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Identifying non-independent anthropogenic risks using a behavioral individual-based model

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ABSTRACT

Anthropogenic disturbances contribute to an animal's perception of and responses to the predation risk of its environment. Because an animal rarely encounters threatening stimuli in isolation, multiple disturbances can act in non-independent ways to shape an animal's landscape of fear, making it challenging to isolate their effects for effective and targeted management. We present extensions to an existing behavioral agent-based model (ABM) to use as an inverse modeling approach to test, in a scenario-sensitivity analysis, whether threatened Alberta boreal caribou (*Rangifer tarandus caribou*) differentially respond to industrial features (linear features, forest cutblocks, wellsites) and their attributes: presence, density, harvest age, and wellsite activity status. The spatially explicit ABM encapsulates predation risk, heterogeneous resource distribution, and species-specific energetic requirements, and successfully recreates the general behavioral mechanisms driving habitat selection. To create various industry-driven, predation-risk landscape scenarios for the sensitivity analysis, we allowed caribou agents to differentially perceive and respond to industrial features and their attributes. To identify which industry had the greatest relative influence on caribou habitat use and spatial distribution, simulated caribou movement patterns from each of the scenarios were compared with those of actual caribou from the study area, using a pattern-oriented, multi-response optimization approach. Results revealed caribou have incorporated forestry- and oil and gas features into their landscape of fear that distinctly affect their spatial and energetic responses. The presence of roads, pipelines and seismic lines, and, to a minor extent, high-density cutblocks and active wellsites, all contributed to explaining caribou behavioral responses. Our findings also indicated that both industries produced interaction effects, jointly impacting caribou spatial and energetic patterns, as no one feature could adequately explain anti-predator movement responses. We demonstrate that behavior-based ABMs can be applied to understanding, assessing, and isolating non-consumptive anthropogenic impacts, in support of wildlife management.

1. Introduction

Measuring the impacts of anthropogenic activities on the responses of wildlife is crucial for their effective management and population persistence (Leu et al., 2008). Ever-increasing industrial landscape change can lead to consequences beyond habitat loss and amount and arrangement of habitat patches. Anthropogenic features or activities can be perceived by animals as risky habitats or threatening stimuli, respectively, and animals will attempt to minimize their exposure or avoid them (Frid and Dill, 2002; Beale, 2007). To understand underlying processes driving habitat selection and movement of prey species, the 'landscape of fear' concept has been invoked as a behavioral mechanism explaining how *perceived* predation risk in heterogeneous environments could alter an animal's use of an area as it tries to reduce its vulnerability to predation (Laundré et al., 2001, 2010; Willems and Hill, 2009). How animals therefore perceive and respond to anthropogenic features is critical for wildlife management as it will impact their decisions of where to forage, how much energy to expend, and what habitats to use (Johnson et al., 2005; Krausman, 2011).

Prey rarely find themselves in single-predator environments and must accordingly evaluate the relative predation risk from

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multiple predators simultaneously (Thaker et al., 2011). With increasing land-use intensification, prey are similarly exposed to multiple anthropogenic features – stressors – that can evoke interactive and/or unpredictable outcomes that aggregate over time and space (Harriman and Noble, 2008). Therefore, an evaluation of how stressors influence an animal's landscape of fear should be examined in an interactive manner. Because multiple anthropogenic effects are characterized by their interdependence between time, space, and activity, this presents a challenging problem in evaluating their relative contributions on wildlife responses (Nitschke, 2008). Studies of this kind are limited by the requisite complexity of experimental designs that often require expert guidance (Frair et al., 2008), and/or use complex statistical analyses for quantifying stressors effects, yet are still unable to adequately quantify interaction terms beyond binary combinations (Glaholt et al., 2012). In addition, studies which examine animal spatial distributions without a behavioral context may also be of limited value, since statistical habitat models parameterized in one area may not be transferable to other areas or conditions in which habitat availability and landscape configuration are different – for example, under future conditions (Beyer et al., 2010). Instead, an integrative modeling framework that allows for the simulation of complex animal movement ecology and behaviors can provide a virtual environment in which to test the interactive effects of multiple stressors on an animal's perception of predation risk and disturbance (Frair et al., 2008; Bennett et al., 2009). Addressing these sources of and pathways to a landscape of fear can resultantly better affect targeted management and mitigation measures should animals respond to anthropogenic effects in graded, interactive, or substitutable fashions (Spaling and Smit, 1993).

In view of this, we use a spatially explicit, behavioral agent-based model (ABM) to assess the effects of multiple industrial developments on animal movement, distribution and habitat use by simulating an animal's perception of landscape risk. Agent-based models (ABMs) are computational simulation tools that rely on a bottom-up approach. They explicitly consider the individual components of a system (the agents) and allow the system's properties to emerge from the interactions among these components (Grimm et al., 2005). Agents are goal-driven and try to fulfill specific objectives, they are aware of and can respond to changes in their environment, they can move within that environment, and they can be designed to learn and adapt their state and behavior in response to stimuli from other agents and their environment. This emphasis on interactions between agents and their environment is what distinguishes agent-based models (also referred to as individual-based models) from other systemic modeling approaches (Marceau, 2008).

We parameterized our model for boreal caribou (*Rangifer tarandus caribou*), a useful model species as their populations have been impacted by expanded industrial development over the last few decades (Vors and Boyce, 2009; Environment Canada, 2011). This expansion has resulted in an increased network of seismic exploration, pipelines and roads, and the loss of habitat of older, lichen-bearing forests due to resource-extraction activities of oil and gas and forestry (Peters et al., 2012). Consequently, the decline of woodland caribou is partly based on an indirect interaction between caribou and industry that has increased the caribou's landscape of fear (DeCesare, 2012). Habitat change from forestry has increased predator biomass as ungulate prey (moose, deer) is attracted to early seral forests (Seip, 1992; Wittmer et al., 2005; Peters et al., 2012) thus increasing predation risk and caribou's tendency to avoid open areas (such as cutblocks). In addition, linear features introduced onto the landscape aid in facilitating predator efficiency (either via sight lines or lowered travel costs through dense forests; Latham et al., 2011; DeCesare, 2012). Resultantly, caribou associate these features with increased predation risk (Vistnes and Nellemann, 2008). Caribou can furthermore be disturbed by industrial activity either directly through the physical footprint, or indirectly through sensory disturbance, and respond similarly, minimizing their exposure. Due to these higher levels of predation pressure and disturbance, the evolved predator-defense strategies of caribou – avoidance/separation behaviors – have augmented the allocation of habitat caribou deem as 'risky'/'fearful' (Smith et al., 2000; Dyer et al., 2001; Polfus et al., 2011).

