



Functional responses to anthropogenic linear features in a complex predator-multi-prey system

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Abstract

Context Anthropogenic linear features can have negative effects on wildlife by altering movements or increasing risk. Spatial responses to linear features vary depending on local conditions (functional responses), including linear feature availability. Several studies explored functional responses of wildlife to linear features, but few examined responses of multiple interacting species.

Objectives We evaluated functional responses of Threatened boreal woodland caribou (*Rangifer tarandus caribou*), moose (*Alces alces*), and gray wolves (*Canis lupus*) to roads and seismic lines (linear features created during fossil fuel exploration) to assess the influence these responses might have on predator–prey interactions.

Methods We estimated median distance to and the density of roads and seismic lines around used and available locations by landcover (peatlands and non-peatlands) and season for each individual. To quantify

functional responses, we regressed use in response to availability in peatlands and non-peatlands across seasons and selected the most parsimonious models for each species.

Results Boreal caribou generally avoided higher road density. Wolves selected areas closer to roads in peatlands and demonstrated selection or indifference to higher road density as availability increased. Female moose generally avoided areas with higher road density, except in early winter. Female caribou and moose demonstrated weaker responses to seismic line density. During calving, late summer, and early winter, wolves often selected for seismic line density, particularly in peatlands, when availability was high.

Conclusions Our analyses suggest that boreal caribou, moose, and wolves respond to linear features in complex ways that alter individual space-use and likely influence predation risk.

Keywords Boreal woodland caribou · Gray wolf · Industrial development · Moose · *Rangifer tarandus caribou* · Roads · Seismic lines

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Introduction

Anthropogenic linear features, such as roads, impact species in a variety of ways (D’Amico et al. 2016) with generally negative results (Fahrig and Rytwinski 2009). Species can be directly affected by roads as

barriers to movement, through vehicle collisions, or via pollutants (Forman and Alexander 1988). Indirectly, anthropogenic linear features can result in a loss of functional habitat (Latham et al. 2011a), or alternatively, serve to increase the susceptibility of wildlife populations to human harvest (McLoughlin et al. 2011) or predation (DeMars and Boutin 2018).

The responses of individual populations to anthropogenic linear features are often inconsistent among species and across systems. The surrounding environmental conditions are the most probable explanation for most of these inconsistencies. For example, high traffic volume or frequent human presence can increase road avoidance of predators and prey (e.g., Eldegard et al. 2012), but also can provide a refugium from predators for unharvested prey populations (Berger 2007; Lesmerises et al. 2017). Additionally, differences in the structure (e.g., width, vegetation height, etc.) of anthropogenic linear features can lead to disparate species responses (e.g., Tigner et al. 2015; Dickie et al. 2017).

The aforementioned context-dependent findings can be broadly described as functional responses. The use of the term functional response was originally used to describe changes in kill rate (number of prey consumed by an individual) as a function of prey availability (Holling 1959). This framework was expanded to explain differences in the use of a specific habitat type as a result of the proportion (availability) of that habitat type within an individual's home range (Mysterud and Ims 1998). More recently, functional responses were generalized to describe individual differences in space-use and selection to landscape features, such as roads (Houle et al. 2010), and as a function of the surrounding conditions beyond the availability of the landscape feature of interest. For example, boreal woodland caribou (*Rangifer tarandus caribou*) selected forage-rich vegetation patches more frequently dependent on the amount of nearby refugium patches (Mason and Fortin 2017).

Although functional responses to anthropogenic linear features have been evaluated for individual species (e.g., Houle et al. 2010; Beyer et al. 2013; Prokopenko et al. 2017), few studies explicitly compare the varying responses of multiple interacting species (but see DeMars and Boutin 2018). Northeast British Columbia (BC) provides an ideal case study to evaluate the functional responses (to anthropogenic linear features) of multiple interacting species,

because it contains an extensive network of anthropogenic linear features and a declining population of boreal caribou likely resulting from interactions among disturbances, other prey species, such as moose (*Alces alces*), and predators, such as wolves (*Canis lupus*) (Mumma et al. 2018).

In Northeast BC and across the western boreal forest, fossil fuel development is the primary cause of land-use change (Hebblewhite 2017). The extraction of oil and natural gas results in resource roads and seismic lines, along with well pads and pipelines. Seismic lines are cleared paths (< 2–10 m wide) created during the fossil fuel exploration process. In the peatlands (fens and bogs) of the boreal forest, seismic lines recover slowly (> 50 years), becoming legacy features in the absence of active restoration efforts (Lee and Boutin 2006; van Rensen et al. 2015).

Boreal caribou are listed under the Canadian Species at Risk Act as Threatened across their geographic range. The most-cited mechanism explaining decreases in boreal caribou abundance is a human-mediated increase in apparent competition as a result of anthropogenic disturbance (Festa-Bianchet et al. 2011). Apparent competition is the indirect, negative interaction of two co-occurring species facilitated by a shared predator (Holt 1977). Anthropogenic landscape features are hypothesized to alter the density of other prey species, which subsequently leads to changes in the density of predator species, thus increasing encounters with predators and mortality for boreal caribou (Latham et al. 2011b). Other studies demonstrate alternative mechanisms that potentially explain decreases in boreal caribou abundance, including the alteration of white-tailed deer distribution via climate change (Dawe et al. 2014; Dawe and Boutin 2016) and changes in predator hunting efficiency (Dickie et al. 2016) and caribou-predator spatial overlap as a result of anthropogenic linear features (DeMars and Boutin 2018; Mumma et al. 2018).

In Alberta, the presence of white-tailed deer was more strongly related to winter severity than land-use change, which suggested that climate change might be having an equal or perhaps stronger influence (than land-use change) on apparent competition (Dawe et al. 2014). Another study in the western boreal landscape demonstrated that wolves select for and travel more quickly on anthropogenic linear features, which is hypothesized to increase wolf hunting efficiency and might increase predation on boreal caribou (Dickie

et al. 2016). Further, the presence of anthropogenic linear features increased wolf and black bear (*Ursus americanus*) selection for peatlands (DeMars and Boutin 2018), which are thought to historically have provided boreal caribou with a refugium from predators (McLoughlin et al. 2005). Similarly, anthropogenic linear features were suggested to increase spatial overlap between boreal caribou and wolves and increase risk for caribou, independent of other prey species (Mumma et al. 2018).

Given the extensive footprint of anthropogenic disturbances in northeast BC and the interwoven relationships among Threatened boreal caribou, other prey species, and predators, it is essential that species responses to roads and seismic lines are better understood. Our objective was to evaluate and compare functional responses of boreal caribou, moose, and wolves to roads and seismic lines as a function of the surrounding environmental conditions (landcover, the availability of anthropogenic linear features, and snow depth). We hypothesized that caribou and moose avoid areas with roads and seismic lines, but that avoidance is greater in landcover classes (non-peatlands) more frequently used by wolves (Mumma and Gillingham 2017). In contrast, we anticipated that wolves select for areas containing roads and seismic lines, but that use of these areas declines when the surrounding availability (density) of linear features is high (Houle et al. 2010), because of a decreasing benefit to hunting efficiency once the landscape is saturated with roads and seismic lines. Because of differences in the energetic costs associated with movement through snow (Droghini and Boutin 2017), we also expected that wolf use of seismic lines declines in winter, which likely have unpacked snow and similar or deeper snow depths in comparison to the surrounding areas, but select for roads in winter where snow is potentially removed or compressed by vehicles (Dickie et al. 2017). This study quantifies functional responses to anthropogenic linear features in a complex predator–prey system and considers the potential community-level implications of these responses.

Methods

Study area

Northeast BC has a northern continental climate that consists of cold winters and short summers (Environment and Climate Change Canada 2017). Our study area (Fig. 1) spanning nearly 69,000 km² has moderate topographic relief (elevations ranging from 214 to 1084 m) and is characterized by vast peatland complexes, mixed-wood and deciduous uplands, and riparian areas (DeLong et al. 1991). The area is largely uninhabited outside of Fort Nelson (pop. 3366, Statistics Canada 2016) and along the two major highways (Alaska and Liard). Resource roads (0.79 km/km²) and seismic lines (1.84 km/km²), however, are widely distributed across the study area (Fig. 1) and can achieve densities of > 2 and > 8 km/km², respectively, in the most heavily developed caribou home ranges. The forest industry contributes resource roads and cutblocks (~ 2% cut within last 45 years), primarily in the western part of the study area. Natural gas development is prevalent across the region and contributes resource roads, seismic lines, pipelines, and well pads. Traffic volume on resource roads is generally low within the study area.

Caribou are the most widespread ungulate species in northeast BC and are concentrated in regions where peatlands predominate. In 2012, all five populations of boreal caribou in BC were assessed as ‘Not Self Sustaining’ (Environment Canada 2012). Population estimates lack precision, but suggest a decline in abundance from 1512 in 2004 to 1279 in 2010 (Culling and Cichowski 2017), which corresponds to a decrease in overall density from 0.031 to 0.027 caribou/km².

Moose are the only other ungulate common across the study area but occur at low densities (0.018–0.246 moose/km², Thiesen 2010; McNay et al. 2013) relative to other regions of BC. Moose primarily use uplands and riparian areas, where they may spatially overlap with caribou during some seasons (Mumma and Gillingham 2017).

