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Evaluating risk effects of industrial features on woodland caribou habitat selection in west central Alberta using agent-based modelling

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Abstract

Alberta woodland caribou (*Rangifer tarandus*) are classified as threatened in Canada, and a local population in the west-central region, the Little Smoky herd, is at immediate risk of extirpation due, in part, to anthropogenic activities such as oil, gas, and forestry that have altered the ecosystem dynamics. To investigate these impacts, we have developed a spatially explicit, agent-based model (ABM) to simulate winter habitat selection and use of woodland caribou, and to determine the relative impacts of different industrial features on caribou habitat-selection strategies. The ABM model is composed of cognitive caribou agents possessing memory and decision-making heuristics that act to optimize tradeoffs between energy acquisition and disturbance. A set of environmental data layers was used to develop a virtual grid representing the landscape over which caribou move. This grid contained forage-availability, energy-content, and predation-risk values. The model was calibrated using GPS data from caribou radio collars (n = 13) deployed over six months from 2004 to 2005, representing caribou winter activities. Additional simulations were conducted on caribou habitat-selection strategies by assigning industrial features (i.e., roads, seismic lines, pipelines, well sites, cutblocks and burns) different levels of disturbance depending on their type, age, and density. Differences in disturbance effects between industry features were confirmed by verifying which resultant simulations of caribou movement patterns most closely match actual caribou distributions and other patterns extracted from the GPS data. The results elucidate the degree to which caribou perceive different industry features as disturbance, and the differential energetic costs associated with each, thus offering insight into why caribou are choosing the

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habitats they use, and consequently, the level and type of industry most likely to affect their bioenergetics and fitness.

1. Introduction and objectives

In Alberta, resource-based industries associated with the forestry and energy sectors have expanded dramatically over the last two decades [1]. This expansion has resulted in an increased network of rights-of-ways for seismic exploration, pipelines and roads, the latter of which are used by both forestry and oil and gas industries. In addition, forestry operations have created landscapes of early seral vegetation communities, effectively resulting in the loss of habitat of preferred old-growth forests. Woodland caribou (*Rangifer tarandus*) which inhabit these regions are classified as threatened in Canada, and a local population in west-central Alberta, the Little Smoky herd, is at immediate risk of extirpation due, in part, to these industrial activities that have altered the ecosystem dynamics. The Alberta government resultantly recommends the assessment and management of cumulative effects on caribou, as well as the identification and provision of adequate habitat (amount and type), to allow for caribou persistence [2].

Measuring the impacts of anthropogenic activities on wildlife population persistence is crucial for effective management. The sustained environmental change wildlife are experiencing may surpass the capacity of developmental, genetic, and demographic mechanisms that populations have evolved to deal with these alterations. In particular, such expanding anthropogenic activities are widely perceived to lead to negative consequences for wildlife beyond habitat loss alone, as animals can perceive human activities as disturbance and predation-risk events and respond accordingly [3]. Indeed, recent studies of risk effects - the costly alteration of prey behavior in response to 'predators' - have demonstrated the impact of these effects to be as great or greater on prey population reproduction and survival than direct effects of predation alone [4]. The cost of predator-avoidance behaviours can manifest in changes in habitat use, reduced foraging effort, and increased energy expenditure in vigilance and altered movement patterns [5].

It has been suggested that the decline of woodland caribou is based in part on an indirect interaction between caribou and resource-extraction industries that has transformed the environs into a landscape of fear. Habitat change from forestry has increased predator biomass as preferred prey (such as elk, moose and deer) are attracted to the new vegetation land cover [6-8]. Second, the linear features introduced onto the landscape aid in facilitating predator hunting and searching efficiency [9]. Resultantly, caribou are being exposed to higher levels of predation pressure, and their evolved predator-defense strategies - avoidance/separation behaviours, may no longer prove effective.

Furthermore, evidence also suggests that caribou perceive industrial development as disturbance. For instance, a study by Tracz et al. (2010) [10] demonstrated that boreal woodland caribou were found to be farther from petroleum-sector disturbances within their home range than expected; however, they remained in peatland complexes containing a large number of petroleum-sector disturbances rather than move to new areas, presumably because the risks of dispersing across upland habitat to reach other suitable habitat are high. Additionally, Smith et al. (2000) [11] showed daily movement rates and individual winter range sizes of woodland caribou in west-central Alberta decreased as timber harvesting progressed. These caribou avoided using recently fragmented areas, with the authors suggesting that the "spacing out" antipredator strategy used by caribou may be compromised.

Lastly, the winter season appears to play a confounding role on caribou risk perception, as over-wintering caribou face the energetic costs of food availability, environmental conditions, predator

avoidance, and disturbance. Specifically, the availability of terrestrial lichen, the main food source for Alberta woodland caribou in winter, is constrained by specific habitat requirements [12]. Also, minimizing costs in winter appears important for female caribou, at times at the expense of increased predation risk [13]. Lastly, winter is the time of year when most industrial development occurs in the study area [14]. Caribou will therefore need to tradeoff the energetic demands of resource acquisition and predator/disturbance avoidance.

