



Protecting wildlife habitat in managed forest landscapes—How can network connectivity models help?

Denys Yemshanov¹  | Robert G. Haight² | Rob Rempel^{3,4} | Ning Liu¹ | Frank H. Koch⁵

¹Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, Sault Ste. Marie, Ontario, Canada

²USDA Forest Service, Northern Research Station, St. Paul, Minnesota

³Ontario Ministry of Natural Resources and Forests, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada

⁴Rob Rempel, FERIT Environmental Consulting

⁵USDA Forest Service, Southern Research Station, Eastern Forest Environmental Threat Assessment Center, Research Triangle Park, North Carolina

Correspondence

Denys Yemshanov, Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen Street East, Sault Ste. Marie, ON P6A2E5, Canada. Email: Denys.Yemshanov@canada.ca

Funding information

The funding for this study was provided by Natural Resource Canada's Cumulative Effects Program

Abstract

Industrial forestry in boreal regions increases fragmentation and may decrease the viability of some wildlife populations, particularly the woodland caribou, *Rangifer tarandus caribou*. Caribou protection often calls for changes in forestry practices, which may increase the cost and reduce the available timber supply. We present a linear programming model that assesses the trade-off between habitat protection and harvesting objectives by combining harvest scheduling and optimal habitat connectivity problems. We formulate the habitat connectivity model as a network flow problem that maximizes the amount of habitat connected over a desired time span in a forested landscape, while the forestry objective maximizes net undiscounted revenues from timber harvest subject to even harvest flow and environmental sustainability constraints. We applied the approach to explore the trade-off between caribou habitat protection and harvesting goals in the Armstrong-Whitesand Forest, Ontario, Canada, a boreal forest area with prime caribou habitat. Our model also incorporates Dynamic Caribou Harvesting Scheduling (DCHS), a harvest policy currently in a place in Ontario that aims to balance the forest management and caribou

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2020 The Authors. *Natural Resource Modeling* published by Wiley Periodicals LLC



protection goals in northern boreal regions. In our study area, the implementation of DCHS appears to have relatively minor impact on timber supply cost. By comparison, maximizing the protection of caribou habitat would lead to a noticeable increase of the mill gate timber cost by $\$3.3 \text{ m}^{-3}$ on average, while enabling habitat protection in an additional 5.0%–9.5% of the range area. Our model is generalizable and can be adapted for assessing habitat recovery and harvest goals in other regions.

Recommendations for Resource Managers:

- Incorporating the concept of long-term habitat connectivity into forest planning can help reduce the negative impacts of harvest activities on caribou populations.
- Prioritizing habitat connectivity leads to a small increase in the overall harvest area because harvest has to be allocated to less productive and more geographically isolated sites to protect prime wildlife habitat containing old conifer stands.
- Maximizing the habitat protection would lead to a noticeable increase of the timber supply cost (by $\$3.3 \text{ m}^{-3}$ on average), while enabling moderate increase of the protected habitat area (i.e., an additional 5.0%–9.5% of the range area).
- Implementation of Dynamic Caribou Harvest Schedules, which is the current harvesting policy in Ontario's boreal forests when caribou populations are present, causes only a minor increase of the timber supply cost in our study area.

KEYWORDS

DCHS, habitat protection, harvest scheduling model I, landscape connectivity, mixed integer programming, network flow model, woodland caribou

1 | INTRODUCTION

Industrial forestry activities in Canada's boreal forests have caused landscape fragmentation and negatively affected the survival of some wildlife species that were originally adapted to function in

undisturbed forest areas. In particular, woodland caribou populations (*Rangifer tarandus caribou*) have been declining in areas of industrial forestry operations (Brandt, Flannigan, Maynard, Thompson, & Volney, 2013; Venier et al., 2014). Harvesting creates a network of clear-cuts in early successional stages, which increases the abundance of competing deer and moose populations and attracts predators of caribou (James & Stuart-Smith, 2000; Latham, Latham, McCutchen, & Boutin, 2011; Wittmer, Sinclair, & McLellan, 2005). Woodland caribou is a threatened species in Canada (SARA, 2002) and declining numbers in its populations pose a serious conservation problem (Festa-Bianchet, Ray, Boutin, Cote, & Gunn, 2011; Hebblewhite, 2017; Hebblewhite & Fortin, 2017). Recovery efforts for protecting caribou populations aim to create larger regions with undisturbed habitat and eliminate open spaces that serve as movement corridors for predators (EC, 2011, 2012; ECCC, 2017).