Considering the important impacts of industrial stressors on caribou fitness, empirical studies face a significant challenge disentangling the relative effects of multiple stressors from each other as well as from underlying habitat configuration. Using the ABM as an investigatory tool, we employ a novel scenario-sensitivity analysis to infer knowledge about caribou responses to different existing industrial features based on characteristics that may affect their relative perception: presence and density of linear features, cutblocks and wellsites; age of harvested forest; and activity status of wellsites. In particular, we test whether industrial features all contribute to a caribou agent's landscape of fear and to what extent by allowing agents to differentially perceive and respond to alternate arrangements of industrial features and their attributes in the landscape. The resultant industrial-landscape configuration causing caribou agents to reproduce the most realistic behaviors is determined by comparing simulated caribou movement patterns with actual caribou data using a pattern-oriented, multi-response optimization approach, and its robustness tested against two null models of caribou movement based on random processes (random locations, and undifferentiated responses to industry). The advantages provided by our approach are a mechanistic understanding of the interrelated role of multiple anthropogenic features on processes governing caribou movements and distributions, and the relative impacts of different industrial stressors, offering a foundation on which decisions and future management actions can be evaluated (Nitschke, 2008).

2. Methods

The caribou ABM comprises two main components: (1) caribou agents and their decision-making heuristics and (2) a landscape representation of the caribou herd's habitat preferences. In this section, an introduction of the study area and a brief presentation of the model overview and agent decision-making rules are first provided, followed by a description of the landscape representation (in terms of different predation-risk scenarios), the simulation framework, and the analysis and comparison of agent responses to the different scenarios tested.

2.1. Study area

The area chosen for the study was the range of the Little Smoky (LS) herd demarcated by the Alberta Fish and Wildlife Division (ASRD, 2010), covering 3100 km^2 in the foothills of west-central Alberta. The LSM range is located in the upper foothills ecoregion of west central Alberta, Canada (54° N, 119° W), with the lands primarily managed by the government for multiple uses including forestry, oil, and natural gas industries. Because the Little Smoky is such a dynamically changing landscape due to industrial development, we confined our study to a single time period, during winter 2004–2005. The LS range has a high level of industrial development for a boreal caribou herd in Canada, with 95% of its range in proximity (500 m buffer) of anthropogenic activities (Environment Canada, 2011), and as such provides an ideal case study to evaluate the interactive effects of the caribou's landscape of fear. Specifically, the activities of four forestry management agreements and numerous petroleum-company operations (WCCLPT, 2008) have generated an estimated 0.45 km/km^2 of infrastructure (roads and pipelines), 3.5 km/km^2 of seismic lines, 439 oil/gas well sites and 9.1 ha/km^2 of cutblock densities in the LS c. 2005. There also continues to be considerable development pressure and increases in allocations to industrial users within the caribou range (Robichaud, 2009).

2.2. Agent-based model overview

Our current work expands on an existing ABM we developed that simulates winter habitat selection and use of female woodland caribou in the LS (Semeniuk et al., 2012). The underlying premise of the ABM is that an individual's internal state influences how it perceives its environment and hence drives its decision-making process (Houston and McNamara, 1992). 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 in the study area. Specifically, the caribou agent can balance its needs to meet its daily energetic requirements and minimize its energetic loss in order to ensure its long-term goal of reproductive success. The caribou also considers its predation risk since relatively safer locations are not always the most profitable in terms of energetic resources.

The intent of the original model was to determine the habitat-selection strategies (i.e., predation-sensitive foraging theories) driving caribou movement. The model has been parameterized with various biological and eco-physiological data specific to woodland caribou, and carefully calibrated with caribou bio-energetic values from literature sources to ensure that agent decision rules are grounded in realism. Simulations had been conducted on alternative caribou foraging hypotheses by assigning different fitness-maximizing goals to agents; for instance, by contrasting caribou agents that were hyper- or insensitive to the predation risk of their surrounding environs at the expense or mercy of their energetic requirements, respectively. The model outcomes were rigorously evaluated using a pattern-oriented modeling approach with actual caribou data using a combination of GPS data from thirteen caribou radio-collars deployed over six months from 2004 to 2005 in the LS, as well as behavioral patterns common to boreal woodland caribou to ensure widespread applicability. The major findings of the ABM allowed us to determine the general processes driving habitat selection. Namely, when navigating their environs, our model suggested caribou make context-dependent decisions, and are indeed responsive to environmental predation risk (natural and industry-related) but only when they can afford to be. Energetic needs for daily maintenance have priority, but once fulfilled, the agent responds to the risk posed by its environment. In our original, existing ABM, the best-fit model comprised agents generally responsive to industry, corroborating a plethora of existing literature; and the model can now be further refined to distinguish any relative degree of responsiveness of agents to oil and gas or forestry industries, and their associated attributes on the landscape.

In recognition that differential perception of industrial features can influence animal movements, and that in turn, the availability and accessibility of habitat can equally affect movement characteristics and energetic constraints (Martin et al., 2008), we employ the caribou ABM to use as a tool to: (1) identify any confounding effects of multiple industrial features and their attributes on caribou movement responses and (2) untangle accessibility of landscape configuration from habitat preference. The ultimate goal of this research is to enhance model predictability for novel environmental conditions such as modeling augmented or mitigated future development scenarios. In this paper we first create diverse industrial landscapes of fear that represent different attributes of industrial features, and parameterized as high risk. We then simulate caribou agents on the landscape possessing adaptive decision-making heuristics, and lastly compare model outputs with actual data using pattern-oriented, multi-response optimization approach. The scenario-sensitivity methodology in this paper represents an entirely novel procedure with the explicit and original goal of understanding and assessing multiple stressors on movement ecology and habitat selection of caribou. Moreover, the patterns used in this model development are unique from those used in Semeniuk et al. (2012), and are explicitly industry-related.

2.3. Caribou agent decision-making heuristics

The caribou agent is provided fitness-maximizing rules: to trade off the competing goals of energy acquisition and conservation (i.e., for somatic and reproductive growth) with minimizing predation risk. Accordingly, at each time step in the model (representing 30 min), the agent first assesses its energetic state; it determines whether it has reached its daily energetic requirements (22–33 MJ day^{-1}, McEwan and Whitehead, 1970; Boertje, 1985) and by what magnitude, and projects whether it will have enough energetic reserves (and by what magnitude) to have a successful birth at the end of the season (an energetic loss of not more than 710–947 MJ, corresponding to a 20% mass loss, Bradshaw et al., 1997; 'A' in Fig. 1). At this stage it also senses the immediate risk in its environment as well as the forage availability ('B'). It then determines whether to minimize its exposure to risk, and does so by assessing whether its energetic requirements have reached a minimum threshold. Based on this decision-making heuristic ('C'), the agent either forages, ruminates, or moves to a new location ('D' and 'E'). The agent then updates its energy reserves – both gained and lost through its actions ('F'), and commits to memory any profitable or safe locations encountered – to which it returns, should it be energetically stressed and surrounded by inhabitable matrix. ('G'). A more detailed description can be found in Semeniuk et al. (2012).

