Incorporating behavioral–ecological strategies in pattern-oriented modeling of caribou habitat use in a highly industrialized landscape

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A B S T R A C T

Woodland caribou (*Rangifer tarandus*) are classified as threatened in Canada, and the Little Smoky herd in west-central Alberta is at immediate risk of extirpation due in part, to anthropogenic activities such as oil, gas, and forestry that have altered the ecosystem dynamics. Winter season represents an especially challenging time of year for this Holarctic species as it is characterized by a shortage of basic resources and is when most industrial development occurs, to which caribou can perceive as increased predation risk. To investigate the impact of industrial features on caribou, we developed a spatially explicit, agent-based model (ABM) to simulate the underlying behavioral mechanisms caribou are most likely to employ when navigating their landscape in winter. The ABM model is composed of cognitive caribou agents possessing memory and decision-making heuristics that act to optimize tradeoffs between energy acquisition and predator/disturbance avoidance. A set of environmental data layers was used to develop a virtual grid representing the landscape in terms of forage availability, energy content, and predation-risk. The model was calibrated with caribou bio-energetic values from literature sources, and validated using GPS data from thirteen caribou radio-collars deployed over 6 months from 2004 to 2005. Simulations were conducted on alternative caribou habitat-selection strategies by assigning different fitness-maximizing goals to agents. The model outcomes were evaluated using a pattern-oriented modeling approach with actual caribou data. The scenario in which the caribou agent must trade off the mutually competing goals of obtaining its daily energy requirement, conserving reproductive energy, and minimizing predation risk, was found to be the best-fit scenario. Not recognizing industrial features as risk causes simulated caribou to unrealistically reduce their daily and landscape movements; equally, having risk take precedence results in unrealistic energetic deficits and large-scale movement patterns, unlike those observed in actual caribou. These results elucidate the most likely behavioral strategies caribou use to select their winter habitat, the relative extent to which they perceive industry features as potential predation, and the differential energetic costs associated with each strategy. They can assist future studies of how caribou may respond to continued industrial development and/or mitigation measures.

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1. Introduction

Woodland caribou (*Rangifer tarandus caribou*) in Alberta are currently designated as *threatened* under Alberta's *Wildlife Act* due to their reduced distribution, a decrease in the number and size of populations, and threats of continued declines associated with human activities (ASRD, 2010). 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. A subset of anthropogenic activities, specifically those of resource-extraction industries such as forestry and oil and gas, affect caribou habitat use in three generally accepted ways. First, they remove large tracts of relatively low-productivity mature to old conifer forests and forested peatlands (i.e., cutblocks), which contain lichens, the primary winter food source for caribou. Second, they increase the predation risk via apparent competition (DeCesare et al., 2010a), and by facilitating hunting and/or searching

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efficiency of predators via linear features such as roads, pipelines, and seismic lines (Dyer et al., 2001). Finally, caribou can perceive human activities and anthropogenic features both as disturbance and predation-risk events, either directly through physical foot-print, or indirectly through sensory disturbance (Frid and Dill, 2002; Vistnes and Nellemann, 2008). Caribou respond accordingly by attempting to minimize their exposure to them, similarly as they would to natural predators (Smith et al., 2000; Dyer et al., 2001; Polfus et al., 2011).

Caribou are also susceptible to harsh environmental conditions. Winter represents an especially challenging time of year as over-wintering caribou face the energetic costs of food availability, periodically harsh environmental conditions, predator avoidance, and disturbance. Specifically, the availability of terrestrial lichen, the main winter food source, is constrained to specific habitat requirements (Dzus, 2001) and is energetically costly to access (i.e., cratering through snow). Next, the minimization of energetic costs in winter appears important for caribou, at times at the expense of increased predation risk, as females are willing to use high-risk areas to minimize travel costs (Johnson et al., 2002). Finally, winter is the time of year when most industrial development occurs in the study area (Neufeld, 2006), and as caribou are sensitive to this form of disturbance, they may experience energetic costs in industrial-feature avoidance (Bradshaw et al., 1998). These energetic costs during winter have the ability to affect female caribou reproduction since maternal condition has a direct impact on fetal viability and subsequent calf survival (Post and Klein, 1999). Therefore, caribou, in particular females, need to trade off decisions between energy management, foraging efficiency, and predation risk, and these choices influence their habitat selection, movement, and reproduction.

Critical habitat for caribou in Canada has been defined as the percentage of range needed to maintain or return that herd at or to a self-sustaining rate (Environment Canada, 2011a). While the impacts of habitat change and industrial features and activities on caribou have been studied in terms of spatial distribution (Fortin et al., 2008), physiological stress (Wasser et al., 2011), energetic costs (Bradshaw et al., 1997), and population viability (Weclaw and Hudson, 2004), the behavioral mechanisms and strategies caribou use when navigating their landscape, and how these are influenced by resource-extraction industries are less clear. Most studies have not explicitly incorporated how caribou concurrently make behavioral tradeoff decisions that are motivated by both the animal's internal state and external environs. Indeed, the Canadian government's determination of critical habitat is not restricted simply to an explicit geographical delineation, but instead ties the designation of critical habitat to a geographic *state* that has a likely probability of supporting a local self-sustaining population (Environment Canada, 2011a).

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 (Semeniuk et al., 2011). By considering the actions of the individual, such information aids in quantifying animal–habitat relationships, describing and predicting differential space use by animals, and ultimately identifying habitat that is important to an animal (Beyer et al., 2010). To address the issue of understanding caribou habitat selection in the face of high-density industrial development, we have developed a spatially explicit, agent-based model (ABM) to simulate winter habitat selection and use of caribou in west-central Alberta. The use of an ABM for our research is advantageous since dynamic interplay between agents and their environment is readily accommodated, realistic conditions can be approximated (such as movement costs across the landscape), and hypothetical scenarios can be
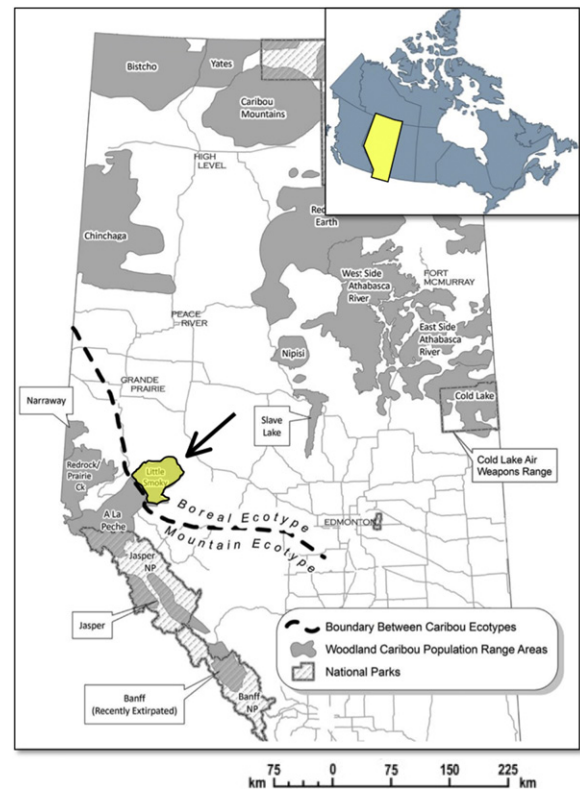

Fig. 1. Little Smoky caribou range (indicated by the arrow) situated amongst other Albertan herds (shaded grey) within the province of Alberta, Canada (ASRD, 2010).

simulated. These models are also amenable to tests of robustness and sensitivity (Grimm and Railsback, 2005). Our caribou ABM incorporates two critical ecological theories involved in habitat selection: animal movement ecology and behavioral ecology. Agents are given fitness-maximizing goals (i.e., survive to reproduce) allowing the model to be used to understand the processes that govern animals' movement, distribution, and selection, and therefore to predict how they might respond to habitat alteration and the presence of industrial features.

2. Methodology

The caribou ABM comprises two main components: (1) a landscape representation of the caribou herd, and (2) caribou agents and their decision-making heuristics. In this section, a description of the study area and datasets is first provided, followed by a presentation of the model parameterization, the simulation framework, and the validation approach.

