



Effects of roads on individual caribou movements during migration



Ryan R. Wilson ^{a,*}, Lincoln S. Parrett ^b, Kyle Joly ^c, Jim R. Dau ^d

^a The Wilderness Society, 705 Christensen Dr., Anchorage, AK 99501, United States

^b Alaska Department of Fish and Game, 1300 College Rd., Fairbanks, AK 99701, United States

^c National Park Service, 4175 Geist Rd., Fairbanks, AK 99709, United States

^d Alaska Department of Fish and Game, P.O. Box 689, Kotzebue, AK 99752, United States

ARTICLE INFO

Article history:

Received 13 May 2015

Received in revised form 17 December 2015

Accepted 25 December 2015

Available online xxxx

Keywords:

Animal movement

Connectivity

Disturbance

Industrial development

Migration

Roads

ABSTRACT

Long distance migrations by large mammals are increasingly imperiled by human development. We studied autumn migratory patterns of caribou (*Rangifer tarandus*) in relation to an industrial road in northwestern Alaska. We built null movement models to determine the expected time to cross the road if caribou movements were not affected by the road. We then identified individuals that took longer to cross than expected (slow crossers) and those that did not differ from that expected from the null model (normal crossers). We identified eight as slow and 20 as normal crossers. Slow crossers took an average of 33.3 ± 17.0 (\pm SD) days to cross the road compared to 3.1 ± 5.5 days for normal crossers. Slow crossers had an average crossing date of 8 Nov. \pm 7.7 days versus 25 Oct. \pm 20.6 days for normal crossers. Movement rates of the two classes did not differ before crossing the road, but slow crossers moved > 1.5 times as fast as normal crossers after crossing the road. Movement patterns were partially explained by environmental attributes, but were most strongly affected by how far a caribou was from the road and whether it was classified as slow or normal crosser. While avoidance is an important aspect of the effects of roads on populations, our results show the importance of other factors, such as how long individuals are delayed in crossing when assessing the influence of development on wildlife.

© 2015 Elsevier Ltd. All rights reserved.

1. Introduction

The preservation of long-distance terrestrial migrations has received increased attention as some migratory populations have been lost due to human development (e.g. Berger, 2004, Bolger et al., 2008, Harris et al., 2009). Migration, the cyclical movement between disjunct ranges, is thought to evolve where the behavior enhances fitness by either accessing ranges with higher quality or quantity of forage or reducing exposure to predation and parasites (e.g., Avgar et al., 2014). With some individuals traveling > 5000 km annually as they migrate between seasonal ranges, caribou undertake one of the longest recorded migrations of any terrestrial mammal species (Fancy et al., 1989). Caribou are facing increased human development across their range (Festa-Bianchet et al., 2011) that have led to shifts in space use (Cameron et al., 2005), reductions in habitat (Nellemann et al., 2003), and impeded movements (Vistnes et al., 2004). All of these changes have the potential to restrict caribou migrations and may lead to population-level effects (Bolger et al., 2008).

While the complete restriction of migration is likely to have the greatest effect on populations (Bolger et al., 2008, Berger et al., 2006), negative effects to populations are possible even if migration is partially

restricted. This is evident in developed areas where animal passage has continued despite a network of roads and buildings (e.g., Lendrum et al., 2013). For example, in the near absence of development, mule deer (*Odocoileus hemionus*) spent 95% of their migration at stop-over sites to take advantage of high quality forage (Sawyer and Kauffman, 2011). When development increased, however, the use of stop-over sites was significantly reduced (Sawyer et al., 2013). Thus, semi-permeable barriers to movement, such as roads, can affect animals even though they are still capable of moving between seasonal ranges.

The influence of roads and other semi-permeable infrastructure on caribou migration is not well documented or understood. The scale and extent to which deflections and avoidance occur remains an unanswered question, particularly for migrating caribou. The majority of the early literature on caribou-infrastructure interactions summarized observations of caribou in the immediate vicinity of a road or pipeline (e.g., Curatolo and Murphy, 1986, Dau and Cameron, 1986, Murphy and Curatolo, 1987, Singer and Beattie, 1986). These studies documented rates of crossing success, distribution, and behavior near infrastructure, but may have included repeat observations of the same individuals, were often unable to account for the entire movement paths of individual animals when they encountered roads, and did not account for individuals that avoided roads at greater distances (Vistnes and Nellemann, 2008). Since the advent of global positioning system (GPS) collars, year-round movement paths of individual animals can be recorded and analyzed at multiple spatial and temporal scales.

* Corresponding author at: 705 Christensen Dr., Anchorage, AK 99501, United States.
E-mail address: ryan.radford.wilson@gmail.com (R.R. Wilson).

Although studies have documented large-scale patterns of caribou responses to infrastructure (e.g., Johnson et al., 2005, Boulanger et al., 2012), few studies have quantified the behavior of individual caribou as they attempt to cross a road or other infrastructure during migration. The few studies that have been conducted on caribou have shown that migratory movements can be hindered by development with the potential for delayed arrival at seasonal ranges (Dyer et al., 2002, Mahoney and Schaefer, 2002, Vistnes et al., 2004, Panzacchi et al., 2013). For example, a recent study by Panzacchi et al. (2013) found that reindeer migration in Norway was delayed approximately five days as individuals moved parallel to the road looking for an optimal crossing location.

Given the importance of preserving the long distance migrations of caribou (Bolger et al., 2008) and the current rate of development in the north (Festa-Bianchet et al., 2011), it is important to understand how developments influence migratory behavior in individuals and how this might translate into population-level effects. This is especially true in northwestern Alaska where there is currently limited industrial development, but large-scale developments are in various stages of planning with many potentially bisecting caribou migration routes (AECOM, 2012, Wilson et al., 2014). Therefore, we sought to understand how autumn migration patterns of caribou in northwestern Alaska were affected by the presence of an industrial road. Specifically, we quantified how movement patterns of individuals were influenced by the road and what the consequences of these changes were for the duration of migration and final wintering location, while accounting for the influence of environmental variables.