2.4. Landscape representation

Because the environment plays a critical role in the decision-making heuristics of caribou, the ABM includes a spatially explicit representation of the Little Smoky region to ensure biological and ecological realism. For integration with the ABM, four categorical raster data layers at a 45 m resolution were used to represent the physical environment where the caribou agents are located: (1) forage-availability layer, (2) a derived energetic-content layer, (3) a predation-risk layer, and (4) an elevation landscape. The forage-availability and predation-risk layers were generated from combined land-cover and industry-feature maps composed of habitat classes and industrial features (roads, pipelines, seismic lines, cutblocks and wellsites), respectively, that in turn were assigned both ranked forage and risk scores (Fig. 2).

The land-cover raster map was developed by DeCesare et al. (2012) and contained ten vegetation classes deemed to be biologically relevant to woodland caribou, ranging from closed conifer forests, to herbs and open water. Individual vector maps of roads, pipelines, seismic lines cutblocks, and wellsites were supplied by Alberta Environment and Sustainable Resource Development (AESRD), and analyzed and updated for accuracy to 2004 (see Appendix A). These AESRD maps included the location of industrial features and associated attributes, such as year of establishment (cutblocks) and activity status (wellsites). The energetic-content layer was produced from combining known caribou daily energetic intake rates and caribou-foraging time budgets with the relative forage-availability of each land-cover class. The elevation layer was represented by a digital elevation

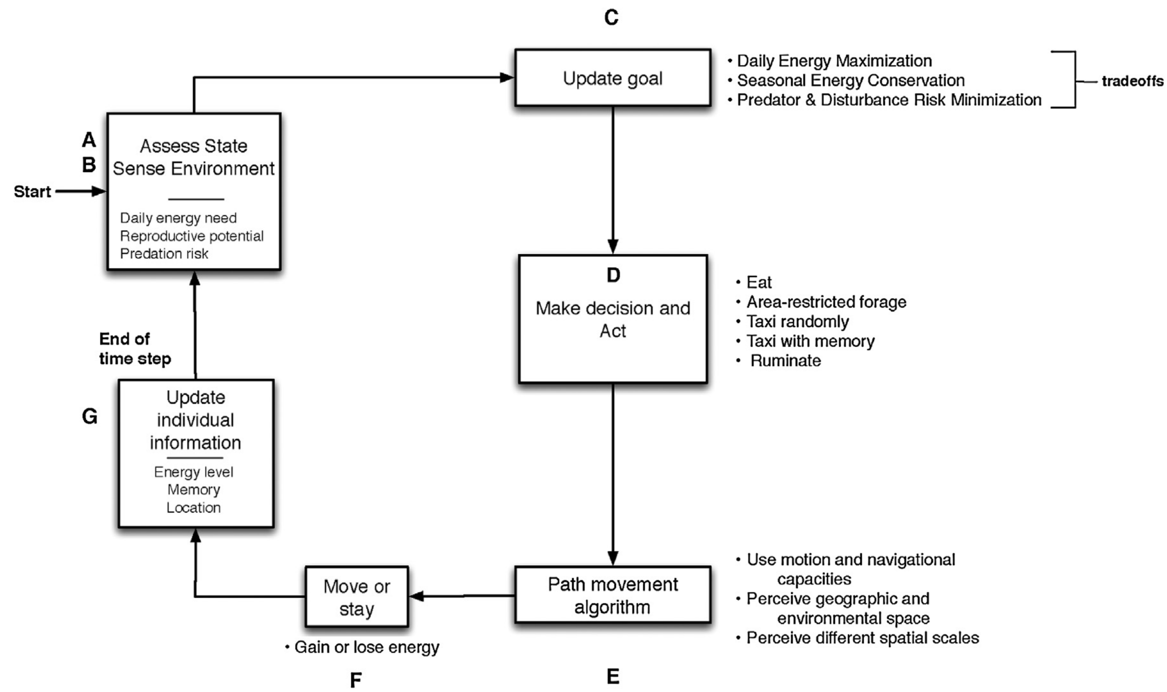

Fig. 1. Steps involved in the caribou agent's decision making. Letters A–G described in Section 2.3.

model (DEM). To provide an environment to the agents and allow their movement, a virtual grid was overlaid on the four layers described above. Each cell in the ABM spatial environment therefore possesses four values accessible by the agent: a forage-availability score (0–5), an associated energetic content (MegaJoules, MJ), a predation-risk score (1–5), and an elevation (m).

2.5. Landscape-of-fear configurations

In our original caribou ABM, caribou agents were responsive to habitat land-cover classes (each assigned a risk score from 1 to 5 and remains unchanged) and industry-feature *presence* (i.e., the actual locations of infrastructure, seismic lines, cutblocks and

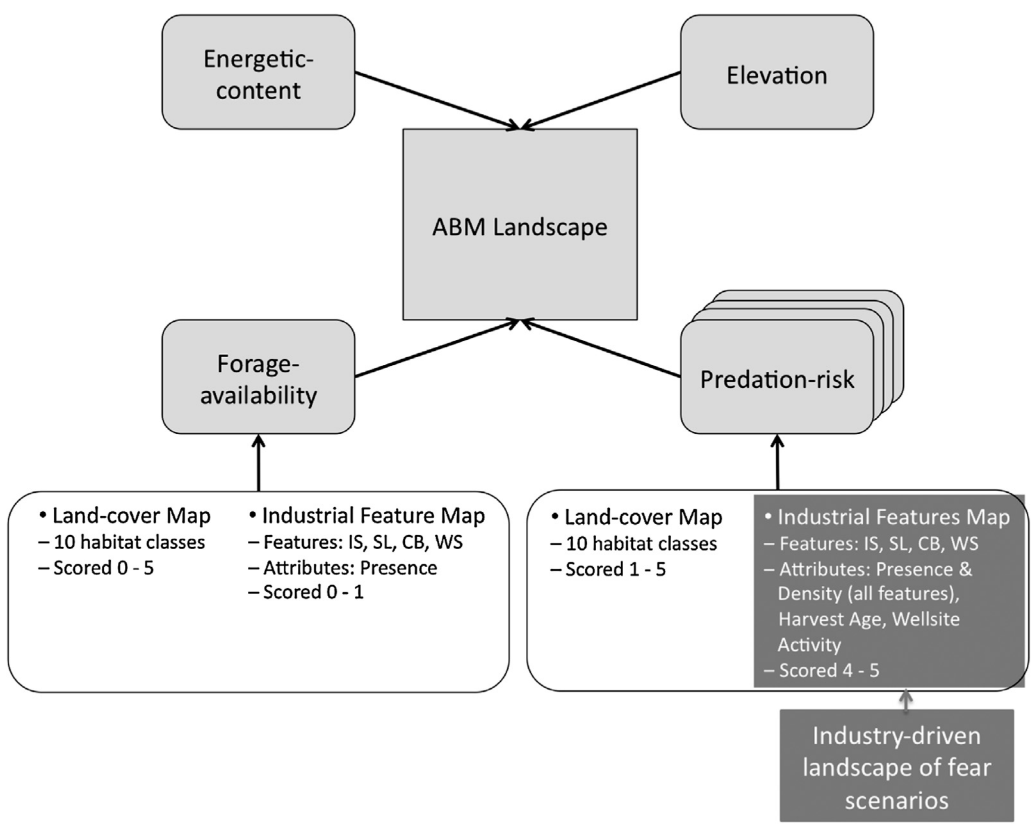

Fig. 2. Elements of the ABM landscape representation with emphasis on (i) the forage-availability and predation-risk data layers and (ii) the contribution of the industrial-feature maps to each. IS – infrastructure; SL – seismic lines, CB – cutblocks; and WS – wellsites.