Although the impacts of habitat change and industrial activities on woodland caribou have been researched, the behavioural mechanisms by which resource-extraction industries contribute to caribou population decline are less clear. Most studies have not explicitly incorporated how caribou concurrently make behavioral tradeoff decisions between energy management, foraging efficiency, and predation risk. Furthermore, traditional approaches to studying wildlife-human-environment interactions do not typically consider individual-level information, account for complexities, or integrate cross-scale and cross-discipline data and methods, resulting in a great loss in predictive or explanatory power [15]. To address these issues, we have developed a spatially explicit, agent-based model (ABM) to simulate winter habitat selection and use of woodland caribou in the face of intense land use by resource-extraction industries. ABMs can readily incorporate two critical ecological theories involved in predator-avoidance strategies: animal movement ecology and behavioural ecology. The movement paths of wildlife result from the dynamic interplay of the internal state of the organism, its motion capacity, its navigation capacity, and the external environment [16,17]. Since agents are also given fitness-maximizing goals and can trade off competing strategies to find optimal solutions to the problems they face (i.e., behavioral ecological theory), this enables the understanding of the processes that govern movement, distribution, and selection, and therefore can predict how animals might respond to habitat loss, industrial activities, and the associated risk effects [18].

This research was undertaken to achieve two goals. The first one is to simulate and recreate the movement behaviors of caribou to explore how they select and use their habitat. The second objective, which is the focus of this paper, is to use these resultant behavioural strategies to determine the relative impacts of different industrial features on caribou habitat selection and movement ecology on the landscape.

2. Methodology

In this section, a description of the study area and the datasets used to calibrate the agent-based model is provided, followed by a presentation of the conceptual model and its implementation.

2.1 Description of the study site

The Little Smoky (LSM) herd is located in the foothills of west-central Alberta, east of Grande Cache. Its range covers an approximate area of 2,400 km^2 (Figure 1). The study area is classed into Upper Foothills and Sub-Alpine Natural Subregions [19], and contains several major rivers, many small creeks, and a few lakes. Elevations range from 850 to 1500 m. The climate is subarctic, with short, wet summers and long, cold winters [11]. Temperatures average 16ºC in July and -13.5ºC in December [20]. The Foothills Region is well forested, and has been described in detail by Edmonds and Bloomfield (1984) [21]. Dry sites support primarily lodgepole pine (*Pinus contorta*) or lodgepole pine/black spruce (*Picea mariana*) forests. The range is bisected by the Little Smoky River, and the area surrounding the Little Smoky River consists of bogs and peatlands, interspersed with upland areas [14].

The LSM range has the highest level of development of any caribou herd in Canada, with 87% of its range in proximity (500 m buffer) of anthropogenic activities [22]. There are currently three forest

management agreements within the Little Smoky range (Canadian Forest Products Ltd., Alberta Newsprint Co., and West Fraser Mills Ltd.). Numerous energy companies also operate in the area (e.g., Canadian Natural Resources Ltd., ConocoPhillips Canada, Devon Canada Corporation, Encana Corporation, Suncor, Transcanada Pipelines Ltd., Talisman Energy Inc., Husky Energy, and BP Canada).
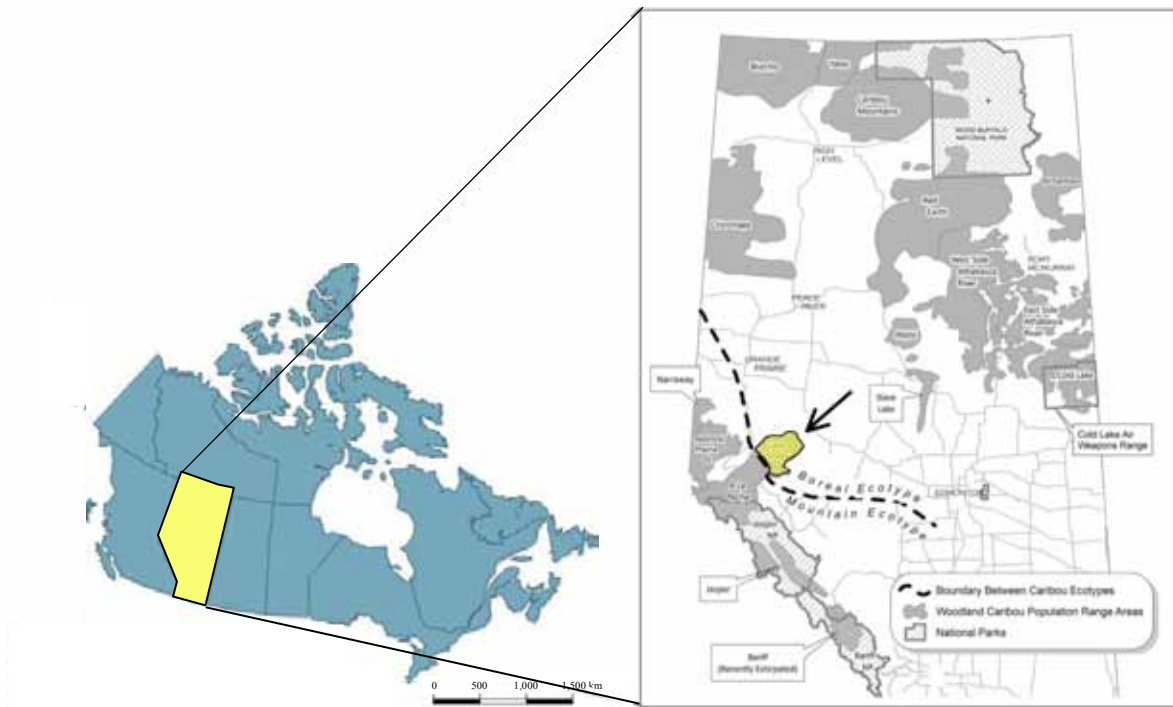

Figure 1. Little Smoky caribou range (indicated by the arrow) situated amongst other Albertan herds (shaded grey) within the province of Alberta, Canada. Inset: distribution of woodland caribou across Canada [2].

