations of collared caribou rarely had roads within their 100-m use buffer—only 5% included roads. These instances were scattered across caribou, with 22 (88%) of the individuals having roads within at least one use buffer. Of the snow trails followed, 82% had roads in their 100-m buffer. The GPS data suggested that caribou avoided densely roaded areas (Tables 2, 4). Road density was 23% lower in use

Table 2. Univariate comparisons for buffers of used and available habitat around caribou GPS locations.

Variable	GPS $N = 25$			
	Used	Available	PD	P
Road density (km/km^2)	0.35 (0.20–0.58)	0.50 (0.41–0.60)	−32.7 (−53.1 to −6.3)	0.110
Age (yr)	175 (157–191)	158 (144–170)	10.1 (2.4 to 17.3)	0.002
Elevation (m)	1600 (1526–1675)	1556 (1483–1625)	2.7 (2.0 to 3.4)	<0.001
Slope (%)	38 (32–43)	42 (37–47)	−11.8 (−16.3 to −7.6)	<0.001
Cedar (%)	6.2 (3.2–9.5)	6.4 (4.3–8.5)	−32.8 (−49.7 to −14.5)	0.855
Hemlock (%)	8.3 (3.5–14)	8.4 (4.6–13.3)	−37.7 (−57.7 to −15.5)	0.909
Fir (%)	38.1 (31.4–44.3)	33.3 (27.9–38.1)	11.0 (4.1 to 18.5)	0.001
Spruce (%)	31.5 (26.8–35.8)	32.2 (28.1–35.9)	−3.4 (−10.2 to 4)	0.475
Other tree species (%)	1.7 (0.7–3.2)	2.3 (1.5–3.3)	−42.7 (−58.7 to −25.5)	0.055
Open (%)	13.9 (8.7–21.4)	17.3 (12.5–23.8)	−7.6 (−34.2 to 27.7)	0.032
Alpine (%)	5.4 (1.3–11.7)	6.2 (2.8–10.3)	−47.8 (−65 to −29.4)	0.509
Primary forest (%)	72.6 (65.7–77.9)	64.6 (59.5–68.5)	11.6 (4.4 to 18.2)	<0.001
Secondary forest (%)	6.6 (4.2–9.6)	8.6 (6.6–10.6)	−19 (−45.7 to 10.4)	0.174
Young natural forest (%)	8.6 (6.7–10.6)	10 (7.8–12.3)	7.4 (−25.3 to 52.7)	0.185
Young cut forest (%)	5.1 (3.1–7.2)	9 (6.5–11.4)	−56.2 (−68.2 to −43.3)	<0.001
Distance into:				
Alpine (m)	79 (66–92)	168 (131–202)	−30.8 (−42.5 to −20.1)	<0.001
Primary forest (m)	198 (159–249)	208 (173–255)	−6 (−13.1 to 0.7)	0.1802
Secondary forest (m)	60 (51–70)	81 (69–94)	−17.6 (−28.5 to −6.9)	0.0043
Young nat. forest (m)	41 (35–49)	51 (44–59)	−16.3 (−25.5 to −6.5)	0.0035
Young cut (m)	66 (55–77)	87 (76–98)	−17.4 (−25.3 to −9.6)	0.0007

Notes: CI, confidence interval; GPS, global positioning system; PD, percent difference. Means, 95% CIs, PD, and *P*-values from paired *t* tests are provided. *N* is the number of caribou from which means were calculated.

Table 3. Univariate comparisons for buffers of used and available habitat around caribou snow trails.