Protection of woodland caribou habitat is a long-term policy that focuses on minimizing human activities that cause fragmentation, such as timber harvesting. However, protecting wildlife habitat may reduce the area of forest available for harvest and increase the cost of timber supply. To plan effectively, decision-makers must be able to assess the interplay between the extent of harvest activities and measures to protect caribou habitat (Martin, Richards, & Gunn, 2016; McKenney, Nippers, Racey, & Davis, 1997; McKenney, Mussell, & Fox, 2004; Felton et al., 2017; Ruppert et al., 2016). Ideally, the habitat protection measures should have minimal impacts on forestry activities, but as a practical matter, caribou populations and harvesting co-occur across many parts of boreal Canada.

Trade-offs between caribou protection and harvesting objectives can be explored using optimization models. For decades, harvest planning has been performed with the aid of linear programming models (Johnson & Scheurman, 1977; M. McDill, Rebain, & Braze, 2002; M. E. McDill, Tóth, John, Braze, & Rebain, 2016; Öhman, 2000; Weintraub, Barahona, & Epstein, 1994), and these efforts have often incorporated habitat protection constraints. In particular, mixed integer programming (MIP) is widely used to solve forest planning problems with landscape management constraints (Constantino, Martins, & Borges, 2008; Crowe, Nelson, & Boyland, 2003; M. E. McDill & Braze, 2000; Meneghin, Kirby, & Jones, 1988; Öhman, Edenius, & Mikusiński, 2011; Snyder & ReVelle, 1996, 1997).

Optimization models have addressed habitat protection by maintaining habitat contiguity (Bettinger, Sessions, & Boston, 1997), maximizing the number of adjacent protected habitats (Williams, ReVelle, & Levin, 2005), applying adjacency restrictions (M. McDill et al., 2002; Snyder & ReVelle, 1997) or maximizing the protected area by selecting among predefined habitat clusters (Tóth et al., 2009). Proposed MIP formulations include selecting a contiguous set of patches to cover a desired amount of habitat for a species of concern (Önal & Briers, 2006), finding a shortest path in a habitat restoration problem (Williams & Snyder, 2005) and optimizing selected spatial properties of a habitat network (Cerdeira, Gaston, & Pinto, 2005; Snyder, Haight, & ReVelle, 2004; Toth et al., 2011; Williams et al., 2005; Williams, ReVelle, & Levin, 2004).

Recently, we proposed a network-based approach to solve a habitat connectivity problem for woodland caribou (Yemshanov et al., 2019). Under this approach, a fragmented forest landscape is depicted as a network of habitat patches (nodes) interconnected by arcs indicating potential movement corridors for animals. Connectivity between adjacent habitats is formulated as a network flow problem through this partially connected habitat network. The work follows from Sessions (1992), who proposed the formulation of the connected habitat problem as a Steiner network. It also relates to Jafari and Hearne (2013) and Jafari, Nuse, Moore, Dilkina, and Hepinstall-Cymerman (2017), who proposed a network flow problem to establish a contiguous protected reserve, as well as



Conrad, Gomes, van Hoes, Sabharwal, and Suter (2012) and Dilkina et al. (2017), who proposed a network flow model to determine minimum-cost corridors to connect a set of core habitat areas.

Habitat connectivity and forest planning problems can be linked, following either of two general approaches. A replanning approach (Martin et al., 2016; Ruppert et al., 2016) combines a spatial simulation model that calculates a habitat priority map for species protection with a harvest scheduling model in sequence. At each planning period t , a heuristic habitat model is applied first to estimate a map of suitable habitat, which is used in a harvest model as the parameter to schedule harvest over a planning horizon starting from t . The estimation of habitat patterns with the heuristic habitat model is repeated in the next planning period $t + 1$, followed by replanning the harvest, and so on.