2. Materials and methods

2.1. Study area

The Red Dog Mine is a zinc–lead mine located in northwest Alaska, approximately 100 km north of Kotzebue, Alaska, and 70 km east of the Arctic Ocean (Fig. 1), and is the world's largest producer of zinc concentrate. The mine has been in operation since 1989 and operates year-round, transporting concentrate to the port facility along an approximately

80 km long road (hereafter, 'the road'). The road only connects the mine to the port and is not accessible by any other road in the state. Traffic along the road, primarily large trucks hauling ore, is constant throughout the year, although it is halted when caribou are on or adjacent to the road. The road is approximately 12 m wide and has no lateral barriers to movement (e.g., fences), nor does it have linear features (e.g., power lines) adjacent to it that might deter caribou from crossing (Tyler et al., 2014). Average traffic levels are approximately 49 round trips per day, or just over 4 vehicles per hour, 24 h a day (Tetrattech, 2009). Some additional traffic occurs seasonally in the form of all terrain vehicles used for hunting, primarily limited to residents of the nearest community, Kivalina (pop. 374).

Two caribou herds contact the road: the Western Arctic (WAH) and Teshekpuk (TCH) caribou herds. The WAH is currently the largest herd in the state (~235,000; Dau, 2013), whereas the Teshekpuk herd is considerably smaller (~32,000; L. Parrett unpublished data). The primary period each year when individuals from both herds interact with the road is during autumn migration (Appendix A), but individuals from the WAH can also encounter the road in summer as they move to and from coastal areas in search of insect relief habitat, or during winter when they are relatively immobile. Neither herd crosses the road during spring migration, which occurs approximately 100 km east of the road (Dau, 2013, Parrett, 2013).

2.2. Data collection and handling

We captured adult female caribou from both herds (TCH: 2004–2012; WAH 2009 – 2012) and fit individuals with GPS collars. During September of each year, we captured WAH individuals (2009 = 39; 2010 = 15; 2011 = 14; and 2012 = 12) as they swam across the Kobuk River at Onion Portage in autumn (Fig. 1; Dau, 1997). We programmed GPS collars for WAH individuals to receive locations every 8 h. We captured individuals in the TCH each year in June (2004 = 10, 2006 = 12, 2007 = 12, 2008 = 27, 2009 = 21, 2010 = 14, 2011 = 9, 2012 = 17, 2013 = 14) with a net gun fired from a helicopter (Rongstad and McCabe, 1984)

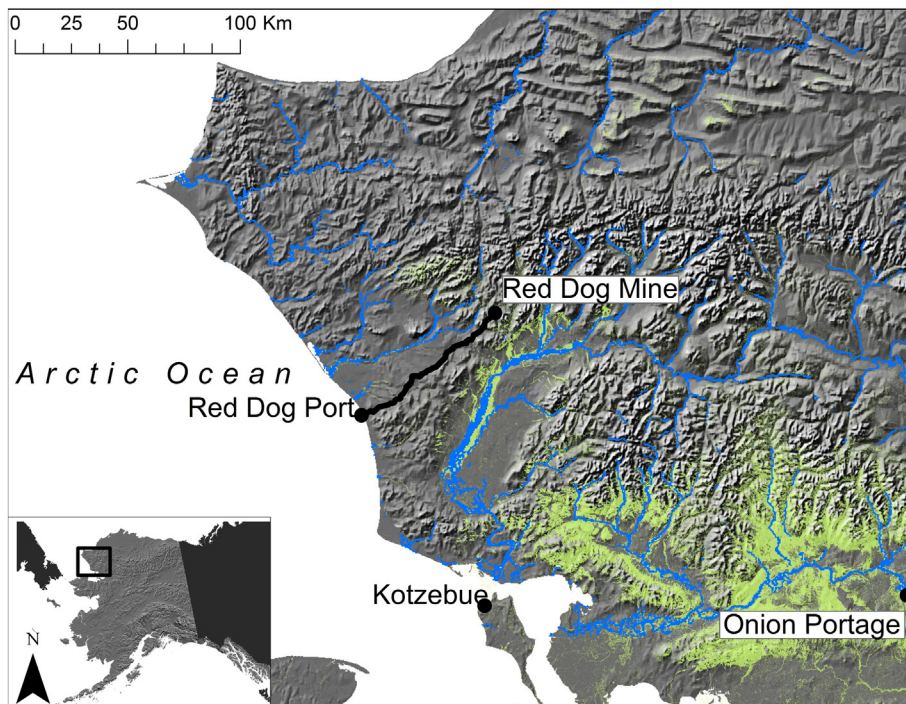


Fig. 1. The Red Dog Mine and its controlled access road in northwestern Alaska (black line); the concentrate storage and port facility is located at the western terminus of the road, whereas the mine is located at the eastern terminus. Major rivers are labeled in blue and areas with dense vegetation are labeled in green. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and programmed their collars to receive locations every 2 h (Parrett, 2013).

We restricted our analysis to the period of autumn migration, which we considered to occur between 15 Aug. and 15 Dec. Although this likely captured periods of movement before and after migration, our primary goal was to ensure that we captured the full duration of migratory movements in autumn. We also did not include an individual's migration path for a given autumn if it was captured that same autumn. We further restricted our analysis to only those animals that came within 15 km of the road during this period. To our knowledge, this is the maximum distance reported in the literature that caribou have been shown to respond to industrial activities (Boulanger et al., 2012). Our use of 15 km allowed us to identify individuals that had a reasonable chance of having their migration directly affected by the road; changing the inclusion criteria to 10 or 20 km did not affect how many individuals were included in the study. Spring migration was not included in this analysis because we did not observe individuals coming into contact with the road then.

2.3. Response to the road

2.3.1. Duration of migration

To determine how the road affected individual caribou migration, we used a null movement model to obtain expected distributions of the time it took a caribou to cross the road after first coming within 15 km of it. In the absence of a control, and given the inherent difficulty in evaluating motivation to cross any obstacle, these simulations were necessary to evaluate each individual's predicted path versus the observed. We restricted this analysis to only those caribou that moved south of the road during migration. To generate a null distribution of movement paths, we used a biased random walk model (e.g., Bartoň et al., 2009) to simulate movement paths beginning at the point an animal first came within 15 km of the road and continued until the number of steps matched the actual number of steps an animal took after coming within 15 km of the road (i.e., until 15 Dec). To simulate steps, we obtained an empirical distribution of step lengths from each individual from the beginning of the migration period until it first came within 15 km of the road. From these same steps we determined the directional persistence of steps by calculating the mean resultant length. We then sampled the direction of each simulated step from a wrapped normal distribution with the concentration parameter set from the mean resultant length and the mean direction set to the location that the individual actually crossed the road using the 'rwrpnorm' function in the 'CircStat' package for R (R Development Core Team, 2013). The mean direction changed at each simulated step. Once a simulated path crossed the road, we changed the mean direction to the location of that individual on 15 Dec. For individuals that came within 15 km of the road but did not cross it, we set the mean direction to the point on the road the individual came closest to. We simulated 100 paths for each individual, based on each individual's empirical distributions of step lengths and turn angles.