Table 1
Landscape-of-fear (LOF) scenarios. Configuration of different attribute layers of industrial features used to represent industry-sourced predation risk. Scenarios are derived from a fractional factorial, mixed-effects orthogonal design.

LOF scenarios	Infrastructure	Seismic lines	Cutblocks	Wellsites
1	Density	Density	Density	Activity
2	Density	Density	No effect	Density
3	Density	No effect	Presence	No effect
4	Density	Presence	Age	Presence
5	No effect	No effect	Age	Density
6	No effect	No effect	Density	Presence
7	No effect	Presence	No effect	No effect
8	No effect	Presence	Presence	Activity
9	Presence	Density	Age	No effect
10	Presence	Density	Presence	Presence
11	Presence	No effect	No effect	Activity
12	Presence	Presence	Density	Density

wellsites). These industry features were randomly given a predation-risk score of either 4 or 5 so as to not overly complicate the model, since deducing the behavioral processes driving overall habitat selection was the original main objective. Nevertheless, the rankings are in accordance with the accepted premise that caribou are sensitive to industry features; and the original model performed significantly better when caribou agents were responsive to industry (instead of ignoring industry when encountered).

For the creation of different industry-driven fear landscapes, a four-step process was required (detailed in Appendix B). First, attribute data layers were created for each industry feature (infrastructure, seismic lines, cutblocks and wellsites): 'presence', 'density', 'age' (for cutblocks only), and 'activity status' (wellsites only). Next, these individual attribute data layers were assigned a high predation risk score. The attribute data layers were then arranged in twelve combinations via a mixed-level orthogonal sensitivity design (Table 1) to generate different configurations of industry-sourced landscapes of fear. An additional response was added to the design: a 'no strong effect', denoting that the industry feature in question (e.g., whether a cutblock or a seismic line, etc.) was not to be deliberately avoided by caribou agents (allowing first for energetic considerations), and instead the agent's perception of its surroundings defaulted to the surrounding habitat class. The last step involved completing the LS landscape representation for input into the ABM's environment. Each of the generated landscapes of fear represented industry-sourced predation risk only; the predation risk associated with the different habitat land-cover classes remained unchanged. Subsequently, the industry landscape was integrated with the land-cover map to represent the complete predation-risk data layer necessary for the ABM (Fig. 2).

2.6. Simulation framework

The caribou ABM was simulated with each of the 12 landscapes of fear in separate runs. The model is run with one agent. The drastically reduced population of LS is currently estimated at 78 individuals (ASRD, 2010), and so we have assumed that conspecific attraction is not a driving force in our system unlike in other ungulate herds. Additionally, while grouped individuals may benefit from the dilution effect, we do not expect conspecifics to have a large impact on the caribou's anti-predator behavior since their dominant predator-avoidance strategy is spatial separation. The simulated agent is female, conservatively assumed to be 132 kg in weight, pregnant, and expected to lose mass over the course of winter (Bradshaw et al., 1997). Accordingly, at the start of simulation, the agent's cumulative energetic loss is set at 0 so as to not bias the model results by initiating the agent in an energetic debt or surplus since we wanted to directly test the environment by perception interaction under standard conditions. The simulation is also begun with the agent at a daily energy intake of 0. Because caribou have distinct summer and winter habitat requirements (including forage), the simulation begins with the agent having no winter locations stored in its memory, as it would be evolutionarily costly to remember locations long term which the animal uses only if energetically or risk-stressed. 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 model outputs, simulations are replicated 65 runs (5 runs $\times$ 13 initial starting positions) per scenario (i.e., fear landscapes). The presented simulation results correspond to the average or median of the values obtained in these replicates.

The model has a reporting mechanism describing the instances of various events at each time step of 30 min on a 3100 km^2 grid surface (1786 $\times$ 1619 45-m cells). The time and areal step are appropriate temporal and spatial resolutions to capture the variability of foraging behaviors that are characteristic of ungulates at the spatial level of the food patch (Owen-Smith et al., 2010). The ABM simulates over a period of 180 days, the span of winter in Alberta. The simulation model was developed using the platform NetLogo v. 4.1.2 (Wilensky, 1999), and verified for proper programming functioning through progressive debugging and uncertainty testing.

2.7. Evaluation of agent responses to fear landscapes

As caribou agents move across the landscape, the ABM outputs various agent behavioral, bio-energetic, and spatial metrics (patterns). Therefore, each landscape-of-fear (LOF) scenario used in the ABM elicited from agents patterns that could be evaluated and compared. To identify the most ecologically realistic LOF scenario, meaningful patterns were selected from radio-collared GPS location data of actual caribou (Table 2 and C1). A total of 5225 location points were obtained at a minimum of 4-h intervals for 13 female individuals from the Little Smoky in winter (November–April) 2004–2005 (see DeCesare et al., 2012 for more details). The patterns from both actual and simulated data for comparison were industry-related variables that comprised: (1) the median nearest distance (m) between caribou point locations and industrial features, (2) the median lineal density of industrial features within 1 km^2 of caribou point locations (km/km^2), (3) the maximum wellsite density (#/km^2) within 1 km^2 of caribou point locations, (4) the percent difference in nearest-proximity to cutblock ages (old vs. young), and (5) the percent difference in nearest-association with wellsite activity status (inactive vs. active). The first two tested patterns differ since high-density features are spatially distinct from feature presence, possibly evoking divergent agent distributional responses. Two regulating criteria were further added as additional patterns to identify biologically

Table 2
Results of sensitivity-analysis patterns of optimized LOF scenario in comparison to twelve other LOF scenarios, null models: (i) random points within LS herd designation and (ii) simulation with industrial features randomly allocated high predation-risk scores, and to actual caribou values. IS – infrastructure; SL – seismic lines, CB – cutblocks; and WS – wellsites.