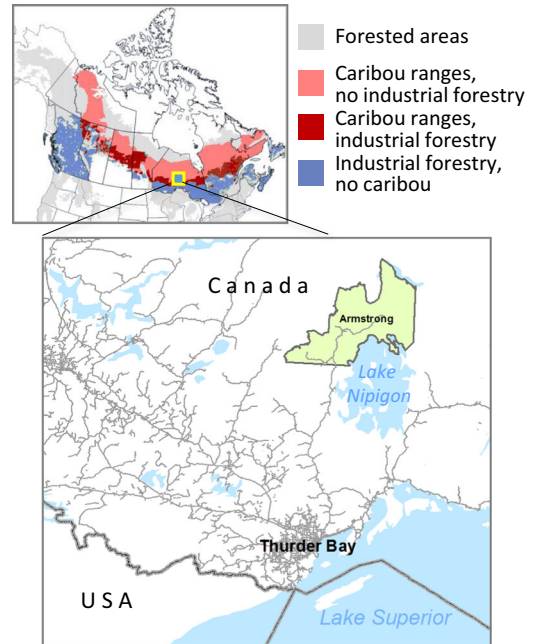
An alternative approach combines harvest planning and habitat connectivity models in a single optimization problem (St. John, Tóth, & Zabinsky, 2018; St. John et al., 2016; Yemshanov et al., 2020). St. John et al. (2016) proposed a multitemporal MIP model for forest harvesting and protection of reindeer habitat and migration corridors. For each harvest planning period t , the model allocated a connected corridor of reindeer habitat while meeting the harvest objective. Similarly, Yemshanov et al. (2020) proposed a network flow model that linked the protection of woodland caribou habitat and harvest planning objectives in northeastern Alberta. For each planning period, the model maximized the amount of connected habitat in the area while meeting a harvest volume target but did not require the protection of fully connected corridors or a contiguous habitat area. In both studies, optimal habitat connectivity patterns were found for each harvest planning period t , yielding a total of T connectivity networks over the planning horizon. This makes the joint habitat connectivity/harvest problem more difficult combinatorially than the replanning approach of Martin et al. (2016). In fact, both St. John et al. (2016) and Yemshanov et al. (2020) required multistage warm start techniques to solve the problem.

In this paper, we adapt the concepts pioneered in St. John et al. (2016) and Yemshanov et al. (2020) and propose a simpler formulation that combines a harvest planning problem with a network flow problem that maximizes the amount of fully connected caribou habitat over a desired timespan. We depict a forest landscape as a network of interconnected patches where any pair of adjacent patches containing suitable habitats is connected by arcs. We assume that a wildlife species can move between patches through corridors defined by the universe of connected arcs. Compared to the previous habitat connectivity model of Yemshanov et al. (2020), the new formulation only tracks connectivity between pairs of adjacent patches with suitable habitat and uses a simpler algorithm to inject the flow into the habitat network, thus ensuring that the connected network is fully contiguous. Instead of finding optimally connected networks for each planning period t , our model finds one long-term habitat network that remains connected for a desired timespan T_{\min} . Our model maximizes (a) the total amount of connected habitat over period T_{\min} or longer and (b) the net revenues from harvest, subject to even harvest flow, environmental sustainability and other operational constraints. For illustration, we present a case study for the Whitesand-Armstrong Forest Management Unit in northern Ontario, Canada (Figure 1), where we incorporate Ontario's current operational policies devised to reduce the impact of harvesting on caribou populations.

2 | MATERIAL AND METHODS

We depict a landscape as a network of N forest patches (nodes). Each patch may have habitat that can support caribou individuals. We assume that caribou may move from neighboring

FIGURE 1 Case study area: Whitesand-Armstrong Forest Management Unit, Ontario, Canada



patches m to patch n if patch n has suitable habitat present over a *continuous* time span, T_{\min} or longer. We depict the connectivity between patches m and n as a bidirectional pair of arcs, mn and nm , which indicate potential movement of caribou individuals between m and n in both directions. Caribou movement through the network of patches N is conceptualized as a flow through a subnetwork of *connected* nodes over a continuous timespan T_{\min} or longer. We introduce the nonnegative variables y_{nm} and y_{mn} to characterize the bidirectional flow through arcs nm and mn connecting a pair of adjacent nodes n and m with habitat.

Caribou require suitable habitat to support their foraging and reproductive behaviour. Each forest patch n may have the amount of suitable habitat. The level of habitat suitability to support caribou individuals depends on the composition and age of the forest in n (Ferguson & Elkie, 2004a, 2004b; Johnson, Parker, Heard, & Gillingham, 2002; OMNRF, 2015). Clear-cut harvesting temporarily destroys the suitable caribou habitat as it reduces the amount of local foraging resources. Early successional stages following the harvest attract deer (*Odocoileus* spp.) and moose (*Alces alces* L.) populations followed by predators (black bears (*Ursus americanus* Pallas) and wolves (*Canis lupus* L.), which further increases the predator pressure on caribou (James, Boutin, Hebert, & Rippin, 2004; Latham et al., 2011; Wittmer et al., 2005). A harvested patch is expected to become suitable again for caribou in 40–60 years, as forest stands mature and adequate vegetation cover is restored. For the current work, we assume that decisions to harvest forest stands in patch n are binary with no partial harvesting options. Harvest decision implies clearcutting all stands in n and resetting their forest age to 0 after the harvest. We assume a patch will undergo a natural regeneration after the harvest.