The main large predators in northeast BC include gray wolves, black bears (*Ursus americanus*), and grizzly bears (*Ursus arctos*). Gray wolves are the primary predator of adult caribou and moose (Culling and Cichowski 2017; Mumma and Gillingham 2017). Black and grizzly bear predation on adult caribou is rare (Culling and Cichowski 2017). Gray wolf

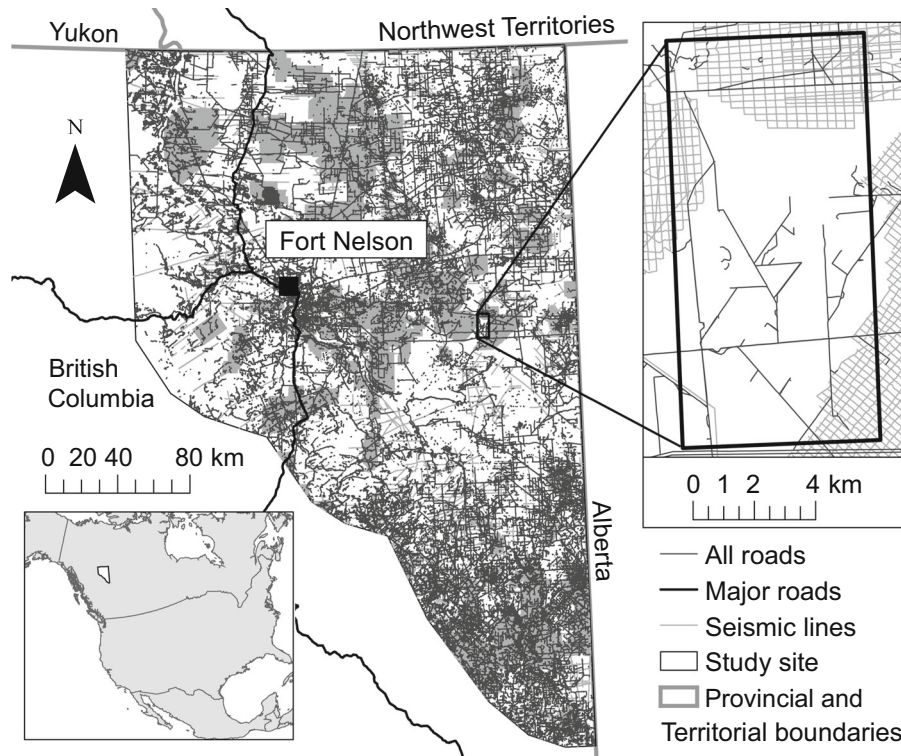


Fig. 1 Study site in northeast British Columbia, Canada depicting the locations of roads and seismic lines. Gray polygons on the large study site map depict areas where seismic line densities are too high for visualization at this scale

densities have been estimated between 0.007–0.016 wolves/km² (Serrouya et al. 2016). Bear densities are unknown within the study area.

Data collection

Female caribou (120 individuals) from all five boreal populations in BC were collared with several models of global positioning satellite (GPS) collars using aerial net-gunning from December 2012–March 2016 (BC Wildlife Permits FJ12-76949, FJ12-80090, and FJ12-83091). Over the same time period, aerial net-gunning was used to GPS-collar wolves (17 males and 12 females) inhabiting parts of the geographic range of all five caribou populations (BC Wildlife Permit FJ14-156487). Collaring of female (42 individuals) and male moose (29 individuals) in March and December 2015 resulted in a similar distribution of GPS-collared moose, overlapping parts of all five caribou ranges (BC Wildlife Permit FJ14-152798).

Collars recorded locations at different rates depending on collar model and settings (4–13 h for caribou,

0.25–8 h for wolves and 12 h for moose). To reduce autocorrelation between wolf locations, we thinned locations from each individual wolf to a minimum of 2 h. At times, more than one wolf was collared from the same pack. To ensure independence, we identified all clustered locations (≤ 100 m within 1 h moving window) of collared wolves from the same pack and then randomly selected a single location from each cluster.

Animal space-use and behaviour may vary across seasons dependent on food availability and reproductive status (Gillingham and Parker 2008; Mumma et al. 2017). We recognized that each of these species has a unique life history that results in seasonal differences in space-use. We, however, were interested in comparing functional responses among these species across the same time periods given the potential for these responses to influence predation risk and survival for boreal caribou. We, therefore, used identical seasons for caribou, moose, and wolves. After considering seasonal changes in environmental conditions and each species' life history, we defined

Table 1 The most parsimonious regression models (linear, second-order polynomial, or third order polynomial) comparing the median distances (m) to and densities (km/km²) of roads and seismic lines (at 500 and 1000 m radii) of femaleboreal woodland caribou (*Rangifer tarandus caribou*) locations in peatlands and non-peatlands as a function of available distances to and densities of roads and seismic lines during the calving, late summer, early winter, and late winter seasons

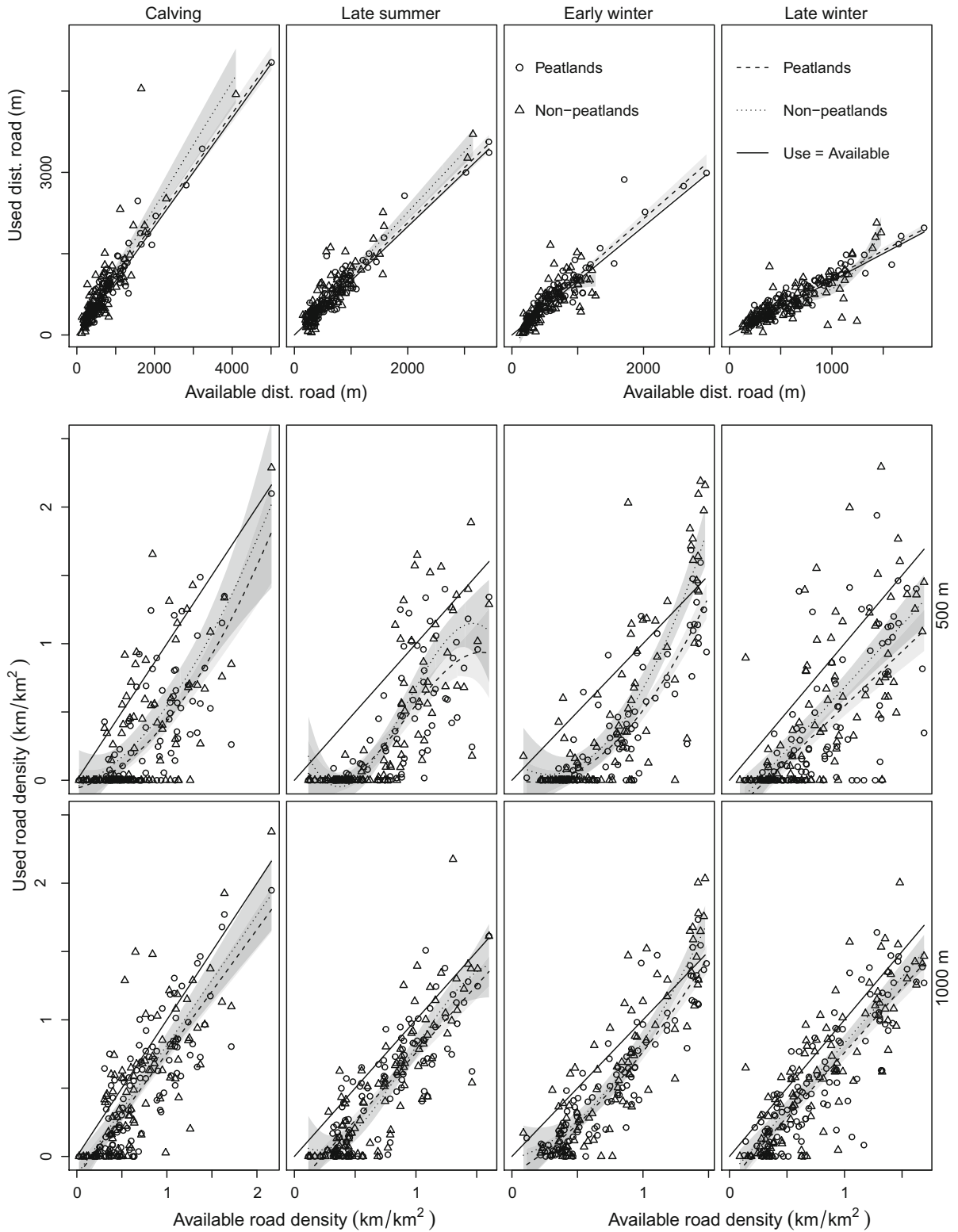
	Distance (m)	Density (500 m)	Density (1000 m)
Roads: peatlands			
Calving	Linear	Second-order ^a	Linear
Late summer	Linear	Third-order ^a	Linear
Early winter	Linear ^b	Second-order ^{ab}	Second-order ^a
Late winter	Linear ^b	Linear ^a	Linear
Roads: non-peatlands			
Calving	Linear ^a	Second-order ^a	Linear
Late summer	Linear ^a	Third-order ^a	Third-order ^a
Early winter	Second-order ^{ab}	Second-order ^{ab}	Second-order ^a
Late winter	Third-order ^{ab}	Linear	Linear
Seismic: peatlands			
Calving	Second-order ^c	Linear	Linear
Late summer	Second-order ^a	Third-order ^a	Third-order ^a
Early winter	Third-order ^{ab}	Second-order ^a	Second-order ^a
Late winter	Linear	Third-order ^a	Third-order ^a
Seismic: non-peatlands			
Calving	Second-order ^a	Linear	Linear
Late summer	Linear	Second-order ^a	Second-order ^a
Early winter	Linear ^{ab}	Linear	Linear
Late winter	Third-order ^a	Second-order ^a	Second-order ^a