A proportion of the Little Smoky herd range (8.6%) is composed of 30 year-old (or younger) cutblocks; it also has the highest road and pipeline density of any caribou range in Alberta and contains substantial industrial infrastructure (e.g. well site, compressor, processing plant, battery) facilities [23]. At present, there is considerable development pressure from all fronts leading to the core of the range and increases in allocations to industrial users within caribou range [24].

The area of interest in this project covers 3100 km^2 and represents the official political and biological range delineation of the Little Smoky herd by the Alberta Fish and Wildlife Division [2]. Because the Little Smoky is such a dynamically changing landscape due to industrial intensification, we chose to confine our study to a single time period, and as such, all spatial and caribou data correspond to the winter 2004-2005.

2.2 Environmental data collection and preparation

Data used to spatially represent the environment comprise remote sensing images and other spatial datasets of the Little Smoky region. These data were collated in an ArcGIS database, and consists of a

land-cover map (including forest cutblock and burns), a digital elevation model, linear-feature network maps (representing roads, seismic lines, and pipelines), and a wellsite industrial-feature map. These datasets were used to characterize caribou habitat suitability for the agent-based model.

The original 30 m spatial resolution land-cover map comprises 12 classes generated from Landsat Thematic Mapper remote sensing images, and was provided by the Foothills Research Institute Grizzly Bear Research Program [25], and the Ungulate Ecology Lab, University of Montana [26]. A value of lichen forage availability was associated to each of the classes, the ranking of which (0 - 5, with 5 representing the highest forage) was determined directly from multiple literature sources [14,21,27-29]. Based on this ranking, an energetic content was then assigned to each cover class. The designation of energetic content was calculated from caribou daily energetic intake rates [30,31], and is described in more detail in the section "Model Implementation - E" (Table 1). Equally, each land-cover class was assigned a predation-risk score, ranked from 1 - 5 (with a score of 5 denoting highest risk). These scores were also derived from the literature [11,14,27,32,33] (Table 1). The digital elevation model at a 30 m spatial resolution [26] remained unchanged.

Data related to industrial features were supplied by Alberta Sustainable Resource Development (ASRD), and consisted of vector maps of roads, seismic lines, pipelines, and well sites. Forest cutblocks and burns were already represented in the landcover map from Decesare et al. (2010)[26]. These data were rasterized at a resolution of 45 m, and were subsequently assigned forage-availability, energetic-content, and predation-risk values, and they were allocated a randomly high predation risk in the baseline ABM (i.e., a value of either 4 or 5; Table 1). For the additional simulations, these industrial features were further categorized according to type, age (based on ASRD designation), density per 1 km^2, and distance from each cell to the closest feature. They were also assigned varying predation-risk weights for the analysis of caribou sensitivity.

For integration with the ABM, four raster maps were generated to represent the physical environment where the agents are located: (1) a forage-availability map, (2) an energetic-content map, (3) a predation-risk map, and (4) a digital elevation model. These raster maps were resampled at a 45 m resolution that was chosen to optimize computational performance and reflect the biologically-realistic size of the foraging patch of caribou [34]. Furthermore, because actual caribou are sensitive to industrial features up to 250 m and 1 km away depending on their type (i.e., they are equally responsive to industry up to this distance; [32], this spatial resolution has no major biasing effect on the caribou agent's ability to perceive them. To provide an environment to the agents and allow their movement from one cell to the next cell, a virtual grid was overlaid on these four maps. Each cell in the ABM spatial environment therefore possesses four values: a forage-availability score, an energetic content, a predation-risk score, and an elevation (m).

Table 1. List of habitat types in the Little Smoky region. Habitat types are based on land cover and industrial-features maps of the study area. Each habitat type is assigned a value for its food availability, energy content, and predation risk attributes. These values are used in the baseline model, with risk randomly assigned either a 4 or 5 to industrial features.

	Lichen Availability[a]	Energy Content (MJ)[b]	Predation Risk[c]
Land Cover[d]			
Closed Conifer Forest	5	1.14	1
Open Conifer Forest	4	0.86	3
Mixed Forest	2	0.29	3
Deciduous Forest	1	0.15	4
Muskeg/Wetland	3	0.58	2
Shrub	1	0.15	4
Herb	1	0.15	4
Barren	0	0	5
Water	0	0	5

Glacier	0	0	0
Forest Cutblocks	1	0.15	4 or 5
Burn	0	0	4 or 5
Industrial Features[e]			
Roads, seismic lines, pipelines	1	0.15	4 or 5
Wellsites	1	0.15	4 or 5

Sources:
a. [14, 21, 27, 28, 29].
b. [30, 31].
c. [11, 14, 27, 32, 33].
d. Original raster maps: [25, 26].
e. Original vector maps: Alberta Sustainable Resource Development 2005.

2.3 Caribou data collection and preparation

Caribou data used to calibrate and validate the model were obtained from a database composed of radio-collared GPS location data of Alberta caribou [35]. A total of 5225 location points were obtained for 13 female individuals from the Little Smoky over the course of winter (November-April) 2004-2005. Using caribou GPS point samples, the spatiotemporal trajectory of each caribou was built and stored within an ArcGIS database. Other sources of biological information necessary for the caribou ABM parameterization include caribou agents' bioenergetic functions, spatial memory (working and reference), and learned decision-making processes. The values for these variables were either derived or obtained from an extensive literature review, and are further described in the section 'Model Implementation' and Table 2.

2.4 Model conceptualization

The model consists of one category of agents, the caribou, represented as a cognitive entity. It has a mental representation of its environment, can plan its activities, and has a memory of profitable and safe patches. Specifically, the caribou agent can balance its needs to meet its minimum daily energetic requirements against the need to minimize energetic loss in order to meet its long-term goal of reproductive success. The caribou must also consider its landscape of fear (i.e., predation risk), for which it must also balance, since relatively safer locations are not always the most profitable.