2.1. Description of the study area and datasets

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 3100 km^2 (Fig. 1). The LSM range has the highest level of industrial development of any caribou herd in Canada, with 95% of its range in proximity (500 m buffer) of anthropogenic activities (Environment Canada, 2011b). The site of four forestry management agreements and numerous petroleum-company operations, 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 (WCCLPT, 2008). 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 (Robichaud, 2009). The area of interest in this project is the official political and biological range delineation of the Little Smoky herd by the Alberta Fish and Wildlife Division (ASRD, 2010). Because the Little Smoky is such a dynamically changing landscape due to industrial practices, 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.

All geographic datasets used in the study are described in detail in Hebblewhite et al. (2010). A major source of data consists of radio-collared GPS location data of Alberta caribou. A total of 5225 location points were obtained for 13 female individuals from the Little Smoky in winter (November–April) 2004–2005. Using caribou GPS point samples, the spatiotemporal distribution of each caribou was built and stored within an ArcGIS database as timestamps corresponding to a 4-h interval. Additional datasets include vector representations of roads, pipelines, seismic lines, and well sites valid to the year 2005, and a raster-based elevation model (DEM) and land-cover map both at a spatial resolution of 30 m. The land-cover map is based on Landsat 5TM imagery of 2005 and includes 12 classes that are deemed to be biologically relevant to woodland caribou (Table 1). For inclusion in the ABM model, all vector layers were rasterized to a resolution of 45 m, with the land-cover map and DEM resampled to the same resolution. The 45 m resolution chosen represents an optimization of computational performance while reflecting the biologically realistic size of the foraging patch of caribou (Bailey and Provenza, 2008). Furthermore, because actual caribou are sensitive to industrial features up to 250 m and 1 km away depending on their type (Dyer et al., 2002), this spatial resolution has no major biasing effect on the caribou agent's ability to perceive them.

For integration with the ABM, four raster maps were generated from the geographic datasets to represent the physical environment where the caribou agents are located: (1) a forage-availability map, (2) an energetic-content map, (3) a predation-risk map, and (4) a digital elevation model. A value of lichen forage availability was associated to each of the land-cover classes, the ranking of which (0–5, with 5 representing the highest forage) was determined directly from multiple literature sources (Edmonds and Bloomfield, 1984; Weclaw and Hudson, 2004; Dunford et al., 2006; Neufeld, 2006; Metsaranta, 2008). 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 (Holleman et al., 1979; Kumpula, 2001), 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 0–5 (with a score of 5 denoting the highest risk). These scores were also derived from the literature (Neufeld, 2006; Smith et al., 2000; Dyer et al., 2002; Weclaw and Hudson, 2004; Sorensen et al., 2008; Table 1). Similarly to the land-cover dataset, the industrial-features dataset was assigned forage-availability and energetic-content, and randomly allocated a medium-high predation risk score (i.e., a value of either 4 or 5; Table 1). This medium-high allocation randomly assigned is based on the premise that caribou are known to be influenced by industrial features (Vistnes and Nellemann, 2008) and respond accordingly. At this point, however, we took a conservative approach, and did not differentiate between the relative influences of forestry vs. petroleum industry practices, instead treating both industry types similarly (medium-high). Finally, we term caribou responses as being 'predation'-sensitive to imply that caribou are likely to have similar responses between landscapes they perceive as risky and features they perceive as risky (whether it is due to a higher predation risk, or a disturbance; Frid and Dill, 2002).

To provide an environment to the agents and allow their movement from one cell to the next cell, a virtual grid was overlaid on the four maps described above. 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). Whereas forage-availability and predation-risk scores are fixed (and it is just the agent's willingness to respond to them that varies), the energy content of the cells is depleted (and hence varies) when agents forage. Sources of biological information necessary for the caribou ABM parameterization include caribou agents' bio-energetic 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 following section.

2.2. Model conceptualization and parameterization

The underlying premise of the model 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. Specifically, the caribou agent can balance its needs to meet its 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 predation risk, for which it must also balance, since relatively safer locations are not always the most profitable.

Fig. 2a 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 Fig. 2a). 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, ruminates, 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 parameterize and calibrate the model.

2.2.1. Assessing states (A)

2.2.1.1. Daily energy requirement.
A caribou's minimum daily energetic requirement (DER) ranges between 22 and 33 MJ day^{-1}, according to different literature sources (McEwan and Whitehead, 1970; Boertje, 1985; Kumpula, 2001). 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 h have passed, DER is reset to zero, regardless of whether the minimum daily threshold was met. The agent can carry over 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; Parker et al., 2005). These restrictions were tested in the model and we found that average daily intake rates fell well within the threshold range. Our agents do not die from starvation since predation is the main source of mortality, which is also in accordance with the survival of all the actual caribou used for comparative purposes during the 2004–2005 winter. We do not assume that increased energetic expenditure may render caribou more vulnerable to predation (McLellan et al., 2011).

Table 1
List of land-cover classes and industrial features in the Little Smoky region. Each land cover and industrial feature is assigned a value for its food availability, energy content, and predation risk attributes. These values are used in the ABM, with risk randomly assigned either 4 or 5 to industrial features.

	Lichen availability[a]	Energy content (MJ)[b]	Predation risk[c]	Mean elevation (m)
Land cover[d]				
Closed conifer forest	5	1.14	1	1178
Open conifer forest	4	0.86	3	1194
Mixed forest	2	0.29	3	1086
Deciduous forest	1	0.15	4	1030
Muskeg/wetland	3	0.58	2	1139
Shrub	1	0.15	4	1144
Herb	1	0.15	4	1146
Barren	0	0	5	1179
Water	0	0	5	1158
Glacier	0	0	0	1175
Forest cutblocks	1	0.15	4 or 5	1170
Burn	0	0	4 or 5	1231
Industrial features[e]				
Roads, seismic lines, pipelines	1	0.15	4 or 5	1110
Well sites	1	0.15	4 or 5	1000

[a] Edmonds and Bloomfield (1984), Weclaw and Hudson (2004), Dunford et al. (2006), Neufeld (2006), Metsaranta (2008). Values are fixed.
[b] Holleman et al. (1979), Kumpula (2001). Values change independently of lichen-availability scores as the agent consumes the resource.
[c] Neufeld (2006), Smith et al. (2000), Dyer et al. (2002), Weclaw and Hudson (2004), Sorensen et al. (2008).
[d] Original raster maps: McDermid et al. (2009), Hebblewhite et al. (2010).
[e] Original vector maps: Hebblewhite et al. (2010).
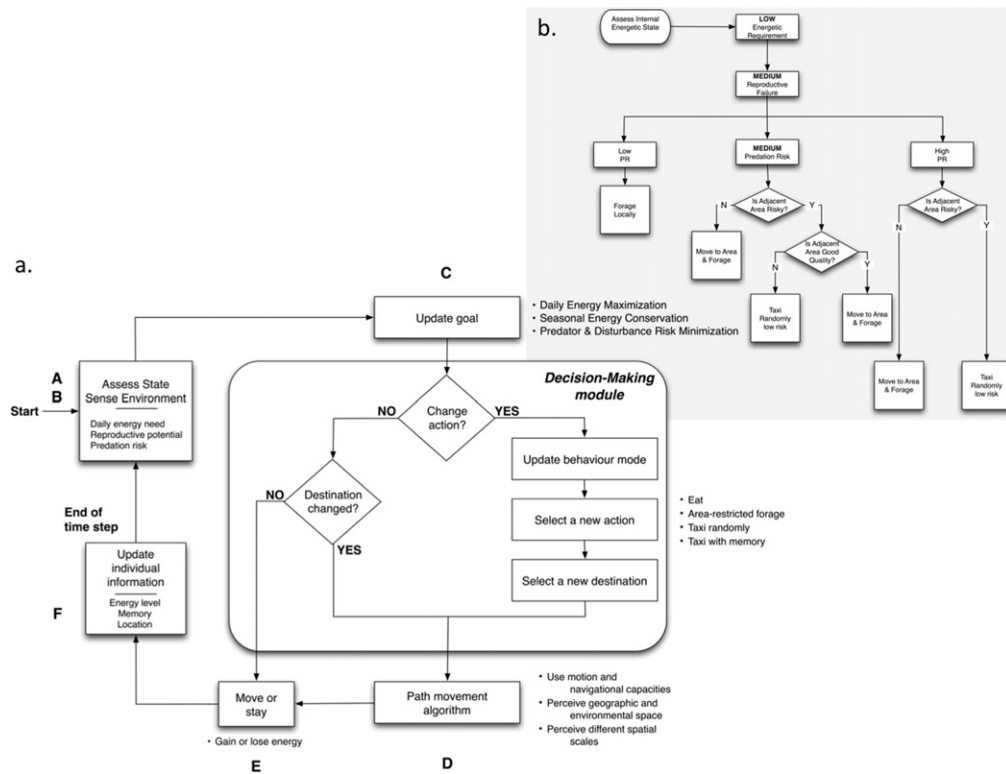

Fig. 2. (a) Steps involved in the caribou agent's decision making (modified from Chion et al., 2011); and (b) flowchart example of the behavioral tradeoffs made by a caribou agent when it has met its daily energetic requirement, is intermediately energetically stressed long term, and faces different levels of predation risk.