^aStatistically significant functional response: altered response as a function of density^bStatistically significant functional response: altered response as a function of landcover^cNon-significant functional response: response overlapping use = available line

four seasons (i.e., calving, late summer, early winter, and late winter). The calving season (May 1st–July 15th) captured the beginning of calving for caribou through the time when late born caribou and moose calves (mid-June) are expected to surpass 1 month of age, representing the period of highest vulnerability for calves (Gustine et al. 2006). The late summer season (July 16th–Oct. 31st) corresponded to decreased calf vulnerability and increased wolf travel distances as wolf pups gained greater mobility. During late summer, caribou and moose also should be maximizing nutritional intake in preparation for winter. We anticipated that caribou and moose might behave differently in early winter (Nov. 1st–Jan. 31st), when body conditions are better and snow depths are low in comparison to late winter (Feb. 1st–Apr. 30th).

We reclassified a boreal vegetation layer (Ducks Unlimited Canada 2013) into peatland and non-peatland landcover classes. Peatlands included nutrient-poor fens (treed, shrubby, and graminoid), nutrient-rich fens (treed, shrubby, and graminoid), and bogs (treed, shrubby, and open bogs). Non-peatlands included uplands (conifer, deciduous, mixed-wood, shrub, and other), swamps (conifer, deciduous, mixed-wood, and shrub), open water, imagery obscured by clouds, anthropogenic (houses, pipelines, and well pads), and burned areas. Open water accounted for ~ 2% of the total study area, and imagery obscured by clouds and anthropogenic areas accounted for ~ 3% of the total study area. Forestry and fire layers (Province of British Columbia 2016) were used to identify cutblocks and younger burns (post-boreal vegetation layer imagery), both of which

Caribou and roads



◀ **Fig. 2** The response (and 95% confidence intervals) to the distance (dist.) to roads and density (500 and 100 m radii) of roads by female boreal woodland caribou (*Rangifer tarandus caribou*) as a function of landcover (peatlands versus non-peatlands) and the available distance to and density of roads, as predicted using the most parsimonious regression model (linear, second-order polynomial, or third order polynomial) for the calving, late summer, early winter, and late winter seasons

were classified as non-peatlands. Roads and seismic line layers (Province of British Columbia 2016; British Columbia Oil and Gas Commission 2016) were used to identify the locations of public and resource roads and seismic lines. Available seismic line layers began in 1996, after which natural gas development increased in our study area.

Table 2 The most parsimonious regression models (linear, second-order polynomial, or third order polynomial) comparing the median distances (m) to and densities (km/km²) of roads and seismic lines (at 500 and 1000 m radii) of female

Data analysis

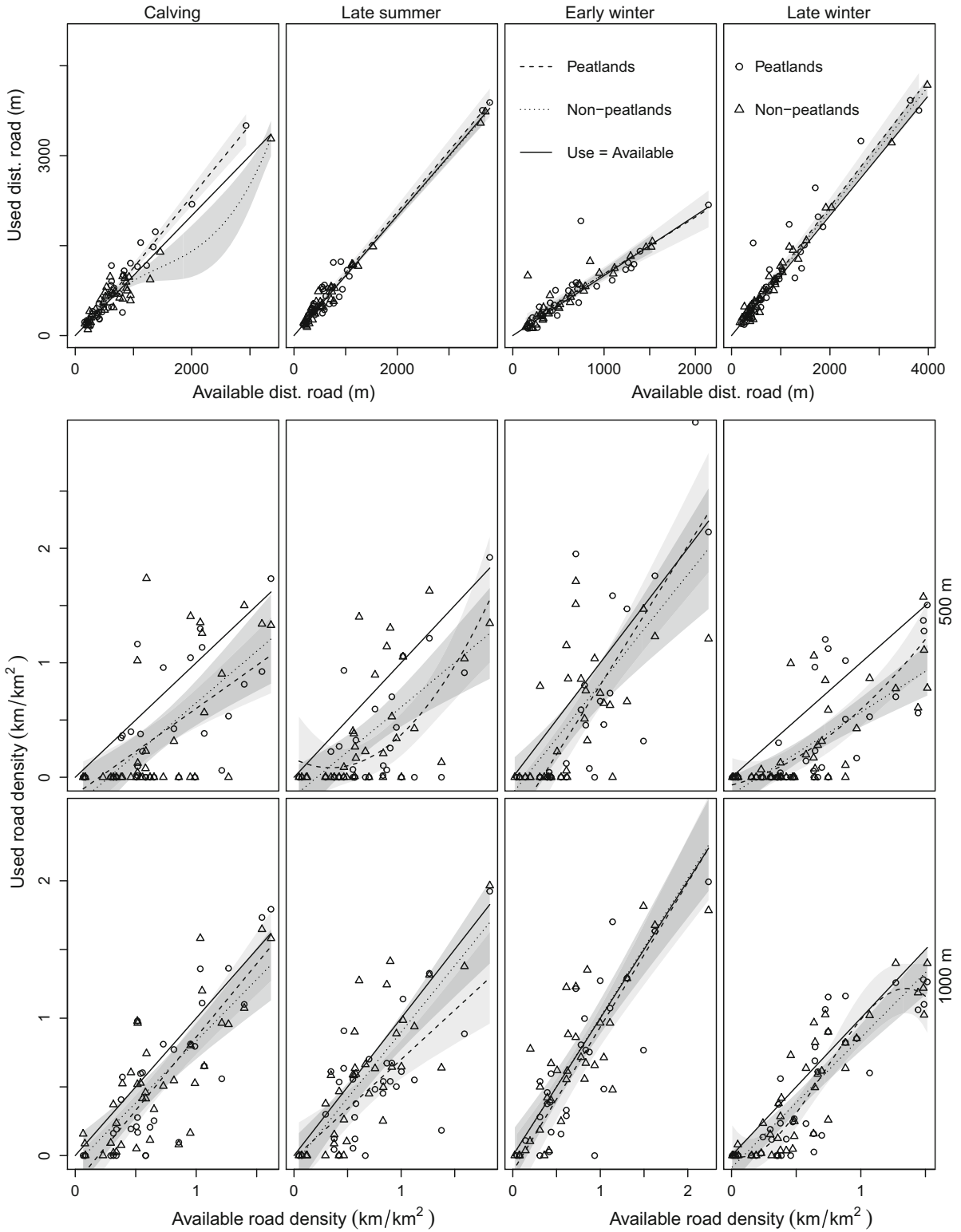
We focused our analyses on space-use within the home range (third order) as opposed to the location of the home range within the geographic range (second order; Johnson 1980), in part because of the potential bias introduced as a result of selectively collaring animals within areas containing linear features, particularly wolves. Because we were interested in examining functional responses, and specifically, the use of areas near or with high densities of linear features as a function of the availability of linear features, we implemented approach one as described by Holbrook et al. (2019), which tests for both linear and non-linear functional responses. We implemented this approach, because we thought that both the potential benefits to wolves (increased hunting efficiency) and costs to caribou and moose (higher

moose (*Alces alces*) locations in peatlands and non-peatlands as a function of available distances to and densities of roads and seismic lines during the calving, late summer, early winter, and late winter seasons

	Distance (m)	Density (500 m)	Density (1000 m)
Roads: peatlands			
Calving	Linear ^{ab}	Linear	Linear
Late summer	Linear	Second-order ^a	Linear
Early winter	Linear	Linear	Linear
Late winter	Linear	Second-order ^a	Third-order ^a
Roads: non-peatlands			
Calving	Third-order ^{ab}	Linear	Linear
Late summer	Linear	Linear	Linear
Early winter	Linear	Linear	Linear
Late winter	Linear	Linear	Linear
Seismic: peatlands			
Calving	Second-order ^a	Linear	Linear
Late summer	Linear	Linear ^b	Second-order ^{bc}
Early winter	Linear ^{ab}	Linear	Linear
Late winter	Third-order ^a	Linear	Second-order ^c
Seismic: non-peatlands			
Calving	Linear	Third-order ^a	Second-order ^a
Late summer	Third-order ^a	Third-order ^{ab}	Third-order ^{ab}
Early winter	Linear ^{bc}	Linear	Linear
Late winter	Linear ^a	Linear	Linear

^aStatistically significant functional response: altered response as a function of density
^bStatistically significant functional response: altered response as a function of landcover
^cNon-significant functional response: response overlapping use = available line

Female moose and roads



◀ **Fig. 3** The response (and 95% confidence intervals) to the distance (dist.) to roads and density (500 and 100 m radii) of roads by female moose (*Alces alces*) as a function of landcover (peatlands versus non-peatlands) and the available distance to and density of roads, as predicted using the most parsimonious regression model (linear, second-order polynomial, or third order polynomial) for the calving, late summer, early winter, and late winter seasons

predation risk) might generate non-linear responses to anthropogenic linear features. For example, wolf hunting efficiency and use of roads might asymptote once linear features are so dense as to add no additional benefit for wolf movement or prey detection. If the benefits decline for wolves, caribou and moose might recognize a concurrent asymptote in risk, and thereby respond accordingly; caribou and moose might increase avoidance of linear features in a linear manner up to a density threshold, and thereafter maintain a consistent avoidance as density increases.