| | Snow trail $N = 63$ | | | |
Variable	Used	Available	PD	P
Road density (km/km^2)	1.48 (1.16–1.81)	1.03 (0.91–1.15)	42.3 (13.2 to 72.9)	0.003
Age (yr)	156 (142–171)	143 (134–153)	12.3 (1.1 to 25.9)	0.033
Elevation (m)	1405 (1324–1482)	1389 (1314–1460)	0.8 (−0.6 to 2.1)	0.029
Slope (%)	30 (26–33)	31 (28–34)	−5.4 (−11.3 to 1.5)	0.136
Cedar (%)	8.5 (5.2–12.1)	8.2 (5.7–10.9)	−30.6 (−45.5 to −17)	0.673
Hemlock (%)	11.2 (6.5–16.5)	9.6 (6.4–13.2)	−23.2 (−38.7 to −6.3)	0.208
Fir (%)	27.8 (22.3–33.6)	27.6 (23–31.9)	−15.5 (−27.2 to −4.6)	0.814
Spruce (%)	37.8 (32.4–43)	37.6 (33.4–41.5)	−6.7 (−18 to 4.2)	0.894
Other tree species (%)	1.2 (0.4–2.5)	1.5 (1–2.3)	−36.3 (−53.2 to −17.5)	0.353
Open (%)	13.1 (9.0–17.9)	15.3 (11.7–19.4)	−8.7 (−31.8 to 17.9)	0.041
Alpine (%)	0.0	0.0		
Primary forest (%)	60.7 (54.8–66.6)	54.4 (50.8–57.8)	14.0 (2.8 to 26.4)	0.006
Secondary forest (%)	6.1 (4–8.3)	11.3 (8.8–14.0)	−44.8 (−59.7 to −27.7)	<0.001
Young natural forest (%)	5.4 (3.5–7.5)	6.3 (4.7–8.0)	−25.4 (−50.1 to 2.9)	0.309
Young cut forest (%)	22 (16.9–27.3)	24.3 (20.4–28.3)	−10.0 (−28.4 to 9.9)	0.232
Distance into:				
Alpine (m)	0.00	0.00		
Primary forest (m)	107.3 (91.7–123.8)	142.0 (123.6–162.2)	−21.4 (−30.5 to −12.6)	<0.001
Secondary forest (m)	39.8 (33.7–46.4)	62.6 (52.7–73.4)	−74 (−82.4 to −65.0)	<0.001
Young nat. forest (m)	25.5 (22.2–29.5)	32.7 (28.1–39.0)	−52.6 (−64.1 to −41.4)	0.016
Young cut (m)	61 (50.6–73.5)	103 (90.1–117.4)	−49.3 (−57.6 to −41.1)	<0.001

Notes: CI, confidence interval; PD, percent difference. Means, 95% CIs, PD, and *P*-values from paired *t* tests are provided. *N* is the number of snow trails from which means were calculated.

buffers compared to available buffers for the GPS data (Table 2). In contrast, trailing data suggested selection for higher road densities (Tables 3, 5; Fig. 1) with average road density 42.3% greater in used buffers (1.48 km/km^2, 95% CI = 1.16–1.81, Table 3) than in available buffers (1.03 km/km^2, 95% CI = 0.91–1.15) (paired *t* test *P* = 0.003). As well, 57% of snow trails had greater use of roads than available (Table 5), whereas only 12% (3/25)

of GPS-fitted individual caribou had positive selection for roads (Table 4).

Selection inferences derived from the GPS and snow-trailing data were not impacted by availability effects. For road density, the bootstrap 95% CIs for PD estimated from the trailing data did not overlap zero. Further, a functional response in selection was not evident using either data set as linear and quadratic relationships between

Table 4. Standardized fixed-effect coefficients (β), 95% CIs, and *P*-values from mixed-effects logistic regression on GPS locations, and the frequency and percent of coefficients from 25 individual caribou showing positive selection for road density or slope.

Variables	Standardized β (95% CI)	P	n Positive	% Positive
Distance from edge	−0.205 (−0.248 to −0.162)	<0.001	n/a†	n/a
Road density	−4.86 (−9.599 to −0.124)	0.044	3	12
Slope	−0.696 (−0.971 to −0.42)	<0.001	2	8
Habitat type				
Alpine	−0.189 (−0.233 to −0.146)	<0.001	n/a	n/a
Secondary forest	−0.42 (−0.462 to −0.378)	<0.001	n/a	n/a
Young clearcut forest	−0.508 (−0.554 to −0.461)	<0.001	n/a	n/a
Young natural forest	−0.244 (−0.283 to −0.206)	<0.001	n/a	n/a
Intercept	−1.348 (−2.615 to −0.082)	0.001	n/a	n/a

Notes: CI, confidence interval; GPS, Global Positioning System. The reference category for habitat types is "primary forest." Nagelkerke's (1991) modified R^2 value for the model was 0.22.
  † Subject-specific (or conditional) coefficients were only estimated for Road density and Slope covariates.

Table 5. Standardized coefficients (β), 95% CIs, and *P*-values from logistic regression of caribou snow trails, and the frequency and percent of trails showing positive selection for each variable.