For each simulated and actual path, we determined the number of days between the animal's first encounter with the road at 15 km and when the animal crossed it. For animals that did not cross but moved south of the road during migration (i.e., skirted the east end of the road; Fig. 1), we calculated the time to cross the road based on when the individual first occurred south of the road. With the expectation that caribou migration could be delayed by the road (Panzacchi et al., 2013), we classified individuals as 'slow crossers' if their observed time to cross the road was >97.5% quantile of the expected distribution of crossing times, and as 'normal crossers' if their crossing time did not differ from the expected distribution (<97.5% quantile).

We tested for differences in the number of days that elapsed between first coming within 15 km of the road and crossing it for slow and normal crossers; although a difference in grouping is established a priori through the partitioning of the groups, the actual magnitude of difference between groups is established through this comparison. We also tested for differences between slow and normal crossers in the

movement rates and total distance moved during three distinct periods: before coming within 15 km of the road, after coming within 15 km of the road but before crossing it, and after crossing the road. Because locations for WAH caribou occurred at 8-h intervals (compared to 2-h interval for the TCH), we corrected movement rates and distances for WAH so they were comparable to 2-h intervals following correction factors found in Prichard et al. (2014). From Prichard et al. (2014) we obtained the average correction factor between Aug. and Dec. (i.e., 1.196) and multiplied this by the observed values for the WAH. We tested for differences in the total distance traveled during migration and the latitude an individual was located on 15 Dec. between individuals classified as slow and normal crossers. We used *t*-tests to perform all one-way tests between slow and normal crossers.

2.3.2. Response to a simulated road

To determine if animals that did not encounter the road displayed similar movements to those that did, we conducted a pseudo experiment with individuals that did not come within 15 km of the road during years that we observed caribou encounter the road (i.e., 2008–2013). We restricted paths of animals that did not encounter to the same period we did for those animals that did encounter the road (i.e., 15 Aug.–15 Dec). We randomly selected the same number of individuals that actually encountered the road with the same distribution of years that animals encountered the road. We then chose a random location along the road and moved the road so that point intersected with the caribou path on 29 Oct. (the mean date we observed animals crossing the real road). We then determined the number of days between an animal first coming within 15 km of the fake road and crossing it for the first time. To determine if the time to cross the road differed between real crossers and fake crossers, we used a Welch *t*-test to control for unequal variance between the two groups. We predicted that if caribou movement was hindered by the road then real crossers would have a mean crossing time significantly greater than fake crossers.

2.3.3. Influence of extrinsic factors on migration

To determine if the road, other environmental attributes, or both, affected caribou movement during migration, we analyzed first passage time (FPT; Fauchald and Tveraa, 2003) within a Cox proportional hazards modeling framework (Freitas et al., 2008). First passage time measures the intensity of use of an area by determining how long it takes an animal to cross a circle of a given radius (Fauchald and Tveraa, 2003; Freitas et al., 2008). We calculated FPT for each individual at radii ranging from 0.5–15 km, at 0.5 km intervals, and found the highest variability across individuals at a radius of 3.5 km (Fauchald and Tveraa, 2003). We then used this radius to calculate FPT for each step of each individual (Freitas et al., 2008). We modeled FPT as a combination of the following variables: distance to the road, the presence or absence of dense vegetation, distance to class 1 rivers (National Hydrologic Dataset; <http://nhd.usgs.gov/>, accessed 16 Oct. 2013), elevation (Gesch, 2007), terrain ruggedness, and snow depth (Brown and Brasnett, 2015). To determine the presence or absence of dense vegetation, we reclassified a vegetation map of the region (Boggs et al., 2012) to pixels where dense vegetation (e.g., riparian, tall shrub, and forested areas) was present. We used the vector ruggedness measure developed by Sappington et al. (2007) to calculate terrain ruggedness at a scale of 1020 m (corresponding to 17 pixels; Joly, 2011). We obtained modeled snow depth from the Canadian Meteorological Centre Daily Snow Depth Analysis Data (Brown and Brasnett, 2015). We included an interaction term for each of these variables with a categorical variable of whether an observation was obtained from a slow or normal crosser (i.e., reference class). We scaled all variables so they ranged between zero and one to allow the magnitude of coefficient estimates to be compared across variables. We restricted data to the period from first coming within 15 km of the road until an individual crossed the road.

We used the 'coxph' function in the 'survival' package (Therneau, 2013) in R to model FPT against the above variables. The interpretation of coefficient estimates for Cox Proportional Hazards models is slightly different than for typical generalized linear models. As such, lower coefficient estimates indicate a longer FPT (i.e., increased duration in an area) and higher values indicate shorter FPT (i.e., shorter durations in an area). We used the robust variance estimator in 'coxph' to help control for multiple observations per individual. We then found the most parsimonious model from the full suite of models (i.e., all combinations of the above variables) based on the model with the lowest Akaike's Information Criterion score corrected for small sample sizes (AICc; Burnham and Anderson, 2002). We predicted that if the road was a reason for the difference in movement between slow and normal crossers, the interaction with distance to road and crossing classification would be retained in the top model and explain more of the variance than the other environmental variables.

We also modeled the number of days it took an individual to cross the road (after first coming within 15 km of it) against the distance from the road they were at the start of migration, the Julian date the individual first came within 15 km of the road, and the herd the individual was from. Because annual snowfall patterns in the region could also potentially influence the time it took caribou to cross the road, we included two snow-based covariates into the model. The first was the average date of first snowfall each year within 15 km of the road derived from MODIS satellite imagery for Alaska (Lindsay et al., 2015). We also determined the average snow depth within 15 km of the road on the day an individual first came within 15 km of the road based on the Canadian Meteorological Centre Daily Snow Depth Analysis Data (Brown and Brasnett, 2015). We scaled all variables so that they ranged from 0 to 1 to allow the magnitude of coefficient estimates to be compared across variables. We used a Poisson regression to model factors that might influence the number of days it took a caribou to cross the road and found the most parsimonious model using AICc scores (as above; Burnham and Anderson, 2002).