	Median nearest distance (m)				Median density (km, well/km^2)				Difference in older CB proximity (%)	Difference WS association (%)	Model comparison	Individual spatial extent (km^2)	Seasonal energy loss (MJ)
	IS	SL	CB	WS	IS	SL	CB	WS (max)					
Optimized LOF-scenario[a]	1449	133	4095	1790	1.03	3.18	1.60	4	41.0	20.0	0.27[c] 0.207[d]	288	865
Simulated models' range[b]	1528–1613	133–174	3221–4392	1724–2058	1.01–1.07	2.41–3.1	1.61–2.69	3–4	18.0–60.1	(−)23.6–24.4	0–0.24[c]	164–262	0–873
(i) Random points	1231	104	4043	1701	1.07	3.07	2.95	4	24.0	15.5	0.212[d]	NA	NA
(ii) Random high risk	1356	132	3866	1767	1.07	3.11	2.33	4	25.0	15.0	0.220[d]	253	859
Actual caribou (quartiles)	1524 (689–2315)	118 (53–204)	4012 (2365–7991)	1327 (830–2231)	0.91 (0.55–1.18)	3.12 (2.1–4.3)	2.43 (0.75–4.30)	3	52.0	18.0		270 (250–290)	(710–947)

[a] Optimized multiple response: infrastructure – presence; seismic lines – presence; cutblocks – density > 3.8 km/km^2; wellsites – active wellsites.
[b] Range of outputs from 12 LOF-scenarios.
[c] Model comparison between LOFs using desirability fit (range 0–1) with higher value indicating better fit with actual value.
[d] Model comparison between optimized LOF and null random models using normalized RMSE. Lower value indicates better fit with actual value.

unrealistic model runs: individual-spatial extent (measured as minimum convex polygon – 270 km^2; Semeniuk et al., 2012), and the cumulative seasonal energy lost by the caribou agent (a normal range should be between 710 and 947 MJ; Bradshaw et al., 1997; Semeniuk et al., 2012).

Once all the 12 LOF were simulated, the patterns produced by the agents were extracted from each output. To determine the LOF scenario that best reproduced the *multiple* patterns generated by actual caribou, a multi-response optimization approach was used, known as 'maximum desirability' (see Appendix C). This technique allows for the simultaneous optimization of several patterns, and can be thought of as being analogous to a linear regression model in which the simulated patterns from an LOF scenario are jointly regressed against observed ones, and the degree of 'fit' estimated (range 0–1). Because this analysis can determine the relative contributions of each industrial attribute to the overall model fit, it can furthermore calculate what multi-response combination should produce the highest fit. Because only a subset of LOF scenarios was evaluated (albeit orthogonal in design), a unique LOF scenario was calculated as having the best fit against actual data. This optimized LOF scenario was subsequently incorporated into the ABM's environment, the model run, and agent patterns evaluated for fit against actual patterns to verify improvement over the 12 other LOFs.

The robustness of the optimized LOF scenario was next tested against two null 'random' models to demonstrate that the refined, mechanistic movement model can outperform models based on randomness. We used (1) a random distribution of points within the LS boundary meant to represent caribou with no underlying mechanistic habitat selection behaviors ($n = 5225$, comparable to the number of caribou GPS point locations) and (2) the original caribou ABM (Semeniuk et al., 2012) that did not distinguish oil and gas from forestry but randomly treated the presence of such features as medium-high or high predation risk. This ABM was re-run using the updated industrial feature datasets (Appendix A). We extracted from the two null random models the same suite of patterns and compared them against the optimized LOF scenario using a normalized root mean square error (NRMSE) approach. To test for model external consistency (Dion et al., 2011), we additionally investigated agent-evoked patterns directly unrelated to industry responses (i.e., not used in the initial evaluations) – the combined spatial extent of individuals and its degree of spatial overlap with the herd range of actual caribou to further assess the performance of the LOF scenario.

3. Results

Caribou agents generated patterns that best reproduced the multiple response patterns of actual caribou when the presence of infrastructure and seismic lines, the density of cutblocks (>3.8 km/km^2), and active wellsites were concurrently considered as the industry-driven landscape of fear (i.e., an optimal fit of 0.27 – see Appendix C; Fig. 3). This optimized LOF was not one of the twelve explicitly modeled during the sensitivity-design process, but instead was estimated by the optimization procedure as producing the closest fit to actual caribou patterns (Table 2). The twelve LOF-scenarios nonetheless had caribou agents produce patterns that fell within the quartile values of actual caribou (Table 2), although scenarios that ignored the effect of seismic lines had very low 'desirability' fits (approximating zero), and caused agents to generate unrealistic spatial extents and lose uncharacteristically minimal amounts of energy. In comparison, the pattern values elicited from the optimized LOF-scenario either generally fell well within the range of the twelve scenarios or as close to the actual-caribou value as possible (Fig. 4a and b).

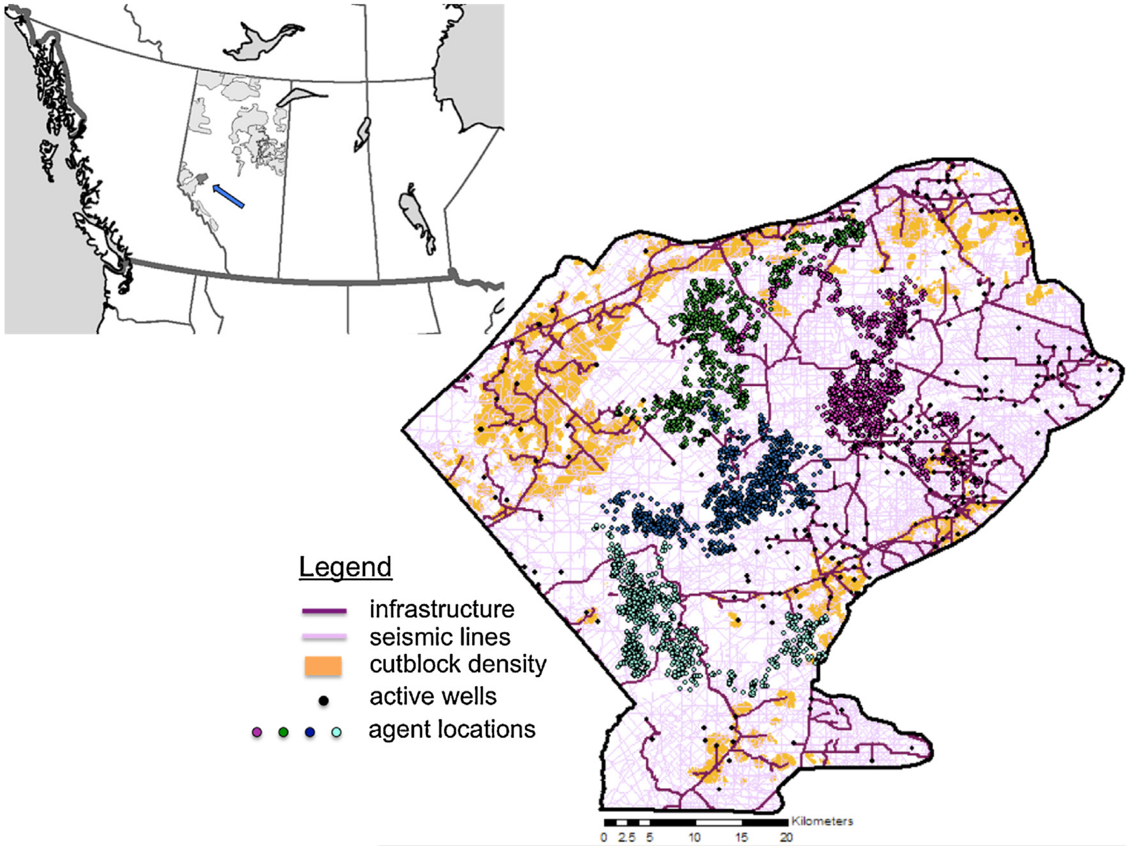

Fig. 3. Map of the study area in west central Alberta, Canada, showing infrastructure (i.e., roads and pipelines) and seismic lines, areas with cutblock density above 3.8 km/km^2, and active wellsites. Also shown are the locations of four simulated caribou agents. Inset: Little Smoky caribou range (indicated by the dark gray) situated amongst other caribou herds (shaded gray) within the province of Alberta, in Western Canada (ASRD, 2010).