We used ArcGIS (V.10; ESRI 2015) to identify species locations as in peatlands or in non-peatlands and to estimate the distance to roads and seismic lines and the density (km/km^2) of roads and seismic lines around each location at radii of 500 and 1000 m. We selected these metrics to emulate species responses frequently modelled in resource selection studies, particularly for our species of interest (Latham et al. 2013; Mumma et al. 2017, 2018). These scales also captured the reported scale of prey detection by wolves (Mech 1966), and one potential mechanism, wolf avoidance, that might influence caribou and moose responses to anthropogenic linear features. We then used the estimated distances to roads and seismic lines and road and seismic line densities at each location to determine the seasonal median distances to and densities (500 and 1000 m radii) of roads and seismic lines used by each individual in each landcover (peatlands and non-peatlands).

We estimated the surrounding availability of distances to roads and seismic lines and the densities of roads and seismic lines by first determining the 90th centile of movement distances between consecutive locations for each individual caribou (median distance = 2830 m) and moose (median distance = 907 m) by season. We calculated the 80th centile of movement distances for wolves (median distance = 4648 m), because of their propensity for sporadic, long distance movements. We buffered each

used location by that individual's 90th centile (80th centile for wolves) of movement distances for the corresponding season. For each used location, we then randomly generated five available locations within their corresponding buffer. Previous studies evaluating habitat use and selection at the third order (Johnson 1980) suggested that a 1:5 ratio (use:available) is adequate to enable reliable inference (Cooper and Millspaugh 1999; Johnson et al. 2005). We estimated the available distance to roads and distance to seismic lines by determining the median distances for each individual's available locations by season and landcover. We then generated seasonal estimates of availability by merging the polygons (buffered area) corresponding to each used location for each individual by season using the method of Walker et al. (2007). We determined the available road and seismic line densities by estimating densities within the seasonal merged polygons of each individual. To ensure that differences in the number of locations per individual, which was a function of collar transmission rate, did not bias our analyses, we plotted available road and seismic line densities against the number of locations per individual by season for each species to visually evaluate the potential for relationships between collar transmission rate and linear feature density (Online Resource 1).

For female caribou, female moose, male moose, and wolves (males and females combined), we regressed the seasonal median distance or density (500 and 1000 m radius) values (used) of each individual per landcover (peatland and non-peatlands) against the corresponding available distance or density values of each individual. We modelled female and male moose separately anticipating seasonal differences in behaviour between sexes (Eldegard et al. 2012), particularly with regards to the presence of vulnerable young for adult females in spring and late summer. We analyzed male and female wolves collectively because of a limited sample size and the tendency of wolves to travel in packs containing both sexes. We built three models (linear, second-order polynomial, and third-order polynomial) in the manner of Holbrook et al. (2017, 2019) for each group by landcover class and season, and selected the most parsimonious models using Akaike's information criteria for small sample sizes (AIC_c , Burnham and Anderson 2002; Bartón 2015). We then plotted response curves using the most parsimonious models.

Male moose and roads

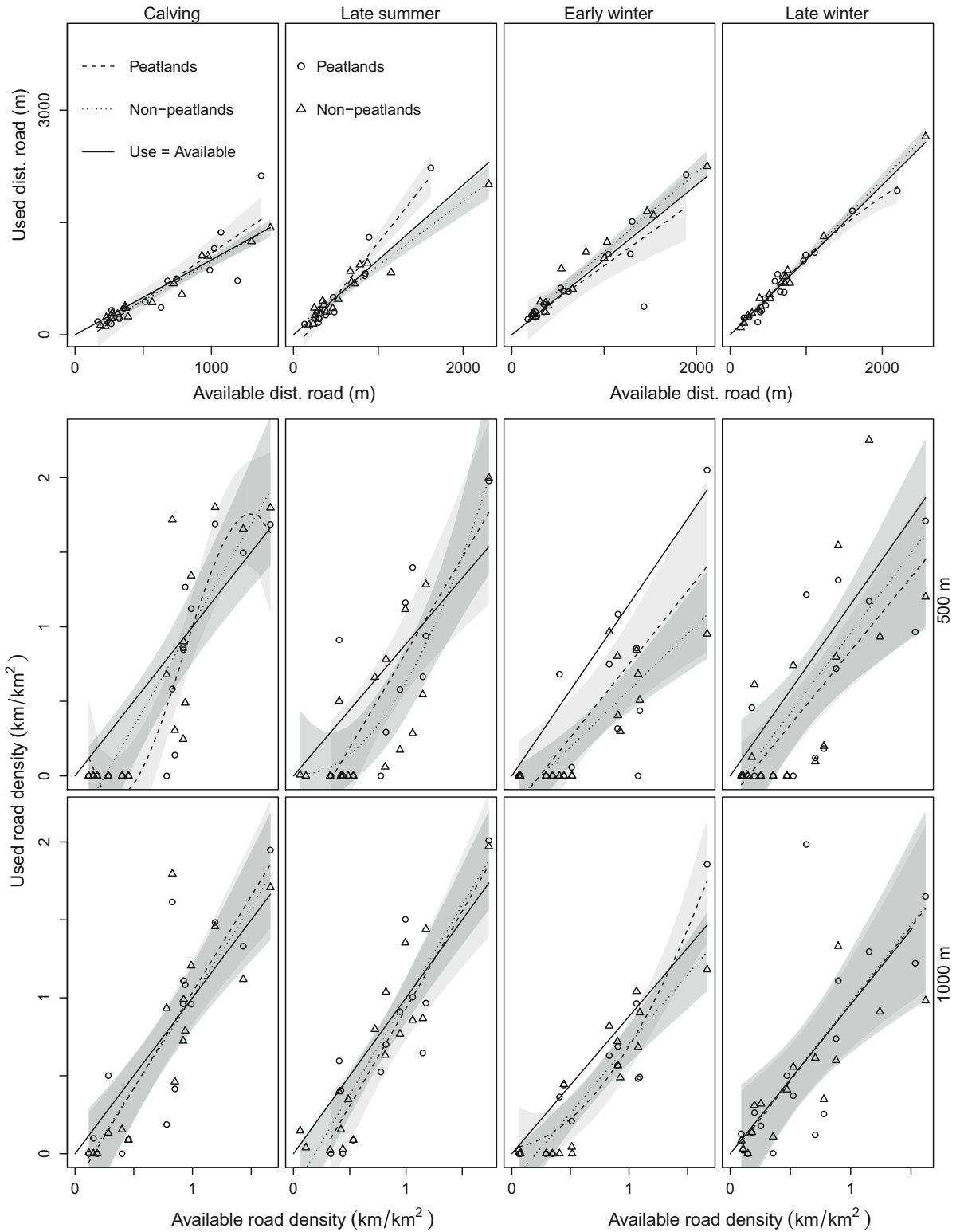


Fig. 4 The response (and 95% confidence intervals) to the distance (dist.) to roads and density (500 and 100 m radii) of roads by male moose (*Alces alces*) as a function of landcover (peatlands versus non-peatlands) and the available distance to and density of roads, as predicted using the most parsimonious regression model (linear, second-order polynomial, or third order polynomial) for the calving, late summer, early winter, and late winter seasons

We evaluated the occurrence of functional responses to the distances and densities of roads and seismic lines as a function of landcover by evaluating overlap between 95% confidence intervals for each response curve (peatland and non-peatland). We used a two-step process to determine the occurrence of functional responses in relation to the surrounding availabilities (distance to or density) of roads and

seismic lines. First, 95% confidence intervals for response curves could not overlap the (must deviate from) use = available line, which indicated that individuals were responding (selection or avoidance) to the distances to or densities of roads or seismic lines. Second, the most parsimonious model had to be a second- or third-order polynomial model or a linear model with a slope parameter (second coefficient) whose 95% confidence interval did not overlap 1. For linear models, a slope parameter of 1 would indicate a constant response regardless of the surrounding (available) distances to or densities of roads and seismic lines.