3. Results

3.1. Duration of migration

From the 216 caribou captured during the period of this study we obtained 263 migration paths (2004 = 10, 2005 = 0, 2006 = 12, 2007 = 11, 2008 = 28, 2009 = 19, 2010 = 44, 2011 = 64, 2012 = 38, 2013 = 37; Appendix A). Of these, 32 came within 15 km of the road during autumn migration (TCH = 15, WAH = 17). Only one individual came within 15 km of the road during autumn migration in multiple years ($n = 2$). Four of the 32 caribou never crossed the road and remained north of it throughout the migration period. Four additional caribou skirted the eastern extent of the road but eventually moved south of the road. The number of caribou that came within 15 km of the road differed across years: 2008 = 11, 2009 = 0, 2010 = 0, 2011 = 11, 2012 = 5, and 2013 = 5.

When observed times to cross the road were compared against those expected from the null models, 20 individuals did not differ from their expected values (Appendix B), but eight individuals took significantly more time to cross than expected (Appendix C). All slow crossers were from the WAH and from 2011. For all animals that moved south of the road, the mean duration of time between first coming within 15 km of the road and finally crossing was 11.8 ± 16.6 days (mean \pm SD). The average time between first coming within 15 km of the road and crossing was 33.3 ± 17.0 days for slow crossers compared to 3.1 ± 5.5 days for normal crossers ($t_{5,4} = 7.7, P < 0.001$). Slow crossers first came within 15 km of the road ($4 \text{ Oct.} \pm 14.9$ days) earlier than normal crossers ($22 \text{ Oct.} \pm 18.5$; $t_{16,1} = 2.6, P = 0.019$). The date caribou crossed the road ranged from 27 Sep. to 3 Dec. with an average crossing date of $29 \text{ Oct.} \pm 18.0$ days. Slow crossers had an average crossing date of $8 \text{ Nov.} \pm 7.7$ days versus $25 \text{ Oct.} \pm 20.6$ days for normal crossers ($t_{26,0} = 2.5, P = 0.021$).

Movement rates did not differ between slow or normal crossers prior to coming within 15 km of the road ($t_{7,6} = 1.0, P = 0.358$, Table 1) nor during the period between first coming within 15 km of the road and crossing ($t_{23,6} = 1.3, P = 0.215$; Table 1). After crossing the road, however, slow crossers traveled nearly 60% faster than normal crossers ($t_{13,4} = 2.9, P = 0.013$, Table 1). The total distance traveled during migration differed significantly ($t_{10,9} = 3.6, P = 0.004$) between slow and normal crossers (Table 1).

Because caribou from the WAH were the only ones to be classified as slow crossers, we also tested for differences in migratory patterns for slow and normal crossers from the WAH only. Within the WAH, slow crossers ($4 \text{ Oct.} \pm 14.9$ days) and normal crossers ($1 \text{ Oct.} \pm 16.4$ days) did not differ in the dates they first came within 15 km of the road ($22 \text{ Oct.} \pm 18.5$ days; $t_{12,3} = 0.3, P = 0.751$). Slow crossers (33.3 ± 17.0 days), however, took significantly longer to cross the road than normal crossers (0.9 ± 0.5 days) within the WAH ($t_{7,0} = 6.0, P = 0.005$). Similarly, the date that slow crossers crossed the road ($8 \text{ Nov.} \pm 7.7$ days) was significantly later than when normal crossers did ($2 \text{ Oct.} \pm 16.1$ days; $t_{8,4} = 5.3, P < 0.001$). Slow crossers from the WAH had significantly longer migrations than normal crossers from the WAH ($t_{12,7} = 2.5, P = 0.026$; Table 1).

We observed no differences in movement rates before encountering the road ($t_{8,5} = 1.0, P = 0.368$; Table 1), after encountering the road and before crossing ($t_{11,9} = 0.5, P = 0.626$; Table 1) or after crossing ($t_{12,8} = 1.0, P = 0.345$; Table 1) between slow and normal crossers of the WAH. We also observed no differences between slow and normal crossers in the distance moved before coming within 15 km of the road ($t_{11,9} = 0.4, P = 0.685$; Table 1). The distance moved after first coming within 15 km of the road and before crossing was longer for slow crossers than normal crossers ($t_{7,0} = 5.5, P < 0.001$; Table 1). Conversely, after crossing the road, the distance moved by slow crossers was less than for normal crossers ($t_{11,1} = 3.1, P = 0.011$; Table 1) and slow crossers wintered significantly further south (1712544 ± 53018 m N, Alaska Albers, North American Datum 1983) than normal crossers (1835129 ± 88697 m; $t_{9,5} = 3.2, P = 0.010$).

Table 1

Changes in the average (\bar{x}) total distance moved (km) and rate of movement (km/h) between caribou classified as slow and normal crossers before coming within 15 km of the Red Dog Mine Road (Before), after coming within 15 km of the road but before crossing it (During), after crossing the road (After), and the total length of migration (Total) for the period August 15–December 15. We present results for normal crossers from all herds combined (All) and from the Western Arctic Herd (WAH) specifically.

Class	Before				During				After				Total	
	Distance		Rate		Distance		Rate		Distance		Rate		Distance	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
Slow crosser	564	186	0.53	0.17	467	226	0.69	0.20	378	129	0.52	0.17	1408	189
Normal crosser (All)	747	226	0.47	0.06	45	50	0.83	0.38	344	254	0.32	0.17	1135	155
Normal crosser (WAH)	520	217	0.47	0.05	25	12	0.75	0.23	619	171	0.45	0.13	1161	191

3.2. Response to a simulated road

The mean time to cross the fake road was 6.2 days (8.03) and was significantly shorter than we observed for caribou that actually crossed (11.8 ± 16.6) the road ($t_{38,8} = 2.75, P = 0.009$). The range of observed times to cross was also lower for fake road crossers (0–35) than real crossers (0–60).