The optimized LOF was robust, outperforming either of the null models more often than the reverse, and resulting in the lowest NRMSE (Table 2). The improvement of the refined caribou ABM over the existing one is not so drastic as to alter the fundamental patterns that had matched well with generally known caribou- and specifically derived GPS-collar behavioral patterns. Indeed, most patterns remain unchanged, as expected: closed conifer forests, muskeg/wetlands and open conifer forests were still the land-cover classes used most frequently by agents; caribou agents in late winter continued to use lower elevations with reduced daily step-lengths; and the single daily peak in activity levels remained unaffected (present values not reported, although see Semeniuk et al., 2012). However, incorporating the landscape of fear into the ABM increased the realism of the model in that caribou agents, in their quest to maximize energetic gain and minimize exposure to the selected industrial features and their attributes, reproduced individual spatial extents still within the observed actual-caribou range (250–290 km^2), but did so with a smaller and restricted herd range than the original ABM, converging more accurately to the areal coverage used by actual caribou c. winter 2004–2005 (Fig. 5).

Each industrial feature was perceived by caribou to be of high risk – 'no strong effect' was never selected during the optimization procedure to maximize overall fit of the multiple caribou response patterns. This result further substantiates that our original ABM, designating industry as being perceived as medium-high to high risk, was appropriate. There was no possibility of having the quantity of cells apportioned as 'high risk' in the spatial datasets overwhelmingly drive the results: the allocation of cells in the 'presence' vs. 'high density' data layers were similar for each industry feature (within 5%). Moreover, the selected active-wellsite attribute, with fewest number of cells deemed high risk in the data layer, was still capable of eliciting a behavioral response from caribou agents. Caribou agents were also most sensitive to linear features (the presence of seismic lines and infrastructure), explaining just over 50% of the agent responses to industry (Fig. 6a). The features' attribute also affected agent responses. Overall fit estimated by the 'desirability' procedure sizably dropped between 30% and 99% when a sub-optimal attribute was imposed by the optimization procedure for an industrial feature (all other feature attributes remaining at their optimum; Fig. 6b). Despite the strength of contribution of linear features in shaping caribou-agent behaviors, there was however no substitution effect: with the exception of seismic lines, overall fit was estimated to approach zero when considering the fit of a sole industry feature (and its optimal attribute) independent of the others. The presence of seismic lines only could explain 4.4% of the variation in agent responses.

4. Discussion

This study represents the first to apply a behavior-based, spatially explicit modeling approach to isolate and specify the contributions of multiple anthropogenic stressors driving the 'industry avoidance' of wildlife, specifically caribou. Using the existing caribou ABM as an investigative tool, the scenario-sensitivity analysis that we performed elucidated caribou responsiveness to different anthropogenic industries, which we described as different scenarios of Landscape of Fear (LOF). Our findings revealed that in addition to resource distribution, the responsiveness of caribou agents to the multiple industry features affects the extent to which caribou distribute themselves on the landscape as well as their energetic reserves (the caribou agent's seasonal

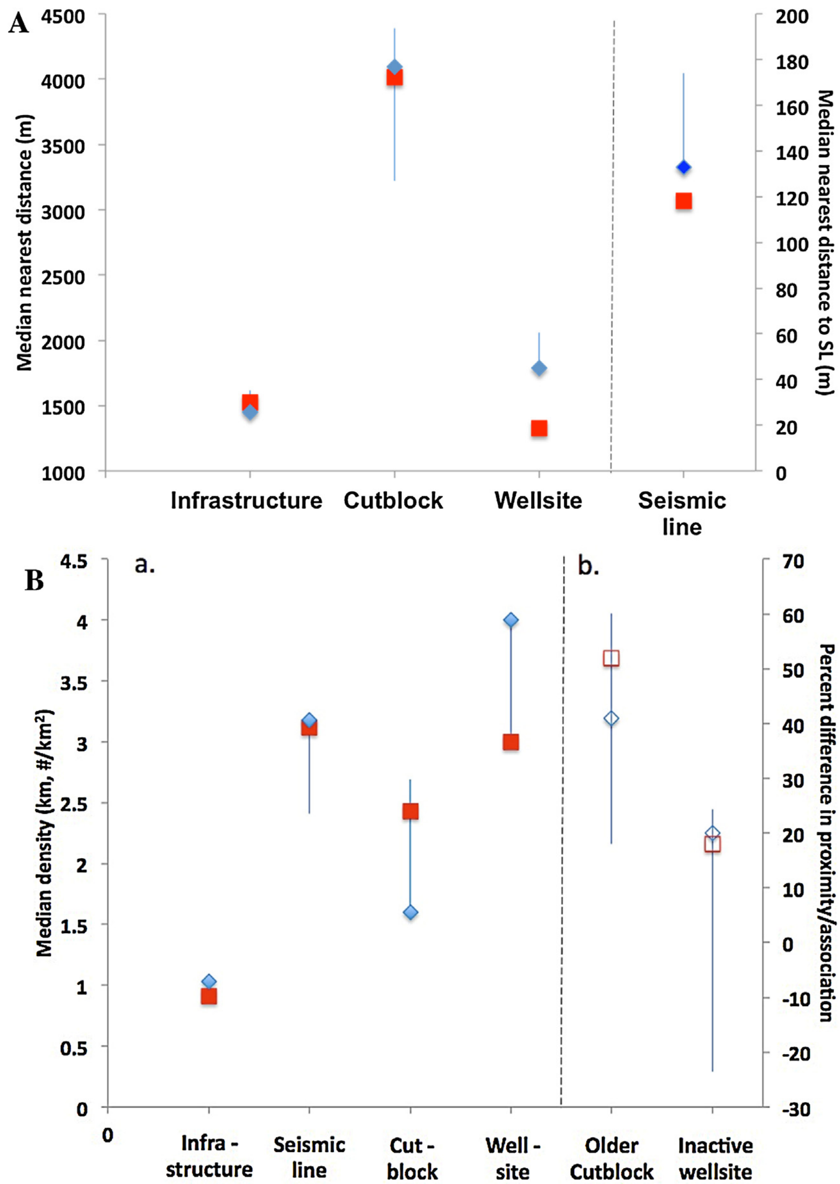

Fig. 4. Comparison of multiple patterns produced by actual and simulated caribou. (A) Median nearest distances (m) to industrial features between agents from the optimized LOF-scenario (diamond) and from actual caribou (square). Note: second *y*-axis corresponds to values for seismic line (SL). (B) Comparison of (a) median densities of industrial features (km, wellsite number) within 1 km^2 and (b) percent difference in: (i) proximity to older cutblocks (vs. younger) and (ii) frequency of association with inactive wellsites (vs. active), between agents from optimized LOF-scenario (diamond) and actual caribou (square). Bars represent output range of values from the twelve LOF-scenarios tested.