Table 3 The most parsimonious regression models (linear, second-order polynomial, or third order polynomial) comparing the median distances (m) to and densities (km/km²) of roads and seismic lines (at 500 and 1000 m radii) of male

moose (*Alces alces*) locations in peatlands and non-peatlands as a function of available distances to and densities of roads and seismic lines during the calving, late summer, early winter, and late winter seasons

	Distance (m)	Density (500 m)	Density (1000 m)
Roads: peatlands			
Calving	Linear	Third-order ^a	Linear
Late summer	Linear ^{ab}	Linear	Linear
Early winter	Linear	Linear	Second-order ^a
Late winter	Second-order ^c	Linear	Linear
Roads: non-peatlands			
Calving	Linear	Linear	Linear
Late summer	Linear ^{bc}	Second-order ^a	Linear
Early winter	Linear	Linear ^a	Linear
Late winter	Linear	Linear	Linear
Seismic: peatlands			
Calving	Third-order ^{ab}	Linear ^a	Linear ^a
Late summer	Third-order ^a	Linear	Linear
Early winter	Second-order ^{ab}	Linear	Linear
Late winter	Linear	Linear	Linear
Seismic: non-peatlands			
Calving	Linear ^{ab}	Linear	Linear ^a
Late summer	Linear	Linear	Third-order ^a
Early winter	Third-order ^{ab}	Linear	Linear
Late winter	Linear	Linear	Linear

^aStatistically significant functional response: altered response as a function of density

^bStatistically significant functional response: altered response as a function of landcover

^cNon-significant functional response: response overlapping use = available line

Results

We did not observe a relationship between the number of locations and the densities of roads and seismic lines, thus suggesting that our characterization of availability for road and seismic line densities was not biased by collar transmission rate (Online resource 1).

Species responses to roads

Caribou demonstrated functional responses to both the available distance to and density of roads during some seasons. Functional responses to the distance to roads in relation to availability were only present in non-peatlands (Table 1). During calving and late summer, the distance to roads curve for caribou in non-peatlands positively deviated from the use = available line as the available distance from roads increased

Table 4 The most parsimonious regression models (linear, second-order polynomial, or third order polynomial) comparing the median distances (m) to and densities (km/km²) of roads and seismic lines (at 500 and 1000 m radii) of gray wolf

	Distance (m)	Density (500 m)	Density (1000 m)
Roads: peatlands			
Calving	Linear ^b	Linear ^a	Linear
Late summer	Linear ^b	Linear ^a	Linear
Early winter	Linear	Linear ^a	Linear ^a
Late winter	Linear	Second-order ^{ab}	Linear
Roads: non-peatlands			
Calving	Linear ^b	Linear ^a	Linear
Late summer	Linear ^b	Linear ^a	Linear ^a
Early winter	Linear ^a	Linear	Linear
Late winter	Second-order ^a	Linear ^{ab}	Linear ^a
Seismic: peatlands			
Calving	Linear	Linear	Linear ^a
Late summer	Linear ^b	Third-order ^a	Third-order ^a
Early winter	Linear	Third-order ^{ab}	Second-order ^{ab}
Late winter	Linear	Third-order ^a	Third-order ^a
Seismic: non-peatlands			
Calving	Third-order ^a	Linear	Linear
Late summer	Third-order ^{ab}	Linear ^a	Linear ^a
Early winter	Third-order ^a	Linear ^b	Linear ^b
Late winter	Linear	Linear ^a	Linear ^a

^aStatistically significant functional response: altered response as a function of density

^bStatistically significant functional response: altered response as a function of landcover

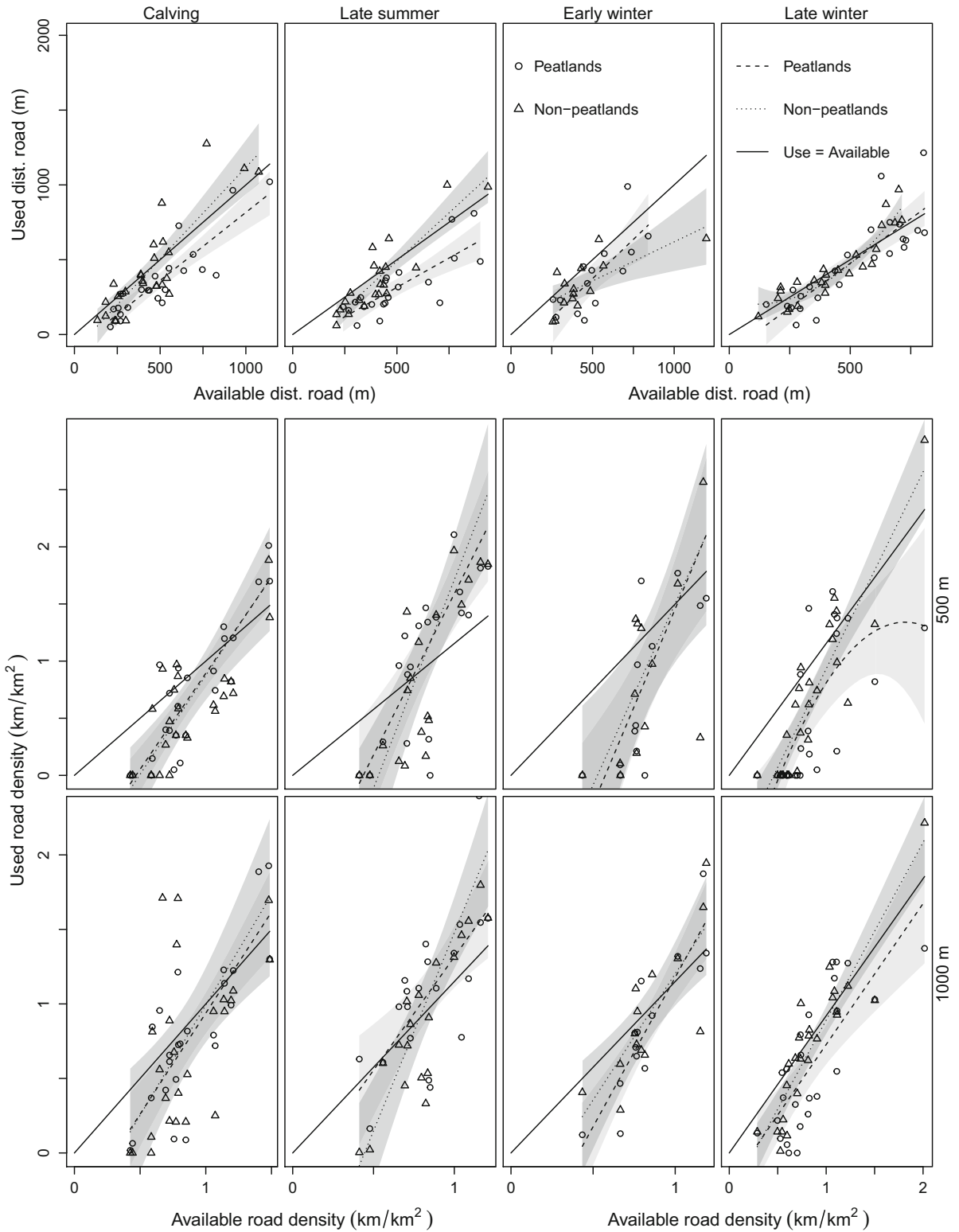
^cNon-significant functional response: response overlapping use = available line

Fig. 5 The response (and 95% confidence intervals) to the distance (dist.) to roads and density (500 and 100 m radii) of roads by gray wolves (*Canis lupus*) as a function of landcover (peatlands versus non-peatlands) and the available distance to and density of roads, as predicted using the most parsimonious regression model (linear, second-order polynomial, or third order polynomial) for the calving, late summer, early winter, and late winter seasons