The agent is characterized by three state-variable types that aid in keeping track of its whereabouts and internal state:

(1) location - the landscape cell it occupies;
(2) energy state variables for:
    a) registering the individual's current energetic uptake,
    b) storing the cumulative amount of energy accumulated over the course of the simulation,
    c) recording the cumulative energy lost, and
    d) calculating the net cumulative energy based on b and c;
(3) multiple lists to store previous locations of high energy return and low predation risk, representing reference and working memory.

Caribou agents forage, rest/ruminate, and travel on a 3100 km^2 grid surface (1786 x 1619 cells). One time step in the model represents 30 min., which is an appropriate temporal resolution to capture the variability of foraging behaviours characteristic of ungulates [36]. The model simulates over a period of 180 days, the span of winter in Alberta

2.5 Model implementation and scheduling

Figure 2 illustrates the sequence of steps involved in the caribou agent's decision making as implemented in the ABM. At each time step, the agent first assesses its energetic state: it determines whether it has reached its daily energetic requirements and by what magnitude, and whether it will have enough energetic reserves (and by what magnitude) to have a successful birth at the end of the season ('A' in figure 2). At this stage it also senses the immediate risk in its environment as well as the forage availability ('B'). It then determines which fitness-maximizing goal is most important to trade off against the others, and does so by assessing which goal has reached a minimum threshold. Based on this decision-making heuristic ('C'), the agent either forages, rests, or moves to a new location ('D'). The agent then updates its energy reserves, both gained and lost through its actions ('E'), and commits to memory any profitable or safe locations encountered ('F'). Each step is described in detail below, with a presentation of the parameter values used to calibrate the model.

- Assessing states (A)

1) Daily energy requirement A caribou's minimum daily energetic requirement (DER) ranges between 22 - 33 MJ per day, according to different literature sources [31,37,38]. We therefore set this range to correspond to the minimum and maximum thresholds, respectively, that an agent must strive to obtain. The agent will gain energy only when it chooses to forage. Once 24 hours have passed, DER is reset to zero, regardless of whether the minimum daily threshold was met. The agent can carryover up to 10 MJ of excess energy at the end of the day, or a deficit of not more than -5 MJ (as caribou are excellent protein recyclers and therefore excessive energetic deficits are unrealistic; [39]). These restrictions were tested in the model and we found that median daily intake rates fell well within the threshold range.
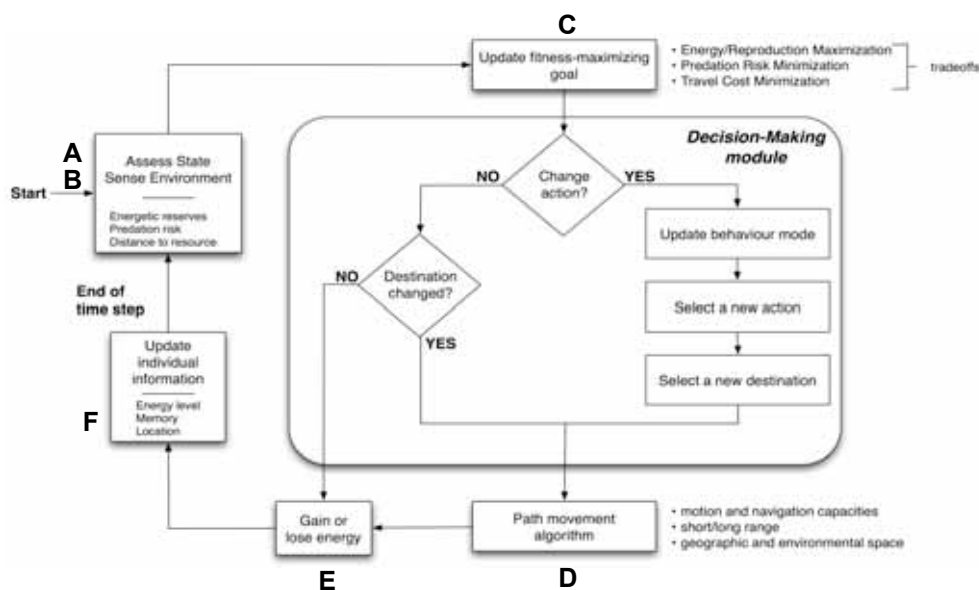

Figure 2. Steps involved in the caribou agent's decision making as implemented in the ABM.

2) Reproductive energy requirement

Caribou lose on average 15% of their autumn mass over winter, via fat and protein catabolism [40]. A loss greater than 20% results in reproductive failure. Therefore, assuming a 132 kg caribou, the agent's

energetic-loss buffer (i.e., minimum and maximum thresholds) is set between 710 - 947 MJ, respectively, for the winter (see [40] for the calculation of converting mass-loss to energy). At each time step, the agent assesses its reproductive energy requirement by calculating the projected cumulative net energetic loss over the course of the season:

At time step t:

net energy = cumulative energy lost - cumulative energy gained   *(1)*

projected loss = (net energy / n_t) * t_{total} ,   *(2)*

where n_t represents the number of time steps elapsed, and t_{total} is the total number of time steps in the simulation (8640 steps = 180 days).

This projection is a simplified version of state-based predictive theory [41,42], in which the organism optimizes the current choice in strategy based on the forecasted conditions. The agent's subsequent foraging decision will depend on where its prediction lies with respect to the threshold range, its daily energetic intake, and its predation risk (see 'Behavioural Strategies' below).