3.3. Influence of extrinsic factors on migration

For our analysis of FPT, there was only one competing model (i.e., $\Delta AIC \leq 2$); the full model (Table 2). Caribou movement patterns were partially explained by environmental attributes, but FPT was most strongly affected by how far a caribou was from the road, and whether it was classified as slow or normal; as indicated by the magnitude of those covariate estimates compared to the others (Table 3). For animals classified as slow crossers, FPT increased as they moved closer to the road, but decreased as animals classified as normal crossers moved closer to the road (Table 3). Based on the results of the top FPT model, prior to crossing the road, normal crossers were 6.3 times more likely to leave an area with a radius of 3.5 km when they were 5 km from the road than slow crossers, when holding all other variables constant (Table 3). Overall, normal crossers were 4.9 times more likely to leave an area with a radius of 3.5 km than a slow crosser, when holding all other variables constant (Table 3).

The most explanatory environmental variable for FPT was snow depth, with slow crossers showing evidence for faster FPT (i.e., positive coefficient) in deep snow than normal crossers (Table 3). Slow crossers exhibited evidence of shorter FPT for all other environmental coefficients than normal crossers, except for distance to rivers, where they had longer FPT the further from rivers they were (Table 3). Most striking of these results is that, even after taking account of a wide-variety of environmental variables that could affect FPT, the distance to the road and whether an individual was classified as a slow or normal crosser still were the most explanatory variables of FPT, indicating the strong role the road played during autumn migration.

Of the 64 models that included factors that might influence the time it took a caribou to cross the road, there was only one competing model (Table 4). The best model contained the terms for Julian day of first coming within 15 km of the road ($1.86 \pm 0.27, \beta \pm SE, P < 0.001$), whether an individual was classified as a slow crosser ($2.49 \pm 0.20, P < 0.001$), the average date of first snowfall within 15 km of the road ($-1.12 \pm 0.36, P = 0.002$) and the average modeled snow depth within 15 km of the road ($-1.63 \pm 0.43, P < 0.001$). The model suggested the number of days to cross the road was longer the later in autumn the road was encountered, whether an individual was classified as a slow crosser, the shallower the depth of snow, and the earlier the date of first snowfall. Even after accounting for other variables that could affect crossing time, whether an individual was classified as a slow crosser was still retained in the final model and had the greatest effect on crossing

Table 2

Top 10 models of the first passage time analysis of time required for a caribou to move beyond a 3.5 km radius. Models were based on first passage time data prior to crossing the Red Dog Mine Road. Top models included variables for the distance to first-order rivers (D.River), distance to the road (D.Road), elevation (Elev), the presence or absence of dense vegetation (Dense), terrain ruggedness (VRM) and whether an animal was classified as being a slow or normal crosser (Class; where Class = 0 for normal crossers, and Class = 1 for slow crossers). Interactions between variables and caribou classification are denoted by **. Main effects were included in all cases where the covariate included an interaction.

Model	AICc	$\Delta AICc$	w_i
D2River*Class + D2Road*Class + Elev*Class + SnDepth*Class + VRM*Class + Dense*Class	9738.0	0.0	0.78
D2River*Class + D2Road*Class + Elev*Class + SnDepth*Class + VRM*Class	9741.6	3.6	0.13
D2River*Class + D2Road*Class + Elev*Class + SnDepth*Class + VRM*Class + Dense	9743.7	5.7	0.05
D2River + D2Road*Class + Elev*Class + SnDepth*Class + VRM*Class + Dense*Class	9744.9	6.9	0.03
D2Road*Class + Elev*Class + SnDepth*Class + VRM*Class + Dense*Class	9745.9	7.9	0.02
D2River + D2Road*Class + Elev*Class + SnDepth*Class + VRM*Class	9748.2	10.1	0.01
D2Road*Class + Elev*Class + SnDepth*Class + VRM*Class	9749.9	11.9	0.00
D2River + D2Road*Class + Elev*Class + SnDepth*Class + VRM*Class Dense	9750.1	12.1	0.00
D2Road*Class + Elev*Class + SnDepth*Class + VRM*Class + Dense	9751.9	13.9	0.00
D2River*Class + D2Road*Class + Elev*Class + SnDepth*Class + VRM + Dense*Class	9752.0	14.0	0.00

Table 3

Results of the top first passage time model relating environmental variables to the time required for a caribou to move beyond a radius of 3.5 km from its current position. The model was built with data from caribou prior to crossing the Red Dog Mine Road. Variables included in the top models were distance to first order rivers (D.River), distance to the road (D.Road), the presence or absence of dense vegetation (Dense), terrain ruggedness (VRM), modeled snow depth (SnDepth), elevation, and whether an individual was classified as being a slow or normal crosser (Class; where Class = 0 for normal crossers, and Class = 1 for slow crossers). Interactions between variables and caribou classification are denoted by **. Coefficient estimates related to distance are based on measurements in km.

Variable	Coefficient	SE	P-value
D.River	0.499	0.486	0.304
D.Road	4.539	1.538	0.003
Dense	-0.513	0.219	0.019
VRM	-1.939	0.431	<0.001
Elev	-2.875	1.781	0.106
SnDepth	-1.657	1.119	0.138
Class	-1.585	0.403	<0.001
D.River*Class	-1.244	0.651	0.056
D.Road*Class	-5.303	1.590	<0.001
Dense*Class	1.109	0.446	0.013
VRM*Class	2.753	0.847	0.001
SnDepth*Class	3.434	1.176	0.004

time of any variable. Additionally, the only variable that was retained in the top ten models was whether an individual was classified as a slow or normal crosser (Table 4).

4. Discussion

Maintaining connectivity between seasonally-important ranges can be vital for the continued viability of migratory populations (Berger, 2004, Bolger et al., 2008). Factors that alter migratory patterns (Panzacchi et al., 2013, Sawyer et al., 2013) might affect migratory populations even though migration continues. We observed changes to movements within the autumn migration of female caribou from an industrial road, however, connectivity between seasonal ranges appeared to be maintained. While most caribou did not respond to the road, the road influenced the movements of ~30% of collared individuals (which represents ~70,000 caribou based on current population estimates). Although calculating the actual delay due to the road is difficult, especially due to confounding factors of timing of first encounter, the time between first encounter and crossing averaged 33 days. This is the longest delay reported for either caribou or reindeer (~5 days, Panzacchi et al., 2013).