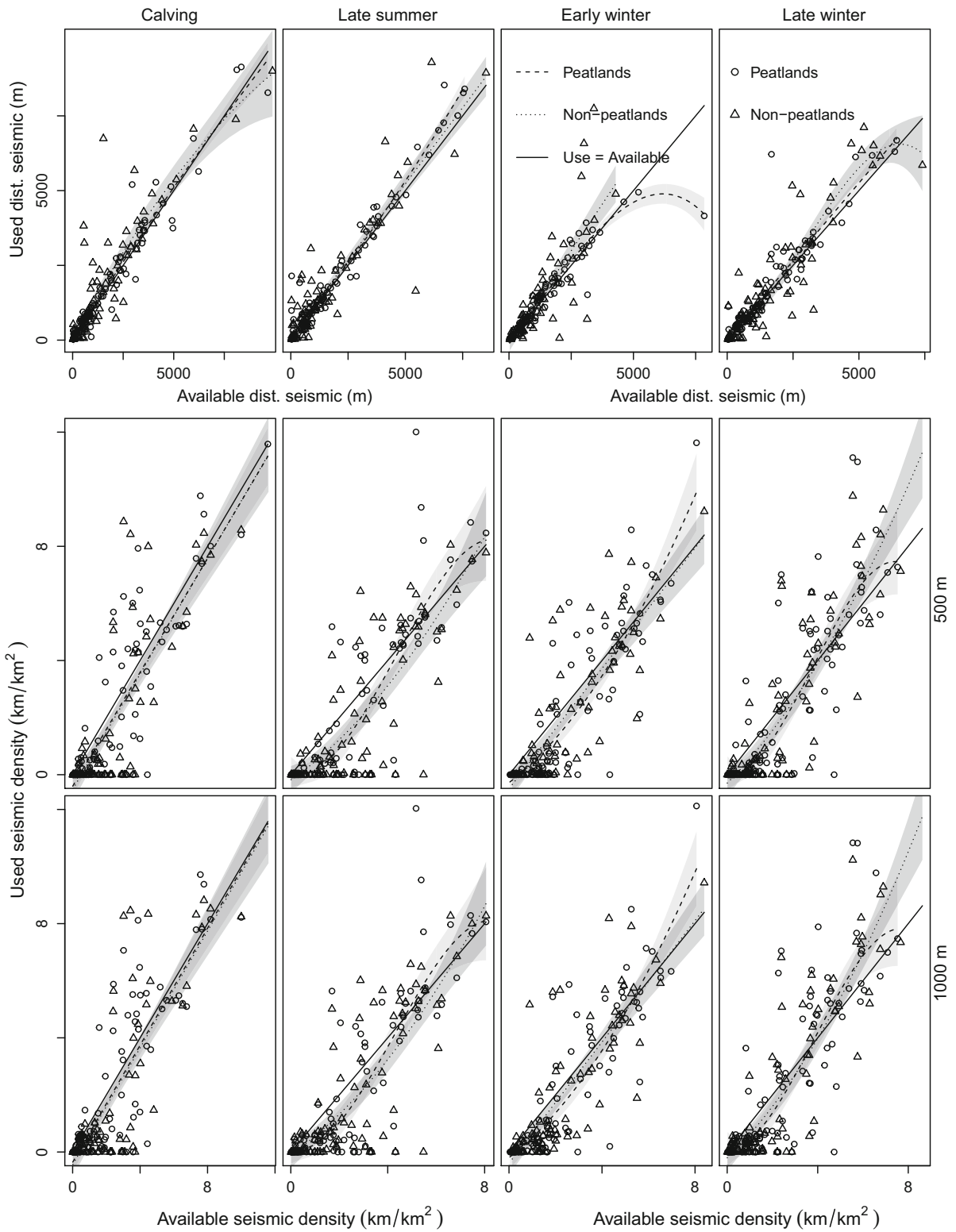
(Fig. 2), thus suggesting selection for areas further from roads when the available distance from roads was high. During early and late winter, deviations from the use = available line with regards to the distance from roads were less obvious (Fig. 2). In contrast, the road density curves generally demonstrated negative deviations from the use = available line (Fig. 2), thus suggesting caribou avoidance of areas with high road density. Functional responses in relation to available

(*Canis lupus*) locations in peatlands and non-peatlands as a function of available distances to and densities of roads and seismic lines during the calving, late summer, early winter, and late winter seasons

Wolves and roads



Caribou and seismic lines



◀ **Fig. 6** The response (and 95% confidence intervals) to the distance (dist.) to seismic lines and density (500 and 100 m radii) of seismic lines by female boreal woodland caribou (*Rangifer tarandus caribou*) as a function of landcover (peatlands versus non-peatlands) and the available distance to and density of seismic lines, as predicted using the most parsimonious regression model (linear, second-order polynomial, or third order polynomial) for the calving, late summer, early winter, and late winter seasons

road density were present at one or both scales (500 or 1000 m) during calving, late summer, and early winter (Table 1; Fig. 2). These responses demonstrated the greatest (negative) deviance from the use = available line when the available road density was at low and intermediate levels (Fig. 2). A functional response in relation to landcover was also present for the 500 m radius during early winter (Fig. 2).

Although functional responses to the distance to and density of roads by male and female moose were less frequently observed in comparison to caribou, they were present during some seasons. Female and male moose demonstrated functional responses to the available distance to roads during calving and late summer (Table 2), but there were few individuals with high available distances, which appeared to exert a large influence on the resulting curves (Figs. 3 and 4). Neither female nor male moose demonstrated a functional response to road density in relation to landcover, but did demonstrate a functional response in relation to the available road density (Tables 2 and 3). The road density curves for female moose negatively (avoidance) deviated from the use = available line at one or both scales during calving, late summer, and late winter (Fig. 3). The road density curves for male moose demonstrated a similar (negative deviance), but less consistent trend with the exception of early winter, although the curves for male moose often demonstrated the greatest (negative) deviance when the available road density was at low and intermediate levels (Fig. 4).

The responses by wolves to the distance to roads varied among seasons, but wolf responses to road density followed a similar pattern across seasons. During calving and late summer, wolves demonstrated functional responses in relation to landcover (Table 4) as evidenced by the negative (avoidance of areas further from roads) deviance from the use = available line in peatlands, but not in non-peatlands (Fig. 5).

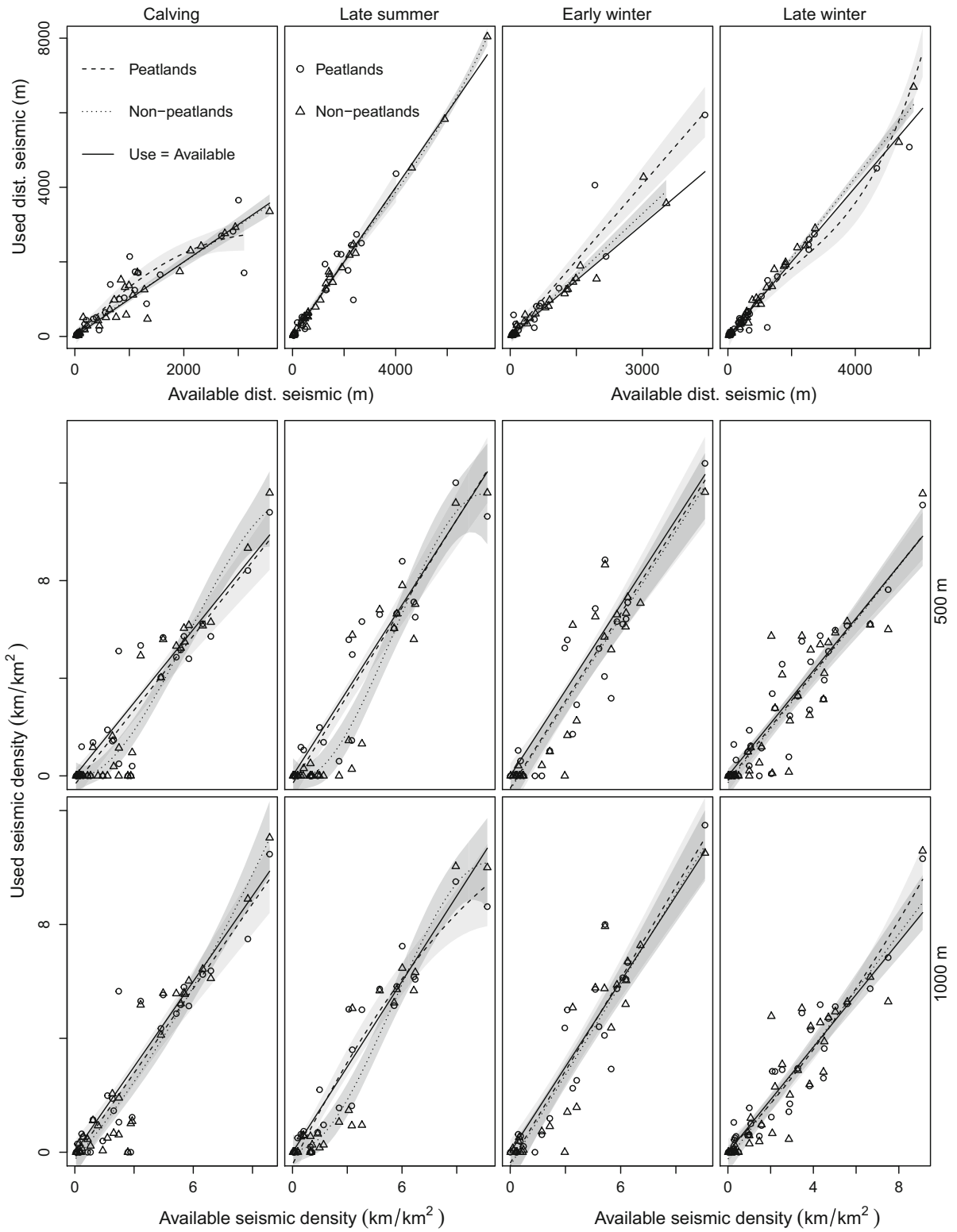
During early winter, the distance to roads curves for wolves negatively (avoidance) deviated from the use = available line in peatlands and non-peatlands (Fig. 5). During late winter, deviations from the use = available line were less apparent (Fig. 5). Although not all responses were significant, the road density curves for wolves were more likely to negatively (avoidance) deviate from the use = available line when the available road density was low and demonstrate no deviance or positive (selection) deviance when the available road density was high (Fig. 5). Model selection results and coefficient values for the most parsimonious models are provided in Online Resource 1.

Species responses to seismic lines

Caribou responses to distance to and density of seismic lines lacked consistency across seasons. During late summer, the distance to seismic lines curve for caribou in peatlands positively deviated from the use = available line as the available distance from seismic lines increased (Fig. 6), thus suggesting selection for areas further from seismic lines when the available distance to seismic lines was high. The same trend was observed in non-peatlands during early and late winter (Fig. 6). In contrast, the distance to seismic lines curve in non-peatlands during early winter negatively deviated from the use = available line, but appeared to be largely driven by a single individual (Fig. 6). Caribou did not demonstrate any response to seismic line density during calving (Fig. 6). During late summer, however, the seismic line density curve for caribou negatively (avoidance) deviated from the use = available line when the available seismic line density was low (Fig. 6). A negative deviation (avoidance) from the use = available line at low available seismic line density was also observed during early winter in peatlands and late winter in non-peatlands, but at higher available seismic line density a positive deviation (selection) was observed (Fig. 6).