- Sensing the environment (B)

Two aspects are considered in the capacity of caribou to sense its environment: risk and forage. The caribou agent can sense the riskiness of its environment up to 1 km in radius, and responds to this risk at two scales: within a 500 m buffer (i.e., during intra-patch foraging), or between 500 - 1000 m (when assessing whether adjacent foraging areas are equally or more safe for inter-patch travel). These buffers correspond to known average avoidance distances of caribou to industrial features [27,32], and predator perception ranges of ungulates [43].

Caribou agents can also perceive food availability in their environment at two scales: intra-patch forage, corresponding to eight neighbouring cells, and within a 450 m in radius for area-restricted (i.e., inter-patch) searches [13]. In addition, caribou agents are also capable of assessing the elevation of their current location, as well as that of their immediate surroundings so that they may choose the cells with minimal elevation when deciding to travel at low energetic cost.

- Behavioural strategies (C)

The baseline model assumes that an agent's goal is to find an optimal balance to its daily energetic requirements, its longer-term reproductive energy requirements, and its predation-risk minimization. Based on its energy calculations and assessment of risk, a caribou can find itself either at the low end or below its energetic and risk thresholds (labeled as 'low'), within threshold range ('medium'), or at the high end or above its thresholds ('high'). Daily energy accumulated is considered low when the amount of gross energy accumulated is below 25.5 MJ, medium between 25.5 and 29 MJ, and high over 29 MJ per day. Risk of reproductive failure is low when the amount of projected net-energy lost is below 789 MJ, medium between 789 and 868 MJ, and high at greater than 868 MJ. Note that the actual lower and upper threshold ranges remain inexplicit, so as not to unduly influence the agent's decision-making. If the resultant agent activity culminates in at least an average of 22 MJ accumulated per day, for instance, this behaviour is more 'emergent' than if we were to tell the agent that it *must* achieve at least 22 MJ day^{-1}. Finally, when sensing its environment, if there are any features (industry or other) within its perception range with a predation risk score of 5, the agent accords a risk of 5; otherwise, it assesses the mean predation risk of its surrounding habitat. A risk of 5 is considered high, 3-4 is medium, and 1-2 is low. The following rules generally apply in governing which action the agent will undertake:

(1) If the agent is highly energetically stressed - both short-term (i.e., daily) and long-term (reproductive potential), predation risk becomes irrelevant and the agent attempts to find a profitable patch in which to forage.

(2) If the agent is energetically flush, minimizing predation risk takes precedence, with the agent seeking out as safe or safer locations in which to forage, if necessary.

(3) If the agent is energetically stressed short-term only, it will attempt to forage and travel in relatively safe locations.

(4) If the agent is energetically stressed long-term only, it will attempt to forage in profitable locations first, and if none available, then forage in safe locations.

(5) An agent will chose to rely on previously-visited foraging sites (i.e., access memory) instead of immediately feeding when the surrounding predation risk is medium and/or low, and both the current and adjacent sites are of low forage availability, and the agent is intermediately energetically stressed.

(6) An agent will chose to rely on previously-visited safe sites in which to forage (i.e., access memory) instead of immediately feeding when predation risk is high, no adjacent safer sites are present, and the agent is intermediately energetically stressed.

(7) The more energetically stressed, the less willing an agent is to taxi long distances.

These strategies are based on literature sources of ungulate movement ecology [34,44], and are drawn from behavioural-ecological principles of optimization behaviours (Figure 3).
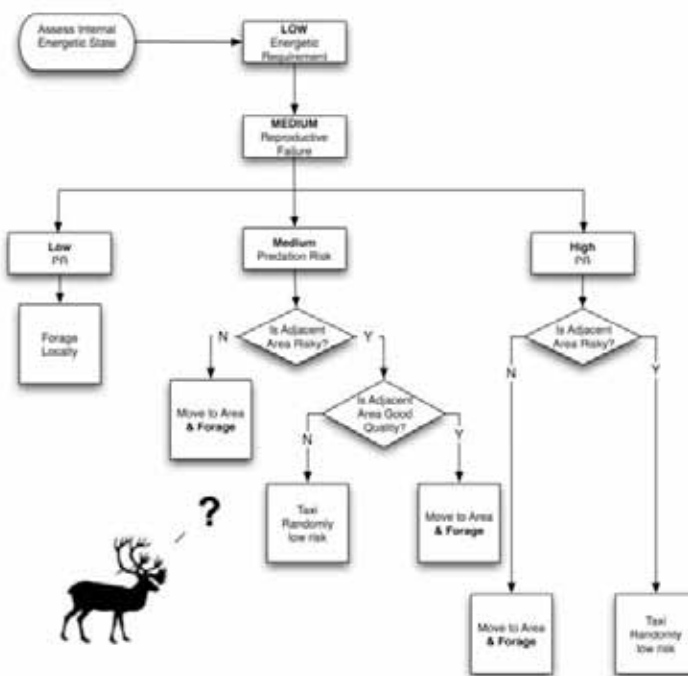

Figure 3. Example of behavioural trade-off flowchart of caribou agents

- Path movement algorithms (D)

Caribou agents engage in four different types of movement, reflecting different scales of habitat selection:

   (1) local, intra-patch foraging, where caribou move one cell at a time;
   (2) inter-patch foraging, also known as 'area-restricted searching' (up to 450 m, and up to two cells at a time);
   (3) random taxiing to an unknown location up to 6 km in distance, either choosing low-risk cells or low-elevation ones and traveling between 2 - 4 cells at a time; and

(4) revisiting a previously-visited patch drawn from memory that is at the same or lower elevation than the agent's current position. This latter movement also traverses 2 - 4 cells per time step, and the agent chooses the minimum-elevation cell in the path to its ultimate destination.