2.2.1.2. Reproductive energy requirement. Caribou lose on average 15% of their autumn mass over winter, via fat and protein catabolism (Bradshaw et al., 1998). A loss greater than 20% of body mass 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 and 947 MJ, respectively, for the winter (see Bradshaw et al. (1998) 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:

$$\text{net energy} = \text{cumulative energy lost} - \text{cumulative energy gained} \quad (1)$$

$$\text{projected loss} = \left(\frac{\text{net energy}}{n_t}\right) \times t_{\text{total}}, \quad (2)$$

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 (Mangel and Clark, 1986; Railsback et al., 1999), 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 'Behavioral Strategies' below).

2.2.2. 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 and 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 (Dyer et al., 2002; Weclaw and Hudson, 2004), and predator perception ranges of ungulates (Laporte et al., 2010).

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 (Johnson et al., 2002). 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.

2.2.3. Behavioral strategies (C)

The baseline model, which we term the 'Energetics and Predation' 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 when above 29 MJ day^{-1}. 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 behavior 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 – short-term (i.e., daily), predation risk becomes irrelevant (even if high) 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, it will attempt to travel at lowest cost (i.e., using minimal elevation); if the agent is not stressed, it will travel in relatively safe locations.

(4) The more energetically stressed, the less willing an agent is to taxi long distances.
(5) An agent will be risk adverse at low to medium daily energetic stress unless it is simultaneously highly stressed long-term. Then it will switch to more risk-prone behaviors (i.e., seek out profitable patches before safe patches in which to forage).
(6) An agent will chose to rely on previously visited sites in which to forage (i.e., access memory) instead of feeding immediately when either: (a) the surrounding predation risk is medium and/or low, both the current and adjacent sites are of low forage availability, and the agent is intermediately energetically stressed, or (b) predation risk is high, no adjacent safer sites are present, and the agent is intermediately energetically stressed.
(7) An agent foraging will not only reduce the energetic content of the cell it occupies, but the agent will no longer feed within it during the same feeding bout. If all neighbouring cells have been used, the agent will then search for a cell within a 450-m radius in which to feed that is of higher energetic content. If none is available, the agent will then randomly recall a high forage-availability cell from memory, and taxi towards it.

These strategies are based on both general principles of behavioral ecology (e.g., foraging-predation risk tradeoff; Lima and Dill, 1990), and literature sources of ungulate movement ecology (e.g., memory and feeding-site selection, Bailey and Provenza, 2008; interplay between internal state and movement decisions, Morales et al., 2005; switches in movement modes, Owen-Smith et al., 2010; Fig. 2b).

2.2.4. 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 and 4 cells at a time; and
(4) revisiting a previously visited patch randomly drawn from memory. If highly stressed, patch chosen is at the same or lower elevation than the agent's current position. This movement traverses 2–4 cells per time step, and the agent also 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 (Owen-Smith et al., 2010). Furthermore, agents do not have perfect knowledge about their landscape. Agents employ a correlated habitat-dependent walk (Kramer-Schadt et al., 2004; Börger et al., 2008) 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 traveling distance of habitat selection for lichen (6 km; Mayor et al., 2007). Lastly, when agents access their memory, they randomly

pick a location that has been stored between 7 and 45 days prior (see 'Memory' below).

2.2.5. Gaining and losing energy (E)

2.2.5.1. Energetic intake per time step.
Caribou consume anywhere between 0.88 and 3.52 kg of lichen per day (Holleman et al., 1979; Kumpula, 2001). Because caribou spend between 50% and 88% of their day actively foraging (Rominger et al., 1996; Kumpula, 2001), this corresponds to caribou consuming, on average (i.e., 69%, or 16.5 h day^{-1}), 0.027–0.106 kg/30 min. (the model's time step).

Using a 10.8 MJ kg^{-1} conversion rate of metabolizable energetic content of lichen (Kumpula, 2001), caribou are assumed to obtain between 0.29 and 1.14 MJ of energy per foraging bout. The amount gained was 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, 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 × 45 m area in one half hour. The depletion is, however, permanent, since lichen re-growth rates are slow, and can take up to 4 months to recover, doing so during summer months only (Gaio-Oliveira et al., 2006).

2.2.5.2. 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; Stuart-Smith et al., 1997). 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.

2.2.6. 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 (Van Moorter et al., 2009). Caribou agents store these patch locations for up to 45 days (reference memory) as a moving window, and subsample locations no fewer than 7 days after 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 (Wolf et al., 2009). Caribou agents only access their memory when no suitable forage and safe areas are available at both the intra- and inter-patch levels *and* when they are energetically stressed. This rule accommodates memory-based movement, known to play a role in ungulate systems in which resources are predictable in time and space (Mueller and Fagan, 2008). It is also based on the information primacy model of exploratory and foraging behavior, which posits that if hunger is great, the animal will choose to search familiar locations that

have in the past reliably yielded food rather than explore unfamiliar locations (Inglis et al., 2001).

The ABM was calibrated 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; walking costs (not accounting for the additional expenditure due to uphill movement and/or in snow) are 1.81 times higher (Fancy and White, 1985). Using these established ratios, we used a variety of energy values in the calibration process to represent the resting metabolic rate. The final values chosen for all scenarios in the ABM were based on whether each produced simulated energetic outputs consistent with three criteria: (1) the daily energy gain by the agent is within known reported ranges (22–33 MJ day^{-1}, McEwan and Whitehead, 1970, Boertje, 1985); (2) the daily energetic expenditure approaches that which has been reported for free-living R. tarandus during winter (28.7 MJ day^{-1}; Gotaas et al., 2000); 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 (Rominger et al., 1996; Kumpula, 2001).

In each of the scenarios, agent caribou had a median daily energy intake of 22–28 MJ day^{-1} (within reported literature values), and experienced a daily loss of energy between 26 and 28 MJ day^{-1}. These values of intake and expenditure are sufficient for body maintenance at the standard metabolic rate (SMR: 403 kJ kg$^{-0.75}$ day^{-1}; Fancy and White, 1985; Barboza and Parker, 2006). Lastly, the average proportion of time agents spent foraging ranged from 65% to 77% (Table 3). 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 for each scenario tested, we felt confident that our model was sufficiently calibrated.

2.3. Simulation framework

Because energy acquisition, energy conservation, and predation-risk minimization are issues which researchers deem important to caribou in winter (e.g., Parker et al., 2005; Cameron et al., 1993; Bradshaw et al., 1998), we have chosen to test five main behavioral strategies with alternative hypotheses in the caribou ABM, beginning with the 'Energetics and Predation' model and then decomposing the framework into biologically relevant alternative strategies:

(1) The caribou agent's goal is to find an optimal balance between its daily energetic requirements (D), its longer-term reproductive energy requirements (R), and its predation-risk minimization (P). Known as the 'Energetics and Predation' scenario (DRP);

(2) Long-term reproductive requirements are irrelevant. Responses to perceived predation risk are unchanged. Known as the 'Energy Acquisition' scenario (DP);

(3) Reproductive requirements take precedence when the risk of reproductive failure is high, regardless of daily requirements. Responses to perceived predation risk are unchanged. Known as the 'Energy Conservation' scenario (RP);

(4) Industrial features are not deliberately avoided. Known as the 'Predation-insensitive' scenario (DR);

(5) Minimizing risk takes precedence over maximizing daily energy and minimizing reproductive energy loss. Known as the 'Predation-hypersensitive' scenario (P).