Variables	Standardized β (95% CI)	P	n positive	% positive
Distance to edge	−1.049 (−1.685 to −0.412)	0.001	16	25
Road density	0.535 (0.006 to 1.064)	0.047	36	57
Slope	−0.208 (−0.635 to 0.219)	0.339	21	33
Habitat type				
Secondary forest	−1.027 (−1.531 to −0.524)	<0.001	7	11
Young clearcut forest	−0.791 (−1.36 to −0.221)	0.006	27	43
Young natural forest	−0.539 (−1.044 to −0.034)	0.036	15	24
Intercept	−0.054 (−0.466 to 0.358)	0.797		

Notes: CI, confidence interval. The reference category for habitat type is "primary forest." The Nagelkerke's modified R^2 value for the model was 0.35.

DISCUSSION

We contrasted time-based and distance-based methods to estimate resource selection of an endangered herbivore, the mountain caribou, when living in human-altered landscapes. Results between the two methods were similar for most explanatory variables. The selection for old forests has been documented across the range of woodland caribou (Apps et al. 2001, Apps and McLellan 2006), and both metrics supported this result. In the rugged mountains where this study occurred, both metrics also indicated selection for gentle slopes, and caribou

selection and availability were weak ($R \leq 0.05$; Fig. 2). For the GPS data, these relationships remained unchanged even after removing three outliers (individuals with selection coefficients ≤ -10; $R \leq 0.04$).

Fig. 1. This example illustrates how roads cover a minute proportion of the available habitat, but 12% of the caribou path is on the road. Even relatively frequent (2-h) telemetry fixes may not detect selection for this road, particularly if the animal moved quickly and settled in the primary forest patch to forage. Selection for habitat edges is also apparent.
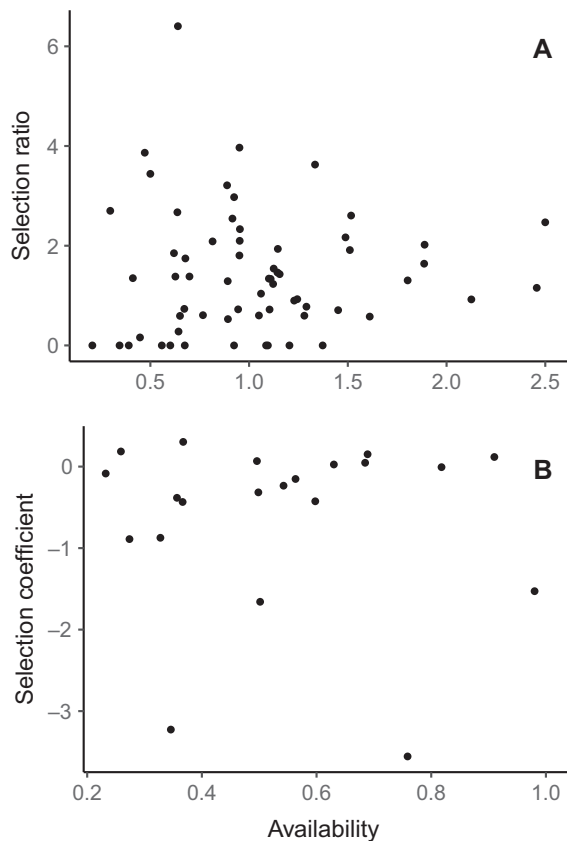
Fig. 2. The relationship between caribou selection for road density and the availability of roads (km/km²) using the snow-trailing data (A) and the Global Positioning System (GPS) data (B). The relationship was weak ($R \leq 0.04$) for both data sets, indicating no support for a functional response in selection. Three caribou with selection coefficients ≤ -10 are not shown on the lower graph, and their removal had no effect on the strength of correlation. Note the scales of the X-axes differ.

were more likely to be found near edges. Field observations often recorded extensive feeding on lichen at edges of cutblocks where litterfall and windthrown trees are more common (Esseen and Renhorn 1998). Selection for edges suggests that caribou avoid entering far into younger stands which may make movement through fragmented landscapes more difficult.

Most studies of resource selection by caribou in managed landscapes have highlighted an avoidance of roads but we found that different methods of investigation generated opposing

inferences. Our distance-based method revealed selection of areas with high road density by most caribou, while the typical time-based method showed avoidance of areas with high road densities. These inferences are not likely affected by a sampling artifact caused by differences in habitat availability, because we found no evidence to suggest a functional response in selection with respect to road density. Furthermore, the range of availability across the two sampling methods overlapped (Fig. 2).