Female and male moose demonstrated functional responses to the distance to and density of seismic lines in relation to availability and landcover during certain seasons (Tables 2 and 3). Several of the distance to seismic lines curves for female and male moose deviated from the use = available line, but appeared to be largely influenced by the few

Female moose and seismic lines



◀ **Fig. 7** The response (and 95% confidence intervals) to the distance (dist.) to seismic lines and density (500 and 100 m radii) of seismic lines by female moose (*Alces alces*) as a function of landcover (peatlands versus non-peatlands) and the available distance to and density of roads, as predicted using the most parsimonious regression model (linear, second-order polynomial, or third order polynomial) for the calving, late summer, early winter, and late winter seasons

individuals with high available distances to seismic lines (Figs. 7 and 8). Regarding seismic line density, the curves for female moose in non-peatlands during calving and late summer negatively (avoidance) deviated from the use = available line when the available seismic line density was low (Fig. 7). A similar trend (avoidance) was observed for male moose during late summer (Fig. 8). During calving, the seismic line density curves for male moose negatively (avoidance) deviated from the use = available line in peatlands and non-peatlands when the available seismic line density was high (Fig. 8). During early and late winter, the seismic line density curves for female and male moose did not deviate from the use = available line (Figs. 7 and 8).

Wolves demonstrated functional responses to the distance to seismic lines as a function of the available distance to seismic lines in non-peatlands during calving, late summer, and early winter (Table 4). During calving, the distance to seismic lines curve for wolves in non-peatlands positively (selection for areas further from seismic lines) deviated from the use = available line when the available distance to seismic lines was high, but during late summer, the curve for wolves negatively (avoidance for areas further from seismic lines) deviated from the use = available line when the available distance to seismic lines was at intermediate levels (Fig. 9). During early winter, the distance to seismic lines curve for wolves in non-peatlands negatively (avoidance) deviated from the use = available line when the available distance to seismic lines was at intermediate levels, but positively (selection) deviated when availability was high (Fig. 9). For seismic line density, the curves for wolves often negatively (avoidance) deviated from the use = available line when the available seismic line density was low, but did not deviate or positively (selection) deviated when the available seismic line density was high (Fig. 9). Model selection

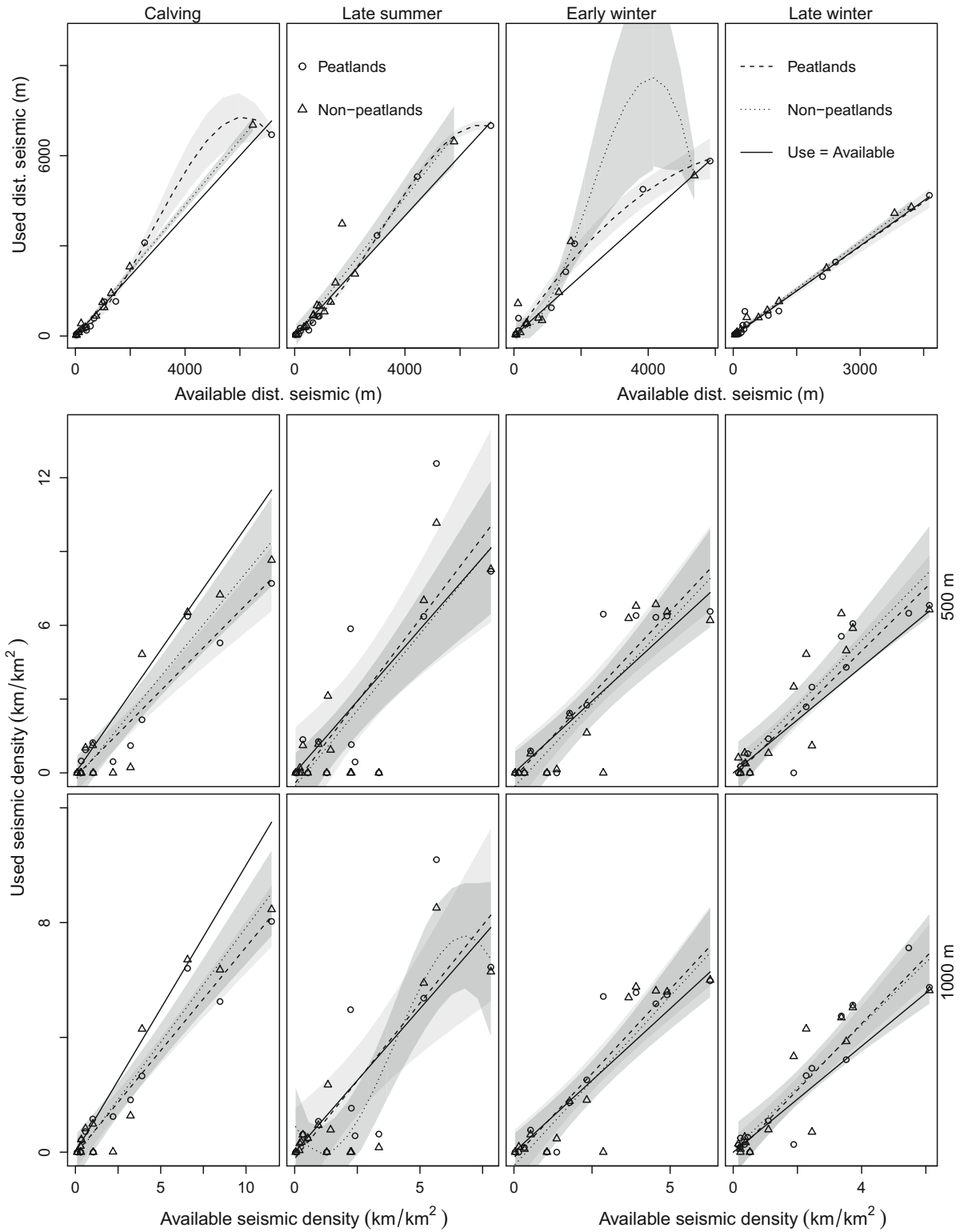
results and coefficient values for the most parsimonious models are provided in Online Resource 1.

Discussion

Our analyses revealed functional responses to anthropogenic linear features that likely have implications for predator–prey interactions. During calving and late summer when calves are most vulnerable, wolves selected for areas closer to roads in preferred caribou habitats (peatlands) and tended to select for areas with higher road and seismic line densities when the available road and seismic line densities were high. These findings support the results of DeMars and Boutin (2018), who suggested a functional response to linear features in relation to landcover (increased selection in peatlands), and aligns with other research demonstrating the selection of anthropogenic linear features by wolves, which was suggested to increase wolf search efficiency and encounter rates with prey (Latham et al. 2011a; Whittington et al. 2011; Dickie et al. 2016).

The positive association between wolves and anthropogenic linear features potentially suggests that boreal caribou could limit predation risk by demonstrating an opposing response to the distance to and the density of linear features if they perceive the increased risk and choose a risk-averse behavioural strategy. Many of the responses of caribou, however, did not seem in opposition to the responses of wolves. Caribou demonstrated selection for areas further from roads during calving and late summer in non-peatlands, which aligned with our first hypothesis that caribou would avoid linear features in habitats frequently used by wolves (non-peatlands) (Mumma and Gillingham 2017). Wolves, however, demonstrated greater selection for areas near roads in peatlands during the calving and late summer seasons, potentially because of restrictions to movement when traveling on wet, soft ground. Caribou also generally avoided areas with higher road densities, but this avoidance often decreased when the availability of road density was high (Fig. 2). In order to mirror the functional responses of wolves to road density, we would have anticipated that caribou increase their avoidance of road density when availability is high. Caribou and wolf responses to seismic line density demonstrated a similar mismatch with caribou avoidance tending to

Male moose and seismic lines



◀ **Fig. 8** The response (and 95% confidence intervals) to the distance (dist.) to seismic lines and density (500 and 100 m radii) of seismic lines by male moose (*Alces alces*) as a function of landcover (peatlands versus non-peatlands) and the available distance to and density of seismic lines, as predicted using the most parsimonious regression model (linear, second-order polynomial, or third order polynomial) for the calving, late summer, early winter, and late winter seasons

occur when available seismic line density was low, and wolf selection tending to occur when availability was high.

The changes (negative to indifferent) in caribou responses to road and seismic line densities as a function of their availabilities might suggest important ecological thresholds for caribou. Although a precise inflection point was not present, many of the response curves for road and seismic line density indicate that caribou generally do not avoid high road and seismic line densities once the available densities exceed ~ 1 and ~ 2 km/km², respectively. While these values might represent an ecologically important threshold as it pertains to caribou behaviour, additional research will be necessary to illuminate the demographic influence of linear feature density on caribou. Indeed, 1–2 km/km² exceeds the recommendation of Forman and Alexander (1988) suggested as necessary to sustain a naturally functioning large mammal community. Further, previous research indicated a multiplicative relationship between linear features and caribou survival (McCutchen 2006), thus suggesting that even low densities (< 1 km/km²) of anthropogenic linear features might affect caribou survival and population growth.