Table 2
Values for parameterizing and calibrating the caribou agent in the ABM.

Caribou agent parameters	Value	Source	Notes
Weight	132 kg	Bradshaw et al. (1998)	
Daily energy requirements	22–33 MJ	McEwan and Whitehead (1970), Boertje (1985), Kumpula (2001)	Used for verification of model calibration
Expected reproductive energy loss	710–947 MJ	Bradshaw et al. (1998)	
Daily energy expenditure in winter	738 kJ kg$^{-0.75}$ day^{-1}	Gotaas et al. (2000)	28.7 MJ day^{-1} for a 132 kg caribou; used for verification of model calibration.
Percent time spent foraging	50–88%	Rominger et al. (1996), Kumpula (2001)	Used for verification of model calibration.
Incremental costs of activities over resting metabolic:		Fancy and White (1985), Boertje (1985), Fancy (1986)	Model calibrated with 520 kJ kg$^{-0.75}$ day^{-1} for foraging, 653 kJ kg$^{-0.75}$ day^{-1} for walking.
Foraging	1.44		
Walking	1.81		
Additional movement costs:			
Uphill	3.640 kJ kg^{-1} km^{-1}	Gustine et al. (2006)	
Downhill	1.293 kJ kg^{-1} km^{-1}	"	
Horizontal high elevation (>1185 m)	2.64 kJ kg^{-1}	Boertje (1985), Gustine et al. (2006)	
Horizontal low elevation	1.72 kJ kg^{-1}	"	
Cratering costs:			
High elevation	3.5 kJ kg^{-1} × h	Fancy (1986)	
Low elevation	1.9 kJ kg^{-1} × h		
Memory:			
Reference	45 days	Unpublished data	
Working	7–45 days, median 13	Wolf et al. (2009), unpublished data	
Range perception:			
Forage – intrapatch	45 m		
Forage – interpatch	450 m	Johnson et al. (2002)	Known as 'area restricted search'.
Forage – taxi	Up to 6 km	Mayor et al. (2007)	
Predation – intrapatch	500 m	Dyer et al. (2002), Weclaw and Hudson (2004)	
Predation – interpatch	1 km	Laporte et al. (2010)	

Table 3
Comparison of calibration parameters between literature-sourced caribou bio-energetic values and the simulated output of five alternative behavioral-strategy scenarios.

	Actual values	Energetics and Predation (DRP)	Energy Acquisition (DP)	Energy Conservation (RP)	Predation-insensitive (DR)	Predation – hypersensitive (P)
Median daily energy gain (MJ, quartiles)	22–33	25.8 (25.5–25.9)	25.5 (24.3–25.7)	25.6 (23.6–25.7)	29.2 (29.1–29.4)	22.2 (21.9–22.4)
Mean daily energy loss (MJ, ±SD)	−28.7	−28.1 (0.65)	−28.1 (0.64)	−26.4 (0.16)	−25.9 (0.55)	−27.8 (0.51)
Percent time spent foraging (%, range)	50–88	76.9 (62–95)	69.6 (58–84)	71.2 (61–93)	74.6 (63–94)	64.9 (54–85)

For simplicity, we use the term 'predation' to denote caribou perception of landscapes and features perceived to be of high risk and of disturbance, as responses are assumed to be similar. In the scenario 'Energy Acquisition', the agent does not consider its reproductive energy at all, and attempts to maximize its daily energetic requirements while minimizing its risk. Essentially, the agent ignores the cumulative energy lost throughout the simulation, and its actions are devoted to foraging in its immediate or adjacent environs, or taxiing to new locations, depending on the quality of the surrounding area and/or perceived risk. In the 'Energy Conservation' scenario, minimizing reproductive failure takes precedence. Accordingly, a high reproductive failure value (i.e., a projected value of greater than a 868 MJ loss) will default the agent into the immediate action of either foraging straightaway, or moving to an adjacent area to forage depending on the degree of predation risk, regardless of the current daily energy already accumulated. In these two scenarios, predation risk is given consideration depending on the interaction of the level of risk and how energetically stressed the agent is. With the 'Predation-insensitive' scenario, the agent does not perceive industrial features as being any more risky than that of the surrounding environment. As such, industrial features take on the predation risk value of their immediate neighbours: a cutblock reverts to a predation risk score of 1 (equivalent to closed conifer forest) but retains its low forage availability, and a linear feature (one pixel wide, but many pixels long), takes on the majority value of its eight neighbours). Agent rules remain unchanged. Lastly, in the 'Predation-hypersensitive' scenario, the agent concerns itself with minimizing predation risk only, and assumes that a minimal daily-energy gain is sufficient and that reproductive loss is not an issue: Resultantly, the agent is driven to reach its daily minimum energetic requirement only. Once having accumulated 22 MJ or more, it concerns itself with minimizing risk. However, if the degree of risk is high, the agent will ignore its current energy level (unless it is excessively low). Despite the different weight an agent accords to a behavioral strategy and which one takes precedence, in all of the scenarios tested

the agent will have access to the four path-movement behaviors that are available in the 'Energetics and Predation' scenario, if necessary: local foraging, area-restricted search, random taxiing, and accessing memory.

The model is run with one agent. The drastically reduced population of LSM 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. Each caribou agent is assumed to be 132 kg in weight, pregnant, and expected to lose mass over the course of winter (Bradshaw et al., 1998). 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. Because caribou have distinct summer and winter habitat requirements (including forage), the agent also begins the simulation with 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 the model outputs, runs are replicated five times per 13 'caribou', for a total of 65 runs per scenario. The simulation results correspond to the average and 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 × 1619 (45-m) cells). The time and areal step are appropriate temporal and spatial resolutions to capture the variability of foraging behaviors characteristic of ungulates at the spatial level of the food patch (Owen-Smith et al., 2010). Important outputs of the model include the spatial distribution of the agent, 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 the cumulative amount of energy lost at the end of the simulation. 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; freely downloadable from http://ccl.northwestern.edu/netlogo/download.shtml), and verified for proper programming functioning through progressive debugging and uncertainty testing.

2.4. Model validation

Our ABM is validated using a pattern-oriented approach that involves comparing model outputs with observed data using multiple patterns across different scales. This protocol is based on the assumption that patterns are both the defining characteristics of a system and are indicators of essential underlying structures and processes (Grimm et al., 1996). By observing multiple patterns at different hierarchical levels and spatiotemporal scales, POM evaluates model behavior and reduces parameter uncertainty. The greater the number of real world patterns the model can predict simultaneously the greater the confidence in the model (Grimm and Railsback, 2005; Topping et al., 2010).

Several metrics were used to compare simulated and observed patterns for validation purposes. These were a combination of (1) spatiotemporal patterns, and (2) spatial distribution patterns at different scales. The spatiotemporal patterns we extracted from the

Table 4
Spatiotemporal patterns observed in actual caribou used for comparison with the model outputs. *Early winter*: months of November and December. *Late winter*: months of March and April.

Spatiotemporal pattern used	Description	
Overall ranked land-cover usage (most to least) in winter	Closed conifer	(CC – 47.7%)
	Muskeg/wetland	(MW – 29.6%)
	Open conifer	(OC – 8.9%)
	Mixed forest	(MF – 5.1%)
	Cutblocks/burns	(CB – 3.7%)
	Deciduous forest	(DF – 1.7%)
	Shrub/herb	(SH – 1.7%)
	Barren	(BA – 1.5%)
	Water	(W – 0.1%)
Differences in major land-cover classes used (>85%) between early and late winter.	CC – slight decrease	(48.8–45.3%)
	MW – increase	(24.2–34.9%)
	OC – decrease	(15.0–2.7%)
Change in use of lower elevation	decreased elevation used in late winter (1211–1186 m)[a]	
Change in mean daily distance traveled	decreased step length in late winter (median 1.9–1.2 km day^{-1})[b]	
Daily step length pattern	Daily single peak of increased movement[c]	

[a] Student's *t*-test assuming unequal variances: $t = -13.25$, $p < 0.001$, $n_{early\_winter} = 2215$, $n_{late\_winter} = 2213$.
[b] Mann–Whitney $U = -9.43$, $p < 0.001$, $n_{early\_winter} = 1931$, $n_{late\_winter} = 1990$.
[c] Significant ($p < 0.001$) negative polynomial fit to the second degree of daily caribou movement displaced over a 4-h interval.

caribou GPS-telemetry data are described in Table 4. The spatial distribution patterns we used for comparison comprise: (1) the mean 100% minimum convex polygons (MCPs) for individuals (i.e., spatial extent of individuals), (2) the total MCP (i.e., for herd range), and (3) the degree of overlap in areal coverage between actual herd MCP and simulated herd MCPs (to compare agreement in space used). These validation metrics were generated from point location data of simulated and real caribou and analyzed for land cover and elevation usage in ArcGIS 9.2. Minimum convex polygons and daily step distributions were calculated using Hawth's Tools in ArcGIS 9.2. All other simulated outputs were generated by NetLogo's reporting mechanism and analyzed in JMP 8.0 (SAS Inc.).