Many studies on large mammals have shown that the magnitude of individual responses to roads increases as the density of roads increases (Lendrum et al., 2013, Sawyer et al., 2013). Our results suggest, however, that even a single road can alter movement behavior for some individuals. This is surprising given that the volume of traffic along this road is low compared to those described in other studies (e.g., >15 vehicles per hour, Curatolo and Murphy, 1986, Dau and Cameron, 1986,

Table 4

Top 10 models of factors that influence the number of days for a caribou to cross the road. Top models included variables for the Julian day caribou first came within 15 km of the road (JD), the herd a caribou was a member of (Herd), whether an individual was classified as being a slow or normal crosser (Class; where Class = 1 for normal crossers, and Class = 0 for slow crossers), the distance from the road the individual began its migration from (D2Road), the average date of first snowfall within 15 km of the road (SnDate), and the average modeled snow depth within 15 km of the road on the date an individual first came within 15 km of the road (SnDepth).

Model	AICc	Δ AICc	w_i
Class + JD + SnDate + SnDepth	180.8	0.0	0.63
Class + JD + SnDate + SnDepth + D2Road	184.0	3.1	0.13
Class + Herd + JD + SnDate + SnDepth	184.0	3.2	0.13
Class + JD + SnDepth	186.8	6.0	0.03
Class + Herd + JD + SnDate + SnDepth + D2Road	187.5	6.7	0.02
Class + JD + D2Road + SnDepth	188.9	8.1	0.01
Class + JD	189.1	8.2	0.00
Class + Herd + JD + SnDepth	189.6	8.8	0.00
Class + JD + D2Road	190.0	9.2	0.00
Class + Herd + SnDate + SnDepth	190.5	59.7	0.00

Murphy and Curatolo, 1987) and the mine has instituted measures to halt traffic along the road when caribou are on or near the road. One notable difference between this road and others may be the regularity and extreme size of most of the traffic; other studies have shown that traffic level is a significant factor in influencing behavior near roads (e.g. Curatolo and Murphy, 1986, Dyer et al., 2002).

We are not sure what caused certain individuals to delay their crossing of the road while others appeared to show no changes to their migration. Individual differences in the response to infrastructure have been previously documented for caribou in Alaska and appear to be the result of different life history conditions. For example, Cameron et al. (2005) found that parturient females exhibited stronger avoidance of industrial infrastructure in northern Alaska than non-parturient females and males. It could be possible that, for at least some caribou, delayed movement was in response to other caribou that responded to the road and not an inherent response to the road per se. Social cues could lead to individuals responding to road disturbance, albeit indirect, at distances greater than 15 km. If something happens to the leaders of migration, those following will respond by altering their migration route (Padilla, 2010, Miller et al., 1972). In a recent model, Guttal and Couzin (2011) found that most migratory species use social cues to determine migration direction and that only a few individuals determine where to migrate. Thus, migratory behavior of caribou could be largely driven by a few individuals responding to the road directly, with the majority of others responding to the behavior of those individuals. Indeed, the zone of influence (Boulanger et al., 2012) may vary by herd as well as time of year, where it is encountered, and the type of disturbance stimulus.

It is curious that we only observed slow crossers during one year (i.e., 2011) of the study. This could suggest that some other lurking variable is causing the movement patterns we observed, however, we controlled for a variety of environmental variables and still the road remained the most significant explanatory variable. Our pseudo-control experiment also showed a strong difference in time to cross a fake road compared to caribou encountering a real road. If the effect was due to some lurking environmental variable, we would likely not have seen this difference. Another possible explanation is that we just did not collar enough individuals each year to obtain a sample of slow crossers, especially given that they appear to be less frequent than normal crossers. Given that our annual sample of individuals in the WAH represents approximately 0.0009% of the population, and the migration route that intersects the road is not the core migration route for the population, this explanation seems possible.

Alternatively, research into animal behavior continues to find strong evidence for individual (Darrow and Shivik, 2009, Bergvall et al., 2011) and context-dependent (Coleman and Wilson, 1998, Visalberghi and Addressi, 2000) differences in behavior. This result does suggest that the effects of infrastructure on caribou migration might not be constant

(as most studies imply; Johnson et al., 2005, Boulanger et al., 2012) and vary from year to year given the context the road is encountered. This result is certainly one that elicits further investigation to determine why the road only affects movement in certain years because it does not appear to be influenced by environmental conditions or annual variation in snowfall. It is also interesting that we observed differences in responses of slow and normal crossers to environmental factors, although this is likely related to the fact that movement is already affected by the road and not an inherent movement trait of slow crossers.

Caribou in the TCH were unaffected by the road in our analysis. Caribou in the TCH might have had greater experience with industrial development on the eastern portion of their range (Person et al., 2007) than caribou in the WAH and thus were less sensitive to the road, despite the lack of data to corroborate habituation in other studies (Haskell and Ballard, 2008). The potential for herd-based differences may also explain the higher crossing success observed in some studies on the Central Arctic Herd (e.g. Curatolo and Murphy, 1986), however the different seasons and different factors (e.g. insect harassment) influencing caribou in those seasons may be more explanatory.

This study highlights the importance of observing a caribou's entire migration path to assess behavior towards roads and other forms of infrastructure. In many earlier studies of caribou responses to roads (e.g., Fancy, 1983, Smith and Cameron, 1985), observations were typically made from or adjacent to roadways. Given our results, caribou could have shown responses to the road at larger scales before being classified as having successfully crossed the road. Indeed, the importance of scale in assessing responses of caribou to infrastructure has been previously noted (Vistnes and Nellemann, 2008) and these results provide additional support for their conclusions.

Aside from the potential effects to caribou populations in northern Alaska, additional development could alter the important relationship between caribou and rural communities (Wolfe and Walker, 1987). Even though the northwestern coast of Alaska is not a major autumn migration corridor for either herd studied (Person et al., 2007; Dau, 2013), communities adjacent to this corridor could still be affected by changes in caribou distribution and timing of movements even if the majority of the herd is not. The faster movement speeds we observed for slow crossers after crossing the road could also decrease the amount of time caribou are available to harvest for communities beyond any infrastructure. Additionally, if other roads are built in the region perpendicular to caribou migration routes (Wilson et al., 2014), more communities might experience the effects of altered caribou migrations. It is unclear if there are population-level effects from the road for either caribou herd studied. Of the seven large (>30,000) caribou herds in Alaska, four herds have infrequent contact with major roads (WAH, TCH, Porcupine Herd, Mulchatna Herd), and three have regular contact, often including a large proportion of the individuals in the herd (Central Arctic, Nelchina, Fortymile). Of the herds that do have significant seasonal interactions with roads, in each case, connectivity between seasonal ranges appears to be maintained (Boertje et al., 2012, Arthur and Del Vecchio, 2009), although responses of individuals to the road (as in our study) have not been undertaken. Our results suggest, however, that there might be herd-specific responses to roads encountered during migration. Therefore, simply finding no effect of roads on one herd does not imply that an effect will not exist on another.