To prevent determinate model runs, stochasticity is introduced into the agent's movement decisions at different scales. When foraging, caribou agents randomly choose one of their eight neighbouring cells; when moving between foraging locations (inter-patch travel), agents also randomly select one cell (satisfying the criteria of being either of the same or greater forage availability or safety). These movements reflect the tortuosity of movement paths typical of area-restricted searches [36]. Furthermore, agents do not have perfect knowledge about their landscape. Agents employ a correlated habitat-dependent walk [45] when taxiing, whereby dispersal direction is dependent on previous direction and local habitat quality (i.e., low risk or low elevation). The agent has no prior knowledge of this destination location; it sets out with a pre-determined traveling distance chosen from a random-exponential distribution that is meant to reflect actual caribou average traveling distance of habitat selection of lichen (6 km; [46]). Lastly, when agents access their memory, they randomly pick a location that has been stored between 7 and 45 days prior (see 'Memory' below).

- Gaining and losing energy (E)

1) Energetic intake per time step

Caribou consume anywhere between 0.88 - 2.64 - 3.52 kg of lichen per day (based on the values from [30,31]. Because caribou spend between 50% - 88% of their day actively foraging [31,47], this corresponds to caribou consuming, on average (i.e., 69%, or 16.5 hours day^{-1}), 0.027 - 0.08 - 0.106 kg per 30 min. (the model's time step).

Using a 10.8 MJ kg^{-1} conversion rate of metabolizable energetic content of lichen [31], caribou are assumed to obtain between 0.29 - 0.86 - 1.14 MJ of energy per foraging bout. The amount gained is specifically linked to habitat type, so that the habitat ranked with the highest forage availability (i.e., open conifer forests) received an energy content of 1.14 MJ; forage availability (FA) of 4 = 0.86 MJ, FA 3 = 0.58 (an intermediate value), FA 2 = 0.29, etc. (Table 1).

In addition, a caribou agent modifies its environment as it forages. Specifically, after completing a 'forage' action at a location, it permanently reduces the energetic content of the cell so that it becomes equivalent to a habitat type with forage availability = 3 (if originally ranked 4 or 5), or 2 or 1 (if originally ranked 3 or 2, respectively). Note that the cell's content does not deplete to zero, as it is unrealistic for a caribou to consume the entire lichen availability in a 45 m^2 area in one half hour. The depletion is, however, permanent, since lichen re-growth rates are slow, and can take up to four months to recover, doing so during summer months only [48].

2) Energetic loss per time step

At each time step, regardless of the action undertaken, the caribou agent expends energy on its metabolism (see 'Model Calibration' for details). When moving from cell to cell, the agent further expends energy on locomotion, with various costs attributed to: (1) an increased or decreased change in elevation, and (2) the absolute elevation of the current position (higher elevation implies greater snow depth which incurs a greater traveling cost). When foraging, the agent sustains an additional cost of cratering through snow (which remained a constant through winter; see Table 2 for values). These losses are additive, and their cumulative value drives caribou reproductive-motivated habitat selection.

- Memory (F)

The caribou agent is able to store habitat assessment information into a variable list resulting in two types of memory: reference and working. The reference memory stores locations for profitable feeding and low-risk areas (as well as their associated elevation), whereas the working memory is used to avoid backtracking on recently depleted patches [49]. Caribou agents store these patch locations for up to 45 days (reference memory) as a moving window, and sub-sample locations no fewer than 7 days post initial

visit (working memory; median = 13 days). These values were derived from actual caribou-GPS data that were used to determine the time interval of a caribou returning to a previously visited site (i.e., 'time-to-return'; unpublished data). These data closely coincide with a study of elk (*Cervus elaphus*) site fidelity, which found a mean return time of 11 days [50]. Caribou agents only accessed their memory when no suitable forage and safe areas were available at both the intra- and inter-patch levels *and* when they were energetically stressed (either short-term, long-term, or both).

Table 2. Parameter values for calibrating the caribou agent in the ABM

Caribou agent parameters	Value	Source	Notes
Weight	132 kg	Bradshaw et al. 1998 [40]	
Daily energy requirements	22 - 33 MJ		
Expected reproductive energy loss	710 - 947 MJ	Bradshaw et al. 1998 [40]	
Daily energy expenditure in winter	738 kJ kg$^{-0.75}$ d^{-1}	Gotaas et al. 2000 [51]	28.7 MJ d^{-1} for a 132 kg caribou; used for verification of model calibration
Incremental costs of activities over resting metabolic:		Fancy and White 1985 [52], Boertje 1985 [38] and Fancy 1986 [53]	Model calibrated with 520 kJ kg$^{-0.75}$ d^{-1} for foraging, 653 kJ kg$^{-0.75}$ d^{-1} for walking
- foraging	1.44		
- walking	1.81		
Additional Movement Costs:			
Uphill	3.640 kJ/kg/km	Gustine et al. 2006 [54]	
Downhill	1.293 kJ/kg/km	"	
Horizontal high elevation (> 1185m)	2.64 kJ/kg	Boertje 1985 [38] and Gustine et al. 2006 [54]	
Horizontal low elevation	1.72 kJ/kg	"	
Cratering Costs		Fancy 1986 [53]	
High elevation	3.5 kJ / kg*h		
Low elevation	1.9 kJ / kg*h		
Memory			
Reference	45 days	unpubl. data	
Working	7 - 45 days, median 13	Wolf et al. 2009 [50], unpubl. data	
Range perception			
Forage - intrapatch	45 m		
Forage - interpatch	450 m	Johnson et al. 2002 [13]	Known as 'restricted area search'
Forage - taxi	up to 6 km	Mayor et al. 2007 [46]	
Predation - intrapatch	500 m	Dyer et al. 2002 [32] Weclaw and Hudson 2004 [27]	
Predation - interpatch	1 km	Laporte et al. 2010 [43]	