The selection of roaded areas (based on the snow-trailing metric) is counter to most, if not all, published work on caribou in managed landscapes (James and Stuart-Smith 2000, Dyer et al. 2001, 2002, Leblond et al. 2011, DeCesare et al. 2012, Appendix S1). The discrepancy between the two metrics of resource selection is readily explained if animals use roads and other linear features for rapid travel. Discontinuous sampling obtained by GPS data can depict underrepresentation of use or selection of any linear feature that facilitates movement (Thurfjell et al. 2014). For animals as varied as domestic cattle and free-ranging wolves, an exponential decay in distance traveled was a function of increasing GPS fix interval (Mills et al. 2006, Johnson and Ganskopp 2008). As the fix interval increased from only 5 to 15 min, measures of distance moved declined dramatically in both studies.

Our results suggest a complexity when trying to link selection of a habitat to the importance of the habitat. In particular, animals may not spend much time in a habitat feature such as a road or a game trail but such features may be important for efficiently exploiting their home range. Conversely, animal movements are very restricted when in a preferred foraging site such as a caribou at a windthrown tree covered with lichen (Serrouya et al. 2007) or a grizzly bear (*Ursus arctos*) at a preferred salmon fishing spot. In such instances, distance-based metrics would be prone to the opposite bias, by underrepresenting stationary feeding sites. Clearly each metric is prone to a bias, and our purpose here is not to advocate one over the other, but to highlight that each metric is better suited to detect selection for different behaviors (e.g., distance for rapid movement and time for foraging). However, a clear advantage of snow trailing is the fine resolution obtained from field

sampling. For example, recording use of narrow features is prone to less error because the observer was on the ground, whereas using remote technology from collars and GIS basemaps, documenting use requires a variety of assumptions (e.g., buffer sizes, telemetry errors; see Dickie et al. 2017).

In terms of underestimating selection for linear features using GPS data, it is difficult to estimate the magnitude of this problem for large mammal studies, but for caribou at least, most resource-based studies used fix frequencies in the range of 2–8 h (Appendix S1). Given the results shown here, and the sensitivity of GPS fix intervals highlighted by other researchers (Mills et al. 2006, Johnson and Ganskopp 2008, Rowcliffe et al. 2012), it is likely that a bias exists against detecting selection for linear features, so results suggesting avoidance of such features should be interpreted with caution.

Advances in state-space models that discriminate among moving and resting/foraging phases (Breed et al. 2012, Owen-Smith et al. 2012, Wilson et al. 2012) may be able to address the biases suggested here. However, an empirical approach would be to program GPS collars to obtain many locations (every five minutes or less) at set periods (e.g., 1 d/week), interspersed with periods of more typical fix intervals to prolong battery life. The high-intensity sampling could be contrasted with typical sampling to estimate the magnitude of this potential bias. Dickie (2015) used a pulsed sampling approach when studying the fine-scale movements of wolves and their interactions with seismic lines. She found that inferences of travel speed and successive movement on lines were highly sensitive to fix intervals. Seismic lines were strongly selected based on five-minute data, but in a directly adjacent study site, Latham et al. (2011) found no selection for seismic lines in winter by wolves, based on two-hour location intervals. This comparison suggests another case where the inference of linear features is apparently affected by the GPS sampling interval.

The selection for roads by some mountain caribou for moving through human-altered landscapes may set an ecological trap (Van horne 1983, Remeš 2003). Wolves, a major predator of caribou, also select roads to move along (Dickie et al. 2017) where they forage more efficiently (McKenzie et al. 2012), suggesting that caribou on or near roads are at greater risk of being killed (Apps et al. 2013). Wolves are likely olfactory predators (Mech et al. 2015), so even though caribou may not spend much time on roads (as suggested by our GPS telemetry and many studies), the disproportionate distance caribou cover on roads would leave a scent path that would be encountered by wolves. The potential for the ecological trap suggests an additional mechanism for the avoidance of roads observed in many caribou studies; individuals that fall into the trap are no longer available to be sampled in telemetry studies. An implication of caribou being attracted to roads and other linear features (e.g., seismic lines) for movement is that these features may have a more adverse effect on population persistence than previously suspected.

When the influence of roads and edges is considered across broad spatial scales, both are negatively associated with the persistence of individuals and populations (James and Stuart-Smith 2000, Apps and McLellan 2006, Apps et al. 2013), likely by increasing encounter rates with predators. Caribou selection of roads for movement and edges for foraging in a human-altered landscape may suggest benefits at a fine scale, but land management that produces these conditions has negative consequences at broad scales that influence populations. Contiguous old forests have been shown to provide consistent foraging opportunities at fine scales (Terry et al. 2000, Kinley et al. 2003, Serrouya et al. 2007), and a much greater chance of persistence at broad scales (Apps and McLellan 2006, Wittmer et al. 2007, 2010).

Acknowledgments

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1730/full