energy loss was slightly higher when compared to the null ABM model; Table 2). Furthermore, no one industrial feature can explain anti-predator responses in caribou; the industries interact in a way to produce non-independent effects, as can be evidenced in their ability to jointly and integratively impact a variety of caribou habitat-selection responses even though predators are not explicitly modeled in the ABM. These findings are comparable not only to LS-specific caribou, but are also consistent with what is known about caribou sensitivities to industrial features in general. They contribute to our knowledge of how anthropogenic effects impact an animal's movement ecology and how they perceive their habitat. These points are discussed below.

While being primarily validated by 13 GPS-collared caribou data, the results of the caribou ABM sensitivity analysis are nonetheless encouragingly consistent with statistical findings from other habitat-selection studies of boreal caribou: our agent represents an individual animal that has chosen a particular location from the available habitats that occur within its home range (known as 3rd order, finer scale resource selection). In this habitat, agents were found to be less responsive to cutblocks and active wellsites than to linear features. These results coincide with two independent resource-selection studies at a herd-specific and regional (western Canada) levels. In the former, Neufeld (2006) found caribou occupancy in winter habitat was influenced only somewhat weakly by the proportion of 1 km^2 area that is cutblock, was not affected by wellsite distance or density, but was strongly influenced by the distance to seismic lines (but not density). Similarly, DeCesare et al. (2012) found woodland caribou herds in western Canada to be responsive to cutblocks at first- and second-order selection – occupying their general geographic and home ranges, respectively. Within an individual caribou's home range, caribou were sensitive to lineal density (when compared to forestry cutblocks) at third-order caribou selection (i.e., the individual). Our comparable model results can be explained by

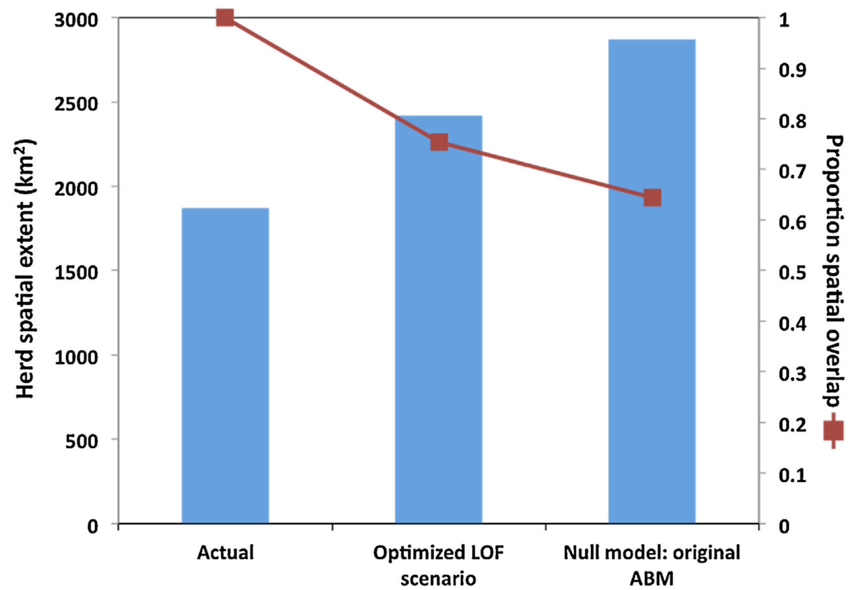

Fig. 5. Optimized-LOF robustness. Comparison between (i) left *y*-axis: spatial extent of actual caribou, agents from the optimized LOF-scenario, and agents from the original ABM where agents did not discriminate between industry features (i.e., the null model), and (ii) right *y*-axis: the proportion of overlap of spatial extents with that of actual caribou.