2.6 Model calibration

   The baseline ABM we chose on which to investigate the differential impacts of industrial features on caribou behaviours underwent a thorough calibration process. The majority of parameters used in the model are fixed - as these have been generally accepted in the literature, and were simply rescaled to either the spatial resolution (e.g., movement costs per cell), or the time frame (e.g., energetic intake per one half hour). However, because we wanted the model to reflect realistic bioenergetics of caribou, we calibrated the model with caribou metabolic rates. Most ecological studies of caribou bioenergetics

consider energetic costs in isolation (i.e., losses due to metabolism, movement, digging for food, or responding to disturbances). These studies are generally not coupled with energetic gains made by caribou (through feeding). As such, the way such losses are counterbalanced by gains of energy via foraging activities remains unclear.

In the baseline ABM, energy is lost and gained at a time interval of 30 minutes (unlike whole-day estimates from literature sources). Energetic gain was parameterized from the literature and remained fixed, and we chose to calibrate energy loss instead. There are two main literature sources for caribou metabolic and activity costs: that of Boertje (1985) and Fancy (1986) [38,53]. The values from the two studies vary widely, and moreover, are at times labeled inconsistently in more recent studies (i.e., calling resting metabolic rate standing metabolic rate). We therefore decided to calibrate the ABM using conserved ratios of the costs of different caribou activities that are considered standard in caribou energetic studies. For instance, the energetic cost of foraging (which incorporates costs of small movements, ruminating, ingesting) is 1.44 times the value used for lying down; and walking costs (not accounting for the additional expenditure due to uphill movement and/or in snow) are 1.81 times more costly [52]. Using these established ratios, we used a variety of energy values in the calibration process. The final values chosen for the baseline ABM were based on whether the model runs produced simulated energetic outputs consistent with three criteria: 1 the daily energy gain by agents is within known reported ranges; 2. the daily energetic expenditure approaches that of what has been reported for free-living *Rangifer tarandus* in winter (28.7 MJ d^{-1}; [51]); and 3. the proportion of time spent foraging (i.e., ingestion and rumination combined with area-restricted searching) is between 50% and 85% of the agent's daily activity budget. Because these criteria were not imposed as top-down rules (i.e., agents were not instructed to attain these values explicitly), and because these multiple parameters fell within the range of validity, we felt confident that our model was sufficiently calibrated. Moreover, the additional scenarios tested (with different risks associated to industrial features based on type, age, density, and distance-to) does not require the baseline model to be recalibrated since variation in the effect of industrial features has already been introduced (with random scores between 4 and 5 being assigned originally to the industrial features). Indeed, this modeling exercise serves to improve model fit with actual caribou activity patterns.

2.7. Simulation framework

One agent is run per simulation. The population of LSM is currently estimated at 78 individuals [2], and so we have assumed that conspecific attraction is not a driving force in our system unlike in other ungulate herds. Each caribou agent is assumed to be 132 kg in weight, pregnant, and expected to lose mass over the course of winter [40]. Accordingly, at the start of simulation, the agent's cumulative energetic loss is set at 0. The simulation is also begun with the agent at a daily energy intake of 0. Lastly, the start coordinates for the agent corresponds to one of the thirteen initial locations of the actual GPS-collared LSM caribou. To account for environmental stochasticity and for variability in the model outputs, runs are replicated 5 times per 13 'caribou', for a total of 65 runs per scenario. The simulation results correspond to the average of the values obtained in these replicates if data are normally distributed, and reports the median for data that are not.

The model has a reporting mechanism describing the instances of various events at each time step of 30 min. Important outputs of the model include the spatial distribution of the caribou, which are represented as a series of point locations (*x*, *y* coordinates and time stamp). This allowed comparison with the *observed* dataset for GPS-collared caribou, which is also comprised of point locations. For this purpose, point locations for simulated caribou were sub-sampled at 4-h intervals similar to the temporal resolution for GPS-collared caribou. The model also reports other critical parameters, such as the

cumulative amount of energy lost at the end of the simulation, the average daily energy gained and expended, the frequency at which the agent accessed its memory, and the proportion of time the caribou spent foraging.

The baseline model does not distinguish between forestry and oil-and-gas industrial features. However, caribou may respond differentially to different features [11,32]. Therefore, additional simulations will be conducted in which industrial features are to be assigned different levels of risk depending on characteristics that may affect their relative risk perception by caribou (e.g., density vs. age, type vs. distance-to). Any differences in risk effects between industry features (forestry vs. oil and gas) is to be evaluated by verifying which resultant simulations of caribou movement patterns most closely match actual caribou distributions and extracted patterns (mentioned below).

The simulation model was developed using the platform NetLogo v. 4.12 ([55]; freely downloadable from http://ccl.northwestern.edu/netlogo/download.shtml), and verified for proper programming functioning through progressive debugging and uncertainty testing.