For evaluating the different scenarios tested, the spatiotemporal patterns were compared to those of the actual caribou by a simple, summed ranking of the degree to which patterns were matched. To compare the spatial distribution patterns, we used a modified distance method, the root mean square deviance (RMSD) to compare actual field data with simulated output, and a ranking method to evaluate the overall best-fit scenario based on a total indicator function (Piou et al., 2007). The total indicator (TI) for each scenario is:

$$TI = \sum_{p=1}^{n} \frac{|Actual - Simulated_p|}{|Actual - Simulated_{Best}|},\qquad(3)$$

where p is the pattern for comparison, and Best is the pattern whose deviance from the actual value is the smallest.

3. Results and discussion

In this section we present the bio-energetic, spatiotemporal, and spatial distribution patterns that emerged from our alternate scenarios, compare and contrast the results, and discuss them in light of what is known about LSM caribou specifically, and boreal caribou, generally.
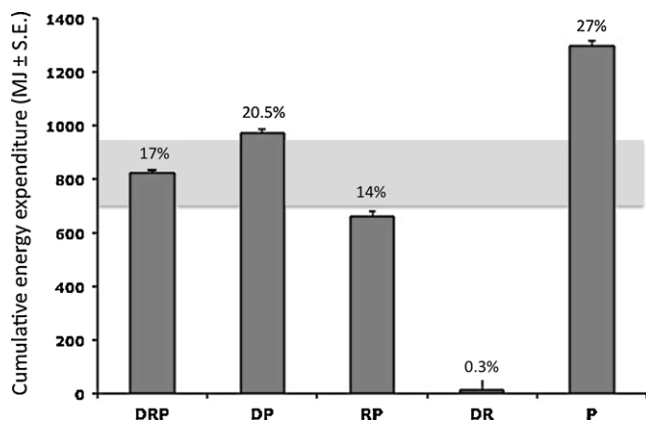
Fig. 3. Mean cumulate energy lost over winter for agents in each alternative scenario. Values over bars correspond to percent body mass lost assuming a 132 kg pregnant female. Grey horizontal bar represents range of expected cumulative energy loss for winter. DRP: 'Energetics and Predation'; DP: 'Energy Acquisition'; RP: 'Energy Conservation'; DR: 'Predation-insensitive'; P: 'Predation-hypersensitive'.
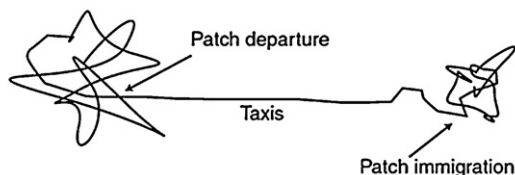
Fig. 4. Movement paths. (a) Diagrammatic representation of typical movement behavior, including: area-restricted search, patch-departure, taxis towards a new location, and patch immigration (after Schick et al., 2008). (b) Movement path of an actual female caribou from the study. (c) Movement path of a simulated caribou agent from the Energetics and Predation scenario.

3.1. Comparison of patterns

3.1.1. Pattern 1: bio-energetic

In all scenarios, agents experienced a cumulative energetic deficit by season's end, typical of over-wintering females (Fig. 3). This energetic debt did not occur via an explicit, perfunctory instruction (i.e., agents were not given rules to meet a daily energetic expenditure); but instead it is a consequence of agents choosing costly daily activities while still satisfying their daily maintenance requirements. There was a great deal of variation in the overall amount of energy lost between scenarios however, mitigated by whether the agent was given the fitness-maximizing goal of conserving reproductive energy and by its responsiveness to industrial features. This is discussed in context when considering spatial-distributional patterns (pattern 8, below).

3.1.2. Pattern 2: movement paths

Caribou agents exhibited typical movement types (exemplified in Fig. 4a) regardless of scenario (Fig. 4b,c). Many models can

reproduce small-scale high tortuosity movements interspersed by straight-line paths – e.g., correlated random walks, Lévy flights, multi-behavioral models (see Schick et al., 2008). While these movement types are coded into our model, we assigned them to specific behaviors: area-restricted foraging vs. taxiing vs. return-to-previous-site. These behaviors were, in turn, driven by the agent's internal state and perception of its environment. Therefore, the exhibition of these different movement behaviors, while available for use by agents, was not pre-determined nor guaranteed.

3.1.3. Pattern 3: land-cover use

Actual caribou did not use the land cover classes in the same proportion as their availability on the landscape. This denotes that caribou actively select habitat for reasons other than random. Simulated caribou used land-cover classes similarly to actual caribou with respect to the overall order, with the exception of the lesser used land-cover classes. Agents in the Energetics and Predation (DRP), Energy Conservation (RP), and Predation-sensitivity (P) scenarios frequented the shrub/herb land cover relatively more than deciduous forest, while the agents in the Energy Acquisition (DP) scenario visited barren areas more often than the deciduous forest. Additionally, agents in the Predation-hypersensitive (P) scenario also frequented open conifer forests less often than they did mixed forests (Fig. 5).

Caribou agents tended to overuse closed conifer forests when compared to actual caribou, due to the broad rankings of the land-cover classes. Habitat rankings were based on landscape traits that have the greatest and most consistent impact on caribou bioenergetics: forage availability, elevation costs, and predation risk. By including a more detailed friction map, for example, attributes such as slope, aspect, and terrain ruggedness, we could possibly redistribute the agent use of the landscape, making some areas more or less attractive (e.g., some open conifer areas can be ranked a 5 for forage availability), but we could also potentially obfuscate the true, underlying processes driving habitat selection and movement. This is because at present, the relationship between the additional landscape attributes and bioenergetics and/or predation risk is less clear, and the influence of these traits on caribou resource-selection functions is variable as well (Neufeld, 2006; Hebblewhite et al., 2010). Nonetheless, our agents did use the different LSM land covers in very similar relative ordering that the actual caribou did, both of which are not in proportion to the relative availability of the land-cover classes. These land-cover class choices by agents were not due to model-driven guidance, but were based on a confluence of perceived forage ability and risk and mediated by agent energetics – not on a preference for one land-cover type over another.