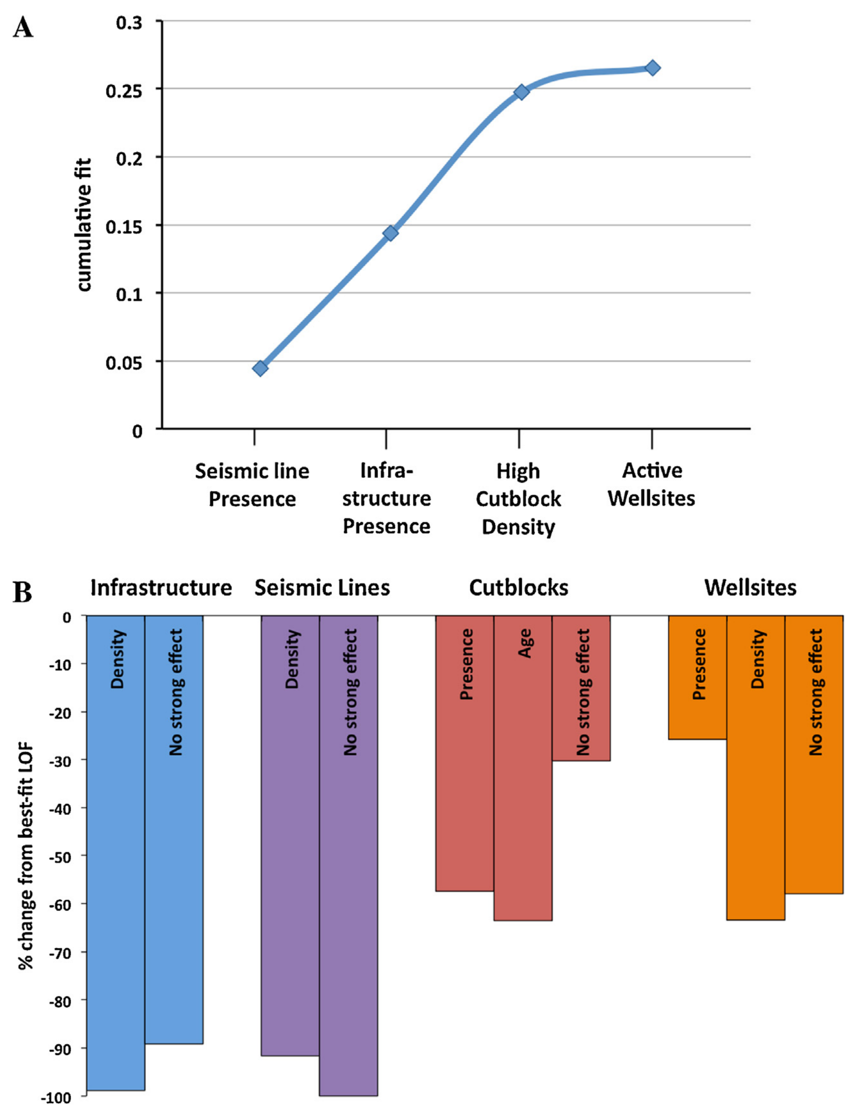

Fig. 6. (A) Cumulative contribution of optimized-LOF industry features to overall model fit (D = 0.27). (B) Relative sensitivity of industrial-feature attributes. Percent change from optimized-LOF fit when alternative attributes are deliberately selected one at a time. Fit estimates are calculated post hoc in the optimization procedure in JMP (Appendix C).

examining the spatially explicit distribution of agents: high cutblock density formed a contiguous movement barrier in the northern portion of the herd range (Fig. 3). Very few agents were found deep within the cutblocks despite their pervasiveness due to high predation risk coupled with low forage. Agents instead spent more of their time in the preferred central area, and were exposed to a higher frequency of occurrence of linear features (and to a lesser extent wellsites), thereby demonstrating high sensitivity to them, as these were the features most often encountered.

A range of models exists to describe wildlife spatial distributions and movements, from resource selection functions to sophisticated state-space models (Schick et al., 2008; Bauer and Klaassen, 2013). These models can produce (and have) similar results as agent-based models. Non-statistical, mechanistic approaches like ABMs offer additional advantages: they can generate spatially explicit landscapes of actual caribou habitat use – a necessary element for conservation planning of critical habitat (McLane et al., 2011). Next, because they explicitly incorporate evolutionary and ecological processes governing decision rules, they can determine the behavioral process of choosing habitat (i.e., habitat *selection* vs. use; Beyer et al., 2010). This approach is resultantly freed from the assumptions underlying traditional species-distribution models that species are at equilibrium with the environments, and that the data used to train (fit) the models are representative only of conditions to which the models are already statistically associated (Elith et al., 2010). Resultantly, ABMs can be fit to conditions which are anticipated. In addition, and as employed in this paper, when coupled with a scenario-sensitivity design, an ABM can be used as an inverse modeling method to infer knowledge about underlying processes from data using meaningful patterns for validation (Schröder and Seppelt, 2006; Topping et al., 2012). Lastly, from a technical perspective, most statistical methods and parameter-sensitivity designs incorporate mainly 2-level interactions or use a one-at-a-time (OAAT) factor approach, respectively, where parameter values are modified one by one while others are kept constant. While an appropriate technique for few variables with little expected variability in parameter values, it does not allow for in-depth exploration of factor space nor does it account for their simultaneous variation, and therefore non-independent effects cannot be effectively examined. Our multi-response optimization approach was able to isolate and jointly test the effects of one stressor from and against the other (Dion et al., 2011), and also prevent over-fitting. Because not any one pattern response is being fit perfectly (although it can happen), and instead all are collectively optimized, the generalization capacity of the model will not be lost and will be labile enough to be easily transferred to other situations – in particular, future scenarios of industrial development within LS.

Agent-based models can further be used as an experimental system in which questions regarding the effects of contrasting environments on animal distribution patterns can be evaluated (Jepsen and Topping, 2004); for example, geographical (e.g., physical connectivity) vs. environmental (e.g., biotic processes) predictors of space use (Semeniuk et al., 2011). First, the caribou model is structured so that agents' decisions are influenced by the landscape in terms of forage availability, travel cost, and predation risk. Next, the use of the 'no strong effect' option in the sensitivity design obliged agents to ignore industry and default instead to using habitat-mediated cues to assess their environment. Taken together, the model was therefore capable of teasing apart the confounding accessibility vs. preference/avoidance space-use of animals (Matthiopoulos, 2003). For instance, the separation distances measured between actual caribou point locations and industrial features could not be explained in our model by features simply being in areas too forage-poor or too costly to encounter – i.e., landscape configuration; otherwise, habitat characteristics alone (the default) would have been enough to explain agent distributions and their seasonal energetic losses. Similarly, the small separation distances to seismic lines still emerged (similarly to actual caribou; Harron, 2007; Fortin et al., 2013) even though agents were given the rule to minimize their exposure to them. These features are ubiquitous, and agents must encounter them as they move through their environment to feed (a top priority). Our model therefore suggests caribou indeed perceive industrial features as akin to threatening stimuli, and respond accordingly when they can afford to do so.

5. Concluding remarks

On a final note, our study emphasizes the importance of understanding how anthropogenic impacts on the landscape shape animals' perceptions of habitat quality. In general, prey respond to predation at the landscape level with temporal and spatial changes in activity and the selection of safer habitats (Peckarsky et al., 2008). Predation 'risk' is typically assessed using habitat cues rather than predator presence, and is a pervasive strategy in terrestrial predator–prey systems. A meta-analysis by Verdolin (2006) revealed habitat characteristics to have a stronger effect on prey behavior as correlates of predation risk than the presence of live predators and associated cues; and more specifically, in a study of North American elk (*Cervus elaphus*), Ciuti et al. (2012) found the effects of human disturbance on elk behavior to exceed those of habitat and natural predators. For wildlife species that rely on spatial-separation strategies to avoid predation, gauging habitats that are risky – such as the case for boreal caribou – is the first line of defense (DeCesare et al., 2010). The spatial extent of caribou agents revealed their distribution to be a consequence of risk-sensitive foraging mediated by perceived geographical-environmental constraints – a finding otherwise challenging to uncover in habitat models. Our model uniquely provides a spatio-temporal and mechanistic explanation of caribou distributional patterns: agents attempt to minimize their exposure to high predation risk areas (i.e., be 'moving away'), but only when they have attained satisfactory energy reserves. Additionally, they respond to specific attributes of industrial features, with some features like cutblocks, from their sheer open contiguousness, acting analogously to semi-permeable barriers (Bolger et al., 2008), potentially increasing exposure of caribou to other risky habitat and features, such as the predation pressure facilitated by linear structures (DeCesare et al., 2013). As such, the type of 'landscape of fear' caribou are experiencing now and under future development or mitigation will play a large role in shaping how an animal uses its habitat, how much energy it expends, and its capacity to minimize exposure to predation, thus having consequences for effective planning and interpretation of conservation measures and outcomes. By using a behavior-based ABM in combination with a validated analysis of differential landscape-risk perception, the ABM can furthermore be used to explore caribou spatial distribution and bio-energetic expenditures to future changes in the LS landscape – an asset to critical-habitat planning, and the next focus of our research.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecocom.2013.09.004.

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