Our results serve as a cautionary note for future development in the region, especially if these developments bisect migration corridors used by a greater proportion of the herd. Developers and resource managers should consider the full suite of effects a road could have on migration and not simply whether animals will cross or not. Other studies on the effects of roads and other linear features on migration typically only consider the level of avoidance of these features (e.g., Curatolo and Murphy, 1986, Dau and Cameron, 1986, Murphy and Curatolo, 1987). While avoidance is an important aspect of the effects of roads on populations, our results show the importance of other factors, such as how long individuals are delayed in crossing and increased movements,

when assessing the influence of development infrastructure on wildlife populations. Future research should focus on the effects of delayed migration on individual survival and reproductive potential as well as what factors delay migration for some individuals and not others. Additionally, future research should attempt to understand why delayed crossing is not observed every year or every herd. Finally, this analysis provides a framework for evaluating the movement behavior of other caribou herds that encounter roads during migration.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2015.12.035>.

Acknowledgments

For financial support and field assistance associated with the TCH, we would like to thank B. Person, G. Carroll, D. Yokel, A. Prichard, ConocoPhillips, the Bureau of Land Management (BLM), and the North Slope Borough. Funding was provided, in part, by the U.S. Geological Survey National Park Monitoring Program, the National Park Service, and the U.S. Geological Survey through the Changing Arctic Ecosystems Initiative (Wildlife Program of the USGS Ecosystem Mission Area). Funding for much of the TCH collaring program came from the North Slope Borough through the State of Alaska, Department of Commerce, Community and Economic Development, as well as through support from ConocoPhillips, BLM, and Pittman-Robertson Federal Aid Funding. The WAH field work was accomplished with the Alaska Department of Fish and Game, National Park Service, BLM, U.S. Fish and Wildlife Service, and students and teachers from local-area high schools. We are extremely grateful to D. Gustine and W. Loya for providing substantive input on this project. We thank J. Rasic, D. Yokel, A. Prichard, P. Bente, L. Adams, and B. Dale for providing comments on previous drafts of this manuscript.