3.1.4. Pattern 4: relative change in use of major land-cover classes between early and late winter

Actual caribou, whether in early or late winter, use closed canopy forests with the same frequency (albeit slightly reduced in late winter) (Fig. 6). Muskeg/wetlands are used more frequently in late winter by caribou, and alternatively, the relative use of open conifer forests is reduced in late winter. The use of these land-cover classes in the simulations exhibited the same trend with the exception of the open conifer class. In the 'Energetics and Predation' (DRP) scenario, the use of the open conifer land cover did not change between early and late winter (2.91–2.96%), whereas in the Energy Acquisition (DP) scenario, the use of this class slightly increased as winter progressed (2.35–2.59%). Again, the under-use of this cover class is based on on the broad-rankings attributed to the land cover categories. Nonetheless, we do not expect future refinement of landscape attributes to affect the choice of best-fit scenario results: if anything, it would redistribute cells marked as
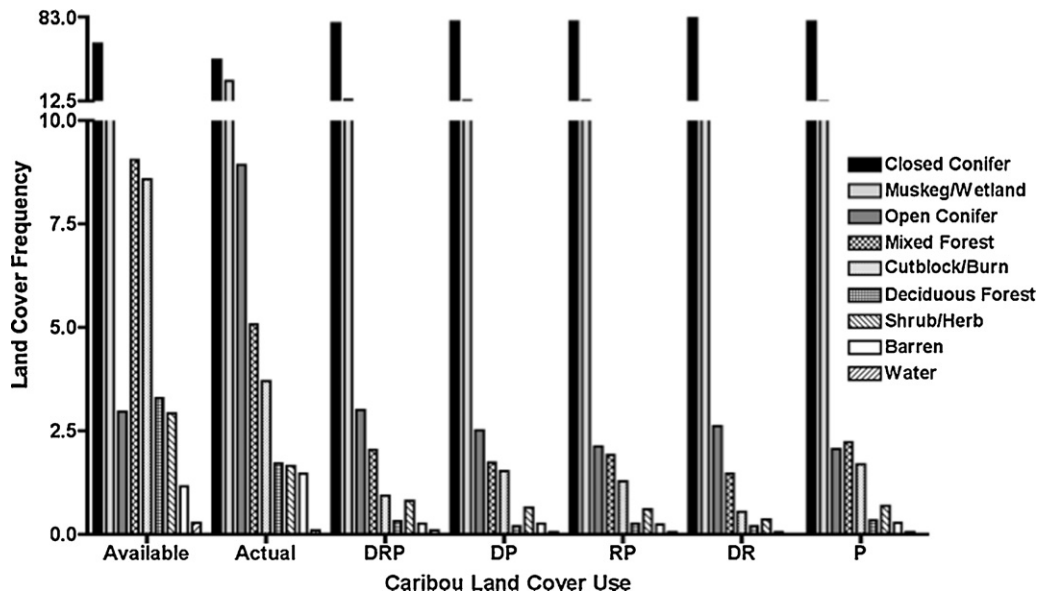
Fig. 5. Land cover used by actual caribou ('Actual') compared to the availability of land-cover classes on the Little Smoky landscape ('Available') and the simulated output of the alternative scenarios.
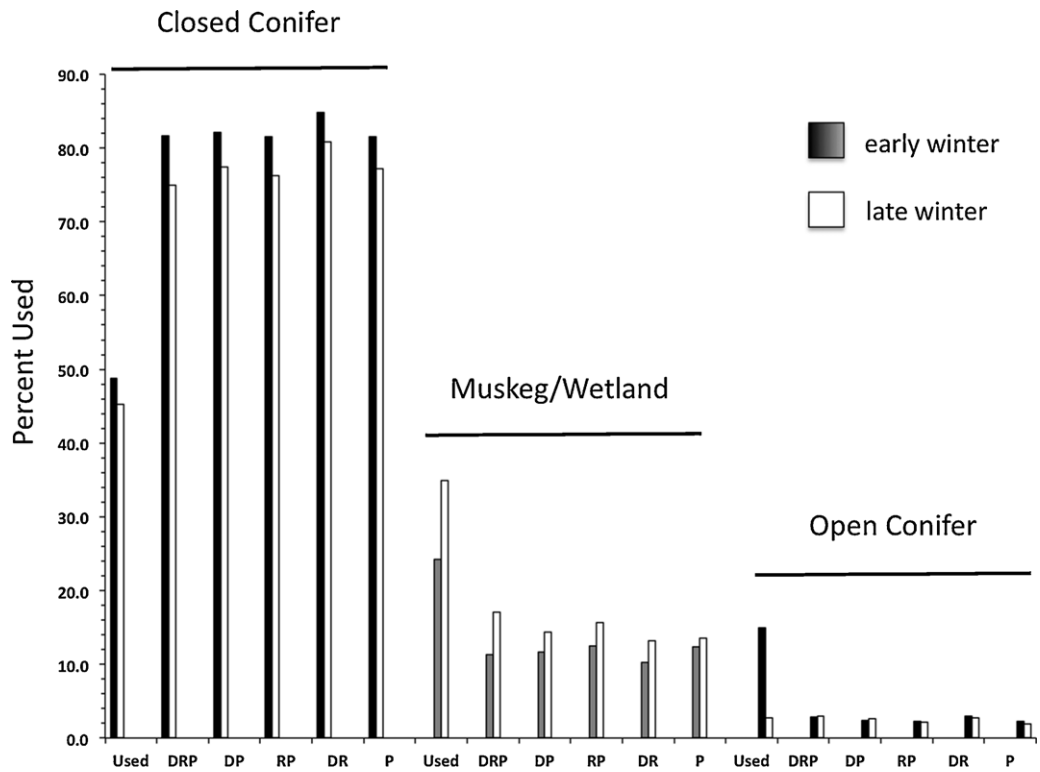

Fig. 6. Use of the three major land-cover classes in early and late winter by actual ('Used') and simulated caribou.

high forage availability without altering the underlying behavioral strategies of agents.

3.1.5. Pattern 5: change in use of lower elevations

The model reproduced the pattern that caribou in late winter use areas significantly lower in elevations, regardless of the scenario tested (Student's t-test assuming unequal variances: ALL $t < -9.0$, $p < 0.001$, $n_{early\_winter} = 23,400$, $n_{late\_winter} = 23,400$; Fig. 7a).

The use of lower elevations in late winter by the caribou agents coincides with what we observe in the actual caribou in the Little Smoky. Using lower elevations can be a function of agents increasing their use of land-cover types such as muskeg (Table 1) since resources in closed canopy forests were being actively reduced, in combination with actively selecting lower areas to conserve energy expenditure as winter progresses, regardless of land-cover class. There were no rules governing agents to frequent lower elevations (or muskeg/wetlands) explicitly in late winter. These ecologically realistic motivations produced very similar patterns to actual caribou in the LSM. Using lower elevations is a common behavioral strategy of boreal caribou, as they have been observed
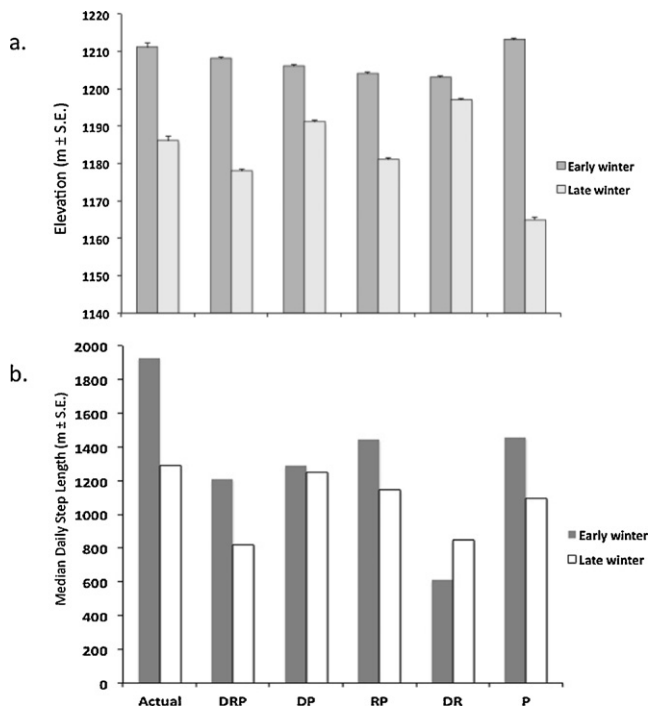
Fig. 7. (a) Mean differences in elevation used by actual and simulated caribou in early and late winter; and (b) median differences in daily step lengths by actual and simulated caribou in early and late winter.

moving across topography with lower energetic costs relative to what is available (i.e., caribou select terrain that facilitated level or downhill movements more often than uphill movements; Johnson et al., 2002).

3.1.6. Pattern 6: decrease in daily distance traveled

The scenarios diverged with respect to whether median daily distance traveled was lower in late winter than in early winter as was observed with actual caribou (Fig. 7b). The Energetics and Predation (DRP), Energy Conservation (RP), and Predation-hypersensitive (P) scenarios reproduced the expected pattern, whereas in the Predation-insensitive (DR) scenario, agents traveled more during a late winter's day. In the Energy Acquisition (DP) scenario, agents traveled similar median daily distances throughout winter. Like changes in elevation, the seasonal patterns recreated by an agent were not 'hard-coded' into the model. These patterns were a consequence of increased cumulative energetic debt based on agent decisions – not of instructions to behave differently in late winter.