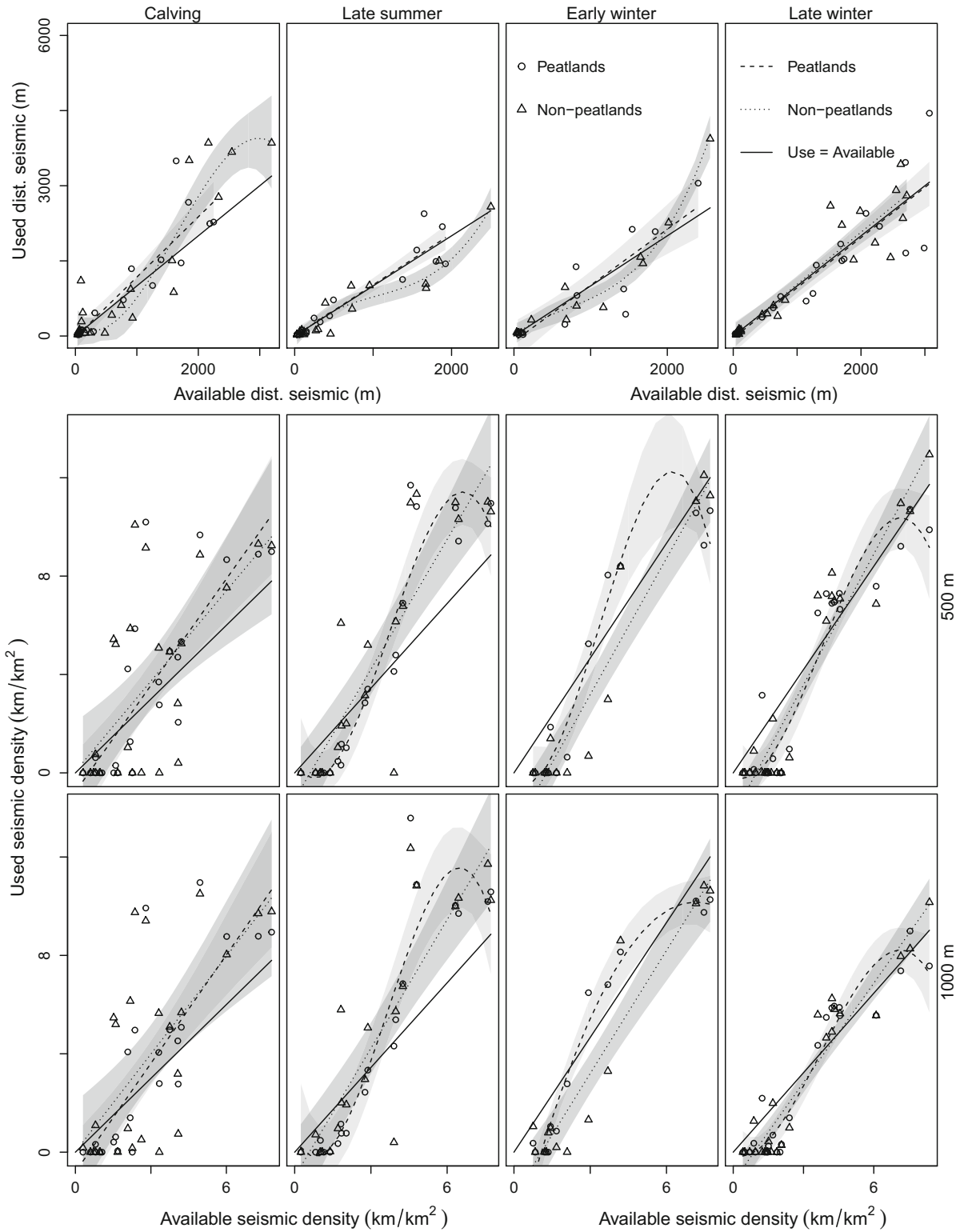
Similar to female caribou, female and male moose did not respond to linear features in a manner that opposed the responses of wolves. Female moose did avoid areas with higher road density during certain seasons, but avoidance did not increase with availability. Notably, male moose avoided areas with higher road density during early winter, which overlaps the legal hunting season (primarily for males) in British Columbia. Moose responses to seismic lines were weak to non-existent. These behaviours might expose moose to greater predation risk from wolves, but might also reflect the balancing of risk against energetic demands and nutritional needs, which might also apply to boreal caribou. Linear features might provide easy travel corridors through dense

vegetation. Further, early successional habitat on the edges of roads and directly on seismic lines might provide foraging opportunities. Numerous studies report selection by moose for early successional vegetation in cutblocks (e.g., Schwartz and Franzmann 1989; Rempel et al. 1997), but results are less clear regarding moose foraging behaviour near linear features (e.g., Laurian et al. 2008; Eldegard et al. 2012). Studies in other systems indicate that moose responses to linear features are dependent on forage quality (Eldegard et al. 2012), traffic volume (Laurian et al. 2008), harvest pressure (McLoughlin et al. 2011), and predation risk (Labbé 2012).

Alternatively, caribou and moose responses might be ideal with regards to risk avoidance as a result of a non-linear relationship between linear feature density and predation risk. We predicted that wolf selection for the distance to and the density of linear features would decline as the availability of linear features increased (Houle et al. 2010) and observed some support for this hypothesis in peatlands, particularly for seismic lines. Likewise, the relationship between linear features and wolf search efficiency might follow a similar non-linear decline as the available density of linear features increases. Therefore, the tendency of caribou and female moose to be indifferent to roads and seismic line density, when the available density is high, might reflect a decreasing benefit with regards to risk avoidance. Further, some research suggests that caribou might be better served via selection or indifference to areas with higher linear feature densities; caribou avoidance of linear features might cause caribou to cluster into smaller habitat patches, which potentially increases their probability of being detected and killed by wolves (Fortin et al. 2013; DeMars et al. 2016).

We also predicted that wolves in winter would demonstrate greater selection for the distance to and the density of roads in comparison to the distance to and density of seismic lines, because of differences in the ease of travel in areas containing roads (Droghini and Boutin 2017). Latham et al. (2011a) postulated that wolves avoid seismic lines in winter, because of higher snow depths in comparison to roads, although other research demonstrated wolf selection for seismic lines in winter (Dickie et al. 2016). We expected snow on many roads to be cleared or packed down, thus lowering the energetic costs of movement (Parker et al. 1984), but vehicle traffic in our system is highly

Wolves and seismic lines



◀ **Fig. 9** The response (and 95% confidence intervals) to the distance (dist.) to seismic lines and density (500 and 100 m radii) of seismic lines by gray wolves (*Canis lupus*) as a function of landcover (peatlands versus non-peatlands) and the available distance to and density of seismic lines, as predicted using the most parsimonious regression model (linear, second-order polynomial, or third order polynomial) for the calving, late summer, early winter, and late winter seasons

variable, but relatively low, which might explain why we did not detect a clear difference between wolf selection for roads and seismic lines in winter.

Other unaccounted for sources of variation include the width of roads and seismic lines, regrowth of vegetation on seismic lines, heterogeneity within our landcover classes, and differences in collar transmission rates among individuals. Other studies have demonstrated the effect of line width on species responses (D'Amico et al. 2016; Dickie et al. 2016) and vegetation height has been shown to influence the use of seismic lines by wolves (Dickie et al. 2017). Although we did not detect any clear bias when evaluating available road and seismic line densities as a function of the number of locations, we are unable to completely dismiss the potential for disparate collar transmission rates to have influenced our inferences as a result of the time between consecutive locations or the specific time of day when locations were transmitted. Further, Serrouya et al. (2017) aptly pointed out that analyses of resource selection using GPS locations from collared animals are an estimate of the time spent in different habitats, but might fail to reflect the distances travelled per habitat if animals use certain habitats or landscape features (e.g., roads) to move between foraging patches. If caribou, moose, or wolves were routinely using anthropogenic linear features for ease of movement, negative responses to linear features might have shifted towards selection (and positive responses might have become increasingly positive) if collar transmission rates were more frequent (Serrouya et al. 2017).

Conclusion

Our analyses indicate that the responses of wildlife communities to anthropogenic linear features are complex and vary across space and time. Studies in other systems also illuminate this complexity and

suggest that linear features are likely having a significant influence on animal abundance (across taxa) and species interactions (Fisher and Burton 2018; Mahon et al. 2019), including processes such as predation risk (Camacho et al. 2017; Lendrum et al. 2018). For boreal caribou, risk is likely, in part, a function of both wolf and caribou responses to roads and seismic lines. Further research will be required to identify tolerable densities of roads and seismic lines for boreal caribou as it pertains to predation risk, survival, and population growth. Here, we demonstrate the value of exploring varying functional responses to landscape features across multiple interacting species to unravel some of the complexity of species interactions.

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Data availability All caribou, wolf, and moose data can be accessed at <http://www.bcogris.ca/boreal-caribou-home>.

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