3. Preliminary results and validation

The baseline model in which the caribou agent must trade off the competing goals of obtaining its daily energy requirement, minimizing reproductive-energy loss, and minimizing predation risk has been simulated. Figure 4 shows the multiple outputs generated by a single caribou agent in the baseline ABM in NetLogo's interface. The output graph 'A' registers the daily energy acquired ('der') over the course of the simulation. It reveals that the agent obtains its daily energy requirements well within the threshold range. Graph 'B' illustrates the cumulative energy lost (line '1') and gained (line '2'), highlighting that the agent is progressively accumulating an energetic debt over the course of the simulation. Graph 'C' reveals that this net loss is within range. Lastly, output 'D' shows the simulated agent's spatial distribution over the LSM environment at 4h-increments (dark shading indicates industry features).

The behavioural strategies employed in the baseline ABM were able to reproduce the following actual, observed descriptive caribou patterns: 1) the same relative ranking of land cover usage in winter, 2) a within-seasonal shift in use of the two major land cover classes (a decrease in closed conifer and an increase in muskeg habitat use from early to late winter), 3) a within-seasonal decrease in the distance to industrial features (including cutblocks), 4) a within-seasonal increase in use of lower elevation from early to late winter, 5) a within-seasonal decrease in the mean daily step length, and 6) a similar step-length pattern of a single peak of increased movement activity during a 24-hr period. The baseline model was also able to reproduce similar absolute numerical values of the following variables: the mean elevation and change in elevation used, mean daily caribou movements, and minimum convex polygons of individual spatial distributions. These closely-fitted patterns are in addition to the model being calibrated to reflect realistic bioenergetics; i.e., a medium daily energy gain and average daily energy loss of 25.4 MJ and 28.1 MJ, respectively, and a cumulative energetic loss of 825 MJ at the end of winter. These caribou agents also allocated 76.9% of their day to foraging activities, and chose to access their memory an average of every 12.4 days.

These combined results provide credible insight into the ways in which caribou use and select their habitat, and further suggest that caribou are, indeed, sensitive to risk on their landscape.
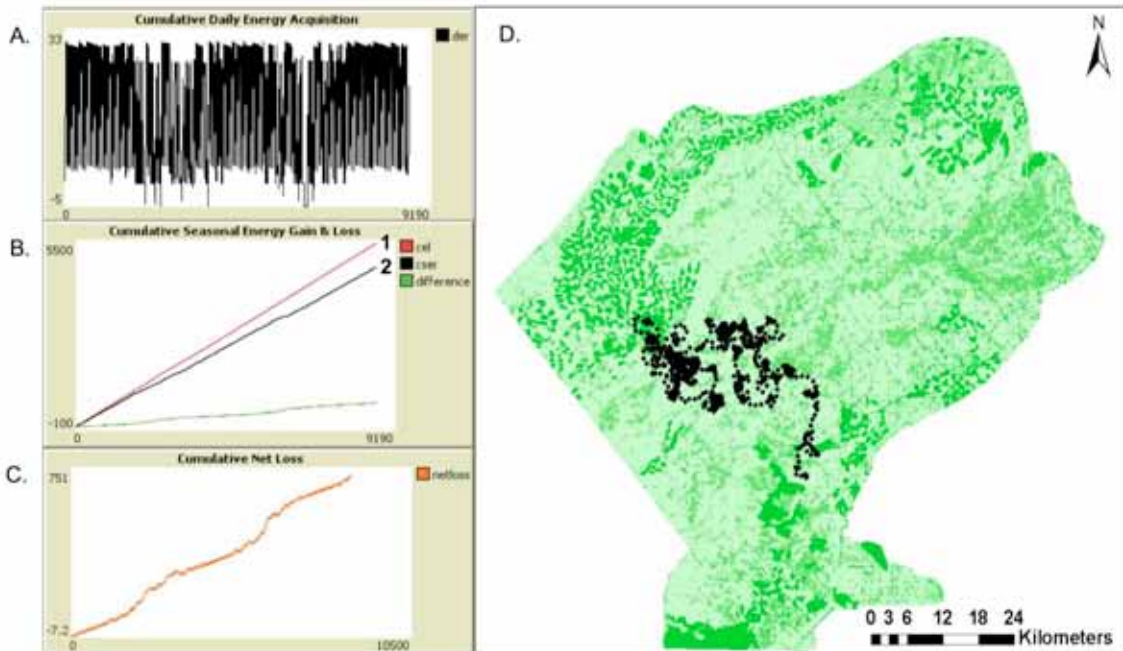
Figure 4. Netlogo interface showing various model outputs to be used for model validation and scenario evaluation

To evaluate the quality of the additional simulations performed to assess caribou responses to different types of risk, a pattern-oriented modeling approach will again be employed that compares the simulated output to multiple patterns extracted from the real system at different hierarchical levels and scales [56]. From the LSM caribou GPS-collar data, additional spatial patterns specific to the interaction between caribou and industry will be used to compare simulation outputs of the different risk scenarios, such as the distance between caribou point locations and specific industrial features, as well as the number of caribou movement paths that intersect with these features.

Finally, the anticipated results from our multiple simulations of predation-risk intensities will have implications for caribou fitness, as we will also be able to elucidate the differential energetic costs associated with each simulation as compared to the best-fit model, using the model outputs of average-daily-energy obtained, lost, and cumulative-seasonal energy lost.

4. Conclusion

By capitalizing on the utility of ABMs to accommodate behavioural mechanisms and movement ecology, we aim to show that carefully designed mechanism-driven models can be used for understanding and predicting how consequences of individual behavioural responses to environmental variation scale up to population-level phenomena such as habitat selection and use [57,58]. Our model findings will offer insight into *why* caribou are choosing the habitats they use, and consequently, the type of industrial activity that is most important in affecting caribou bioenergetics and fitness. Consequently, our ABM results will have benefits for conservation and industry-management purposes, serving as an applied, science-based decision tool for managing potential effects of resource extraction activities on valued resources.

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