The overall daily movement rates of agent caribou were lower than actual caribou in the Little Smoky. We believe that this is due to the strong positive skew of step lengths by certain individual caribou that moved great distances during a 4-h interval (e.g., 10 km). These events were restricted to isolated occurrences that may have been in response to a disturbance on the landscape or predator avoidance. We did not explicitly model predation events or indeed include wolves in the ABM as additional agents or objects for two specific reasons: we have no specific data on the encounter rates of wolves and caribou in LSM (for example, as in Whittington et al., 2011), and we do not believe that incorporating infrequent, random flight initiation behavior of agents would gain us any additional insight into the underlying impetus of caribou movement. Secondly, a caribou's 'landscape of fear' is an extremely effective operant in shaping an individual's perception of risk. This response is especially applicable in terrestrial predator–prey systems in which habitat characteristics have been shown to have a

stronger effect as correlates of predation risk than the presence of live predators (and associated cues; Verdolin, 2006). Nevertheless, the daily movement rates recorded for simulated caribou were well within the range reported in the literature for woodland caribou in winter (0.64 ± 0.13 km/day: Stuart-Smith et al., 1997; 0.9–2.5 km day^{-1}: Ferguson and Elkie, 2004; 0.47–1.2 km day^{-1}: Gustine et al., 2006). Moreover, woodland caribou both in LSM and elsewhere have lower movement rates in late winter similar to our agent caribou (Ferguson and Elkie, 2004; Gustine et al., 2006). This reduction in movement rates may be a function of increased snow depth at winter's end, or, as Bradshaw et al. (1997) also suggest, it can be an energy-saving strategy.

3.1.7. Pattern 7: single peak in daily activity

During a 24-h cycle, actual caribou steadily increased their step length from 0 h (midnight) until it reached a peak at 8h00. This pattern was reproduced to some extent by all scenarios as they, too, display a circadian movement pattern, shown by a significant negative quadratic fit to their step length data (log transformed to satisfy assumptions of normality) recorded at 4-h intervals. A closer inspection of the medians reported for each time interval reveals that only the Energetics and Predation and the Predation-insensitive scenarios produced a single daily peak. The remaining scenarios exhibited two daily peaks separated by 8 h, each (Table 5).

The display of a peak in daily activity denotes that agents are indeed engaging in various activities; a constant step-length rate instead would suggest that agents were (1) insensitive to their internal state/and or their surroundings, or (2) in the extremes of either energetic deficit or surplus. Secondly, this zenith in daily activity levels is also a realistic phenomenon, emulating actual behaviors of animals affected by circadian events. Our model therefore demonstrates both internal (i.e., model architecture) and biological robustness.

By ranking each scenario based on the extent to which they reproduce the actual, generated spatiotemporal patterns in comparison to the other scenarios, and summing these scores to produce an overall ranking, the best-fit scenario is shared between 'Energetics and Predation' and 'Energy Conservation' (Table 6).

3.1.8. Pattern 8: spatial distributions

The spatial-distribution patterns reveal the greatest pattern divergence between the alternative scenarios (Table 7). Individual spatial extent, herd range, and degree of spatial overlap with actual caribou were sensitive to the degree in which caribou were willing to trade off energetics vs. predation risk. When risk was ignored, agents did not engage in predation-sensitive foraging, and were capable of meeting their short- and long-term energetic needs. While we know this to be an unrealistic strategy, we could still expect this outcome in a herd with a small industrial footprint. Indeed, in a study of LSM that spanned from 1979 to 1984 – before the first cutblock appeared on the landscape and with very little oil and gas industrial development, female caribou had a reported annual winter range (km^2) of 147 ± 30 (Edmonds, 1988; similar to our simulated 153 km^2 in the Predation-insensitive scenario). When predation risk was considered in our ABM, caribou agents traveled in wide-ranging distances and directions as a minimization-strategy, unless their energetic needs became pressing. They were then less inclined to travel far, and relied more on returning to previously visited sites, resulting in a more restricted range that coincided with actual caribou (i.e., the Energetics and Predation scenario). This realistic strategy has a solid theoretical basis: home-range patterns have been shown to emerge with simulated animals tracking a dynamic resource landscape using a biologically plausible two-part memory system, i.e. a reference- and a working-memory (Van Moorter et al., 2009). Our ABM reached similar conclusions, thus emphasizing that the inclusion

Table 5
Median step lengths (m) at 4-h intervals. Bolding denotes the peaks.

Hour	Scenario					
	Actual	Energetics and Predation (DRP)	Energy Acquisition (DP)	Energy Conservation (RP)	Predation-insensitive (DR)	Predation-hypersensitive (P)
0	159	136	185	178	109	185
4	186	**143**	**195**	**192**	111	**193**
8	**523**	141	184	188	**113**	192
12	368	140	**194**	**190**	111	**204**
16	365	135	178	179	103	188
20	182	126	169	165	93	173

Table 6
Ranking of descriptive patterns by how closely they match actual patterns of actual caribou in LSM.

Spatiotemporal patterns						
Scenario	Land cover ranking	Change in land-cover use	Increase use of lower elevation	Decrease in daily distance	Peak in daily activity	Overall ranking (total score)
Energetics and Predation (DRP)	1	2	1	1	1	1 (6)
Energy Acquisition (DP)	2	3	1	2	2	4 (10)
Energy Conservation (RP)	1	1	1	1	2	1 (6)
Predation-insensitive (DR)	1	1	1	3	1	2 (7)
Predation-hypersensitive (P)	3	1	1	1	2	3 (8)

Table 7
Comparison of spatial distribution patterns. *RMSD*: root mean squared deviance (within scenario evaluation), and *TI*: total indicator (between scenario evaluation). The lower the scores for both RSMD and TI, the closer the simulated scenario matches the real-world patterns of LSM caribou.

Spatial-distribution patterns	Actual	Energetics and Predation (DRP)	Energy Acquisition (DP)	Energy Conservation (RP)	Predation-insensitive (DR)	Predation hypersensitive (P)
Mean individual MCP ($km^2 \pm$ S.E.)	271 (38)	297 (37)	444 (55)	446 (55)	153 (19)	458 (57)
Herd MCP (km^2)	1867	2578	3257	3202	2628	3611
Proportion spatial overlap	1	0.715	0.573	0.583	0.709	0.517
RMSD		411	809	777	445	1013
Total indicator		3.0	10.1	10.0	6.6	11.3

of memory processes can be a crucial component in the study of ungulate foraging systems with home-range behaviors.

3.2. Ecological context of best-fit scenario

Our detailed study of caribou distributions offered us insights into the animal's decision-making process as being the ultimate confluence of individual behavior, physiological constraints, and fine-scale environmental influences (Patterson et al., 2008). Established patterns helped us to develop a model with enough detail to reproduce the system's essential dynamics that was at once based in physiological realism, yet without excess complexity (Railsback and Johnson, 2011). With the Little Smoky region undergoing rapid development, we did not wish to dilute the strength of our comparisons with caribou from different years that were likely experiencing different levels of disturbance. However, the patterns we chose are largely universal patterns of either non-migratory and boreal caribou or ungulates in general, and not necessarily unique to a specific herd in a given year. While all five scenarios were calibrated to faithfully reproduce daily caribou bioenergetics and foraging time budgets with little intra-scenario variation, there existed enough variation in these scenarios that when we compared how well they satisfied the multiple patterns of actual caribou, we were able to show that one scenario is the most useful for modeling caribou of the Little Smoky. The scenario that most consistently produced patterns that coincided with actual caribou data was 'Energetics and Predation'. In this scenario, each of the three behavioral strategies – acquiring energy for daily use, conserving energy for reproductive needs, and minimizing predation,

was given consideration whenever the need arose, with energetic needs taking precedence.

To lend further justification to the ranking of the alternate caribou strategies, it is helpful to interpret the model outputs in an ecological context. Agents reproduced the fewest number of patterns exhibited by actual caribou in the Energy Acquisition scenario, since they did not consider their long-term energetic reproductive needs. Agents were more likely to randomly travel to new locations (as evidenced by their spatial distributions), since surrounding areas of high risk became unacceptable and they were unwilling to trade off these costs against increased foraging. Additionally, at the end of the simulation, caribou agents incurred a cumulative energetic deficit corresponding to a mass loss of approximately 27 kg (20.5%). Although it seems intuitive that meeting daily energy needs while reducing the risk of predation is a likely strategy, it ignores the considerable literature which states that relatively small shifts in mass result in relatively large changes in caribou parturition rate (Cameron and Ver Hoef, 1994). In other words, it is non-adaptive for a female caribou to ignore her reproductive needs.