References

- AECOM, 2012. Fine Scoping Report Foothills West Transportation Access Environmental Impact Statement. AECOM.
- Arthur, S.M., Del Vecchio, P.A., 2009. Effects of Oil Field Development on Calf Production and Survival in the Central Arctic Herd. Alaska Department of Fish and Game.
- Avgar, T., et al., 2014. On the adaptive benefits of mammal migration. *Can. J. Zool.* 92, 481–490.
- Bartoń, K.A., et al., 2009. The evolution of an 'intelligent' dispersal strategy: biased, correlated random walks in patchy landscapes. *Oikos* 118, 309–318.
- Berger, J., 2004. The last mile: how to sustain long-distance migration in mammals. *Conserv. Biol.* 18, 320–331.
- Berger, J., et al., 2006. Connecting the dots: an invariant migration corridor links the Holocene to the present. *Biol. Lett.* 2, 528–531.
- Bergvall, U.A., et al., 2011. Personality and foraging decisions in fallow deer, *Dama dama*. *Anim. Behav.* 81, 101–112.
- Boertje, R.D., et al., 2012. Fortymile caribou herd: increasing numbers, declining nutrition, and expanding range. Alaska Department of Fish and Game, Wildlife Technical Bulletin. 14 (ADF&G/DWC/WTB-2012-14).
- Boggs, K., et al., 2012. Vegetation map and classification: northern, western and interior Alaska. Alaska Natural Heritage Program. University of Alaska Anchorage.
- Bolger, D.T., et al., 2008. The need for integrative approaches to understand and conserve migratory ungulates. *Ecol. Lett.* 11, 63–77.
- Boulanger, J., et al., 2012. Estimating the zone of influence of industrial developments on wildlife: a migratory caribou *Rangifer tarandus groenlandicus* and diamond mine case study. *Wildl. Biol.* 18, 164–179.
- Brown, R.D., Brasnett, B., 2015. Canadian Meteorological Centre (CMC) Daily Snow Depth Analysis Data, Version 1. NASA National Snow and Ice Data Center Distributed Active Archive Center, Boulder, Colorado USA (<http://dx.doi.org/10.5067/W9FOYWH0EQZ3>. [27 Nov 2015]).
- Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. second ed. Springer-Verlag.
- Cameron, R.D., et al., 2005. Central arctic caribou and petroleum development: distributional, nutritional, and reproductive implications. *Arctic* 58, 1–9.
- Coleman, K., Wilson, D.S., 1998. Shyness and boldness in pumpkinseed sunfish: individual differences are context-specific. *Anim. Behav.* 56, 927–936.
- Curatolo, J.A., Murphy, S.M., 1986. The effects of pipelines, roads, and traffic on the movements of caribou, *Rangifer tarandus*. *Can. Field Nat.* 100, 218–224.
- Darrow, P.A., Shivik, J.A., 2009. Bold, shy, and persistent: variable coyote response to light and sound stimuli. *Appl. Anim. Behav. Sci.* 116, 82–87.
- Dau, J., 1997. Caribou survey-inventory management report. Units 21D, 22A, 22B, 23, 24, 26A. In: Hicks, M.V. (Ed.), Caribou. Federal Aid Wildlife Restoration Survey-Inventory Activities 1 July 1994–30 June 1996. Grant W-24-3 and W-24-4. Study 3.0. Alaska Department Fish and Game, pp. 158–185.
- Dau, J., 2013. Units 21D, 22A, 22B, 22C, 22D, 22E, 23, 24 and 26A caribou management report. In: Harper, P. (Ed.), Caribou Management Report of Survey and Inventory Activities 1 July 2010–30 June 2012. Alaska Department of Fish and Game, pp. 201–280.
- Dau, J.R., Cameron, R.D., 1986. Effects of a road system on caribou distribution during calving. *Rangifer Spec. Issue* 1, 95–101.
- Dyer, S.J., et al., 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in northeastern Alberta. *Can. J. Zool.* 80, 839–845.
- Fancy, S.G., 1983. Movements and activity budgets of caribou near oil drilling sites in the Sagavanirktok River Floodplain, Alaska. *Arctic* 36, 193–197.
- Fancy, S.G., et al., 1989. Seasonal movements of caribou in arctic Alaska as determined by satellite. *Can. J. Zool.* 67, 644–650.
- Fauchald, P., Tveraa, T., 2003. Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* 84, 282–288.
- Festa-Bianchet, M., et al., 2011. Conservation of caribou (*Rangifer tarandus*) in Canada: an uncertain future. *Can. J. Zool.* 89, 419–434.
- Freitas, C., et al., 2008. A novel method for quantifying habitat selection and predicting habitat use. *J. Appl. Ecol.* 45, 1213–1220.
- Gesch, D.B., 2007. The National Elevation Dataset. In: Maune, D., ed. Digital Elevation Model Technologies and Applications: The DEM User's Manual. American Society for Photogrammetry and Remote Sensing.
- Guttal, V., Couzin, I.D., 2011. Leadership, collective motion and the evolution of migration strategies. *Commun. Integr. Biol.* 4, 294–298.
- Harris, G., et al., 2009. Global decline in aggregated migrations of large terrestrial mammals. *Endanger. Species Res.* 7, 55–76.
- Haskell, S.P., Ballard, W.B., 2008. Annual re-habituation of calving caribou to oilfields in northern Alaska: implications for expanding development. *Can. J. Zool.* 86, 627–637.
- Johnson, C.J., et al., 2005. Cumulative effects of human developments on arctic wildlife. *Wildl. Monogr.* 160, 1–36.
- Joly, K., 2011. Modeling influences on winter distribution of caribou in northwestern Alaska through use of satellite telemetry. *Rangifer* 19, 75–85.
- Lendrum, P.E., et al., 2013. Migrating mule deer: effects of anthropogenically altered landscapes. *PLoS One* 8, e64548.
- Lindsay, C., Zhu, J., Miller, A.E., Kirchner, P., Wilson, T.L., 2015. Deriving snow cover metrics for Alaska from MODIS. *Remote Sens.* 7, 12961–12985.
- Mahoney, S.P., Schaefer, J.A., 2002. Hydroelectric development and disruption of migration in caribou. *Biol. Conserv.* 107, 147–153.
- Miller, F., et al., 1972. Group cohesion and leadership response by barren-ground caribou to man-made barriers. *Arctic* 25, 193–202.
- Murphy, S.M., Curatolo, J.A., 1987. Activity budgets and movement rates of caribou encountering pipelines, roads, and traffic in northern Alaska. *Can. J. Zool.* 65, 2483–2490.
- Nellemann, C., et al., 2003. Progressive impact of piecemeal infrastructure development on wild reindeer. *Biol. Conserv.* 113, 307–317.
- Padilla, E.S.R., 2010. Caribou Leadership: A Study of Traditional Knowledge, Animal Behavior, and Policy Thesis University of Alaska Fairbanks.
- Panzacchi, M., et al., 2013. A road in the middle of one of the last wild reindeer migration routes in Norway: crossing behaviour and threats to conservation. *Rangifer* 33, 15–26.
- Parrett, L.S., 2013. Unit 26A, Teshekpuk caribou herd. In: Harper, P. (Ed.), Caribou Management Report of Survey and Inventory Activities 1 July 2010–30 June 2012. Alaska Department of Fish and Game, 355, p. 314.
- Person, B.T., et al., 2007. Distribution and movements of Teshekpuk caribou herd 1990–2005: prior to oil and gas development. *Arctic* 60, 238–250.
- Prichard, A.K., et al., 2014. The effect of frequency of telemetry locations on movement rate calculations in arctic caribou. *Wildl. Soc. Bull.* 38, 78–88.
- R Development Core Team, 2013. R: A Language and Environment for Statistical Computing R Foundation for Statistical Computing.
- Rongstad, O.J., McCabe, R.J., 1984. Capture techniques. In: Halls, L.K. (Ed.), White-tailed Deer: Ecology and Management. Stackpole Books, pp. 655–676.
- Sappington, J.M., et al., 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. *J. Wildl. Manag.* 71, 1419–1426.
- Sawyer, H., Kauffman, M.J., 2011. Stopover ecology of a migratory ungulate. *J. Anim. Ecol.* 80, 1078–1087.
- Sawyer, H., et al., 2013. A framework for understanding semi-permeable barrier effects on migratory ungulates. *J. Appl. Ecol.* 50, 68–78.
- Singer, F.C., Beattie, J.B., 1986. The controlled traffic system and associated wildlife responses in Denali National Park. *Arctic* 39, 195–203.
- Smith, W.T., Cameron, R.D., 1985. Reactions of large groups of caribou to a pipeline corridor on the Arctic coastal plain of Alaska. *Arctic* 38, 53–57.
- Tetratch, 2009. Red Dog Mine Extension: Aqaluk Project. Final Supplemental Environmental Impact Statement. Tetratch.
- Therneau, T., 2013. A package for survival analysis in S. R Package Version 2, pp. 37–44.
- Tyler, N., Stokkan, K.-A., Hogg, C., Nellemann, C., Vistnes, A.-I., Jeffery, G., 2014. Ultraviolet vision and avoidance of power lines in birds and mammals. *Conserv. Biol.* 28, 630–631.
- Visalberghi, E., Addessi, E., 2000. Seeing group members eating a familiar food enhances the acceptance of novel foods in capuchin monkeys. *Anim. Behav.* 60, 69–76.
- Vistnes, I., Nellemann, C., 2008. The matter of spatial and temporal scales: a review of reindeer and caribou response to human activity. *Polar Biol.* 31, 399–407.
- Vistnes, I., et al., 2004. Effects of infrastructure on migration and range use of wild reindeer. *J. Wildl. Manag.* 68, 101–108.
- Wilson, R.R., et al., 2014. Evaluating potential effects of an industrial road on winter habitat of caribou in north-central Alaska. *Arctic* 67, 472–482.
- Wolfe, R.J., Walker, R.J., 1987. Subsistence economies in Alaska: productivity, geography, and development impacts. *Arct. Anthropol.* 24, 56–81.