The second alternative scenario, 'Energy Conservation', acknowledges the energetic requirements necessary to ensure successful parturition. In this scenario, caribou agents are unwilling to trade off the costs of future failed reproduction even though their daily needs have been met. As a result, agents performed well in matching the patterns of real caribou, and lost a minimal amount of energy over the winter (18.4 kg or 14% body mass). However, because of the abundance of energy, agents were also more likely to engage in long-distance forays, and covered more area spatially than actual caribou. In many animal systems, adaptive behaviors

are updated as environmental conditions and individual state change, and prediction is widely accepted as essential to decision-making (Levin, 1999). While real caribou may indeed engage in state-based predictions, they do not do so at the exclusion of other competing strategies. In essence, the fundamental difference between the Energy Conservation scenario and the real world is that the former assumes animals have perfect foreknowledge when in reality, animals rarely do; i.e., their predictions are based on best available assimilated information that has intrinsic error. It is for this reason that the Energetics and Predation scenario fits better overall: the agents still trade off short- vs. long-term needs, thus inexplicitly reflecting the naturally occurring imperfection involved in decision-making.

For the estimated remaining 78 individual caribou, it would appear that available food is non-limiting in a 3100-km^2 range. This occurrence provides the ability to test competing hypotheses about the sensitivities of caribou to predation. In the first case, if caribou are insensitive to industrial features, caribou should not minimize their exposure to them on the landscape. And with food being in such plentiful supply (as intraspecific competition is a non-issue), then caribou should be more than capable of meeting their energetic requirements over a small geographic area. These are indeed the results we observe from the Predation-insensitive scenario, with caribou agents reducing their daily and landscape movements; however, this was a mismatch to actual patterns produced. Moreover, this scenario resulted in agents losing an unrealistic estimated 0.3% in body mass by winter's end. It would thus appear that predation risk plays a significant role in influencing caribou movement decisions. At the other extreme, however, if caribou are hypersensitive to industrial features and attempt to minimize their exposure by moving away from the source while being capable of meeting their daily minimum energetic needs, then we would expect the opposite outcomes. Our results confirmed that having predation risk take precedence resulted in highly unlikely energetic deficits (a mass loss of 27%) and the greatest large-scale movement patterns – again, a mismatch with what actual caribou displayed. Instead, the Energetics and Predation scenario provides a more likely explanation: caribou respond to the pervasive predation risk of their environment when they can afford to (and in doing so, incur additional energetic costs) with energetic needs taking priority. While there is incomplete understanding of the mechanics behind the observed caribou avoidance of industrial features in Canada, our model suggests it to be an intuitive link to predation risk. In this case the source of predation risk is the industrial features themselves, being perceived as caribou agents as either direct or indirect disturbance, and/or being associated with predator presence.

While our ABM does not model population-level processes, we can infer consequences for caribou fitness based on the bioenergetics results. The predominant energy requirement for wintering caribou is maintenance, and it must be met chiefly by foraging (Adamczewski et al., 1993). Therefore, if a female caribou experiences benign winter conditions, she can afford to increase her allocation of energy to reproduction. However, the condition of a female caribou also has a direct impact on fetal viability and subsequent calf survival (Cameron et al., 1993; Post and Klein, 1999). If a female caribou experiences harsh winter conditions (i.e., via increased snow depth, predation, and/or disturbance), failed reproduction can occur, manifesting itself either in the form of stillbirth, low birth-weight calves, or deformities (Cameron et al., 1993), with the latter two situations increasing calf vulnerability to predation. While the absolute availability of winter food may not be limiting, the need to minimize predation risk and/or disturbance can impel female caribou to adopt predation-sensitive foraging that essentially results in the loss of usable habitat despite its ubiquity (Wittmer et al., 2005). Functional habitat-loss coupled with increased expenditure of energy to minimize exposure to

perceived predation risk can indeed result in female caribou becoming nutritionally stressed. Lastly, carry-over effects of previous nutritional deprivation may ultimately affect pregnancy rates of caribou and hence population dynamics if animals are unable to replenish reserves following severe winter conditions (Parker et al., 2009). Consequently, bioenergetics can play a significant role in caribou population processes.

In the Energetics and Predation scenario, the mean cumulative energy lost by caribou agents was equivalent to a 17% loss in body mass. This value is slightly higher than the 10–15% that caribou are assumed to normally loose of their autumn mass during winter (Bradshaw et al., 1998). While not beyond the critical 20% loss, it does suggest that acquiring enough energy for both somatic and reproductive growth may be an issue. In actuality, the Little Smoky herd, although it has a high pregnancy rate, has one of the lowest calf recruitments of Alberta herds, with a mean of 0.07 female calves per female (range 0.01–0.11; ASRD, 2010); however, the portion attributable to calf predation vs. unfit offspring or stillborns is currently unknown.

4. Conclusion

An unavoidable challenge in the conservation of endangered species is that their ecologies can sometimes be poorly or only broadly understood, making targeted conservation management particularly difficult. ABMs as a tool can provide answers when knowledge is limited (Topping et al., 2010), and our current focus on ABM validation by pattern-oriented modeling (POM) demonstrates that the conclusions our model draws on the behavioral motivations of caribou are robust. The patterns chosen in this study refer to characteristic, non-random, identifiable states of the system (Grimm et al., 1996), and the robustness of the ABM lies in the simulation of multiple patterns across different hierarchical and spatio-temporal scales, and in the exploration and contrast of alternative, competing hypotheses of habitat selection and movement. In particular, a model might be relatively likely to reproduce fortuitously a single feature of the system, but simultaneous reproduction of several system-level characteristics is much less likely (Grimm and Railsback, 2012). As such, our caribou ABM sheds light on caribou behaviors, which can contribute to discussions and assessments of boreal caribou recovery plans.

Under current consideration by the Canadian federal government are four broad management strategies proposed for boreal caribou: to undertake coordinated and comprehensive landscape-level planning for caribou ranges, conduct population monitoring, and, where our ABM may be particularly informative, to manage both caribou mortality and caribou habitat to meet current and future habitat requirements (Environment Canada, 2011a). Our best-fit scenario demonstrates that caribou (in LSM) are sensitive to industrial features on the landscape that evoke anti-predator responses and bioenergetic costs even in the absence of any explicit predators modelled. In essence, mortality tools such as managing predators and alternate prey may stabilize population growth rates, but functional habitat loss is still a serious issue with ensuing energetic costs. Management efforts should also ensure that caribou: (1) are not increasingly energetically stressed by their anti-predator behaviors induced by actual predators and industrial features on the landscape, and (2) have enough high-forage, functionally available habitat to meet their energetic needs required for somatic and reproductive growth and 'predator' avoidance. With continuous land-use development in the already highly industrialized landscape, caribou may end up allocating too much time and hence energy avoiding predation/disturbance, even though food availability may remain readily available. On-the-ground management efforts must therefore also include limiting new development and

restoring old anthropogenic changes in LSM. Although our focus on LSM can be considered regional and represents a herd in a highly developed landscape, 28 local populations of boreal caribou across Canada are considered non-sustaining (Environment Canada, 2011a). Our ABM has established an investigative methodology for establishing why caribou choose the habitats they use, and can be readily and easily adapted to herds of different ecotypes (mountain vs. boreal) experiencing varying levels of development.

Next, because conservation planning of wildlife habitats also involves the analysis of habitat-linked population demographics under various land-use development scenarios, the ABM can be used as a scenario-planning tool. By considering multiple possible future landscapes within a spatially explicit context, and then modeling caribou responses to the changes in their habitat (both spatiotemporal and bio-energetic), scenario planning with ABMs can offer managers a method for creating more resilient conservation policies by increasing understanding of key uncertainties, incorporating alternative perspectives into conservation planning, and providing greater resilience of decisions to surprise (McLane et al., 2011). This is the next phase of our research focus.

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