For each patch n , we define a set of harvest prescriptions i , $i = 1, \dots, I$, where each prescription defines a possible sequence of harvest events over a planning time horizon T , including a scenario without harvest. We enumerate all possible prescriptions that can be assigned to forest patch n by a set of binary vectors of length T , $p_{ni} = \{(1, 0, \dots, 0), (0, 1, \dots, 0), \dots\}$, $p \in P$. The elements of each vector denote the harvest or no harvest conditions in a particular time period t , $t = 1, \dots, T$. A binary variable x_{ni} , $x_{ni} \in \{0, 1\}$ selects whether a patch n follows a



harvest prescription i with a vector of harvest times p_{ni} . Only one harvest prescription can be selected for a patch.

The time since harvest and tree species composition defines the amount of suitable habitat in patch n in period t as well as the continuous time span $t, t + 1, t + 2, \dots$ during which the habitat remains suitable. For each prescription i , the parameter b_{nit} defines the amount of suitable habitat that could support caribou individuals in patch n in period t , $t \in T$ (see the description of the parameter b_{nit} in the Data section). A binary parameter, λ_{nit} , identifies the presence or absence of suitable habitat in n in prescription i in period t ($\lambda_{nit} = 1$ when $b_{nit} > 0$ and forest stands in n are older than 40 years, and $\lambda_{nit} = 0$ otherwise). We use the λ_{nit} values to estimate the parameter τ_{ni} , $\tau_{ni} \in [0; T]$, which defines the maximum number of consecutive time periods when the habitat remains suitable over a planning horizon T in patch n in prescription i . The habitat capacity in patch n in prescription i in period t is defined as follows:

$$\sum_{i=1}^I b_{nit} x_{ni} \lambda_{nit}. \quad (1)$$

2.1 | Habitat connectivity problem

Our habitat model tracks connectivity between patches with suitable habitat that remains connected for *continuous* time span T_{\min} or longer, $T_{\min} < T$. A binary variable w_{nm} , $w_{nm} \in \{0,1\}$, defines whether a species flow is established between patches n and m throughout the continuous timespan T_{\min} or longer. We find a network of connected patches in the landscape that maximizes the total habitat amount in the network. To ensure their spatial connectivity, we formulate a network flow problem that injects flow into the network of selected patches. Each selected patch must receive flow from at least one neighbouring selected patch. We introduce a root node, $n = 0$, that is used to inject the flow into the habitat network. The root source node 0 is connected to all other nodes (patches) $1, \dots, N$ and can inject the flow into any node in the network (Figure 2). Adding a root node is a standard approach in formulating network flow models that aim to find a spatially contiguous set of land units (see Jafari & Hearne, 2013).

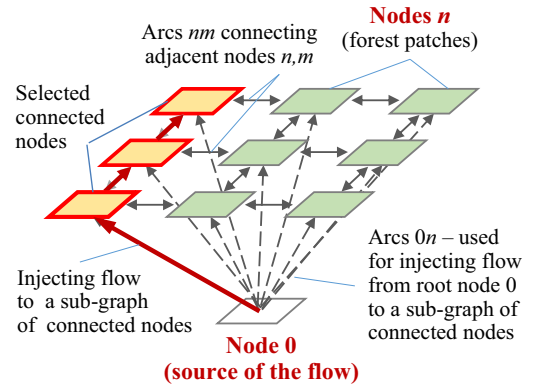
We assume that connected nodes can be fed by no more than a single incoming arc from one node, and the flow only comes to a node from one source. This assumption prevents the creation of loops in the connected network. A node n with incoming positive flow from nodes m (i.e., with one of the w_{mn} values set to 1) becomes a part of the connected network, that is,

$$\sum_{m=1, \{0\}}^{N_n^-} w_{mn} = 1. \quad (2)$$

In Equation (2), set N_n^- defines nodes $m = 1, \dots, N$ which are connected to node n and can transmit flow to n , including the root node $\{0\}$.

Since only nodes with suitable habitat available over a continuous timespan T_{\min} can be connected, node selection must include the selection of a harvest prescription i (which defines the forest stand age and so the node's habitat suitability status). We define a binary variable z_{ni} , $z_{ni} \in \{0,1\}$, as the product of the selection of flow to a node n and harvest

FIGURE 2 The network flow model concept. Arrows show the universe of arcs, or potential connections between the neighboring patches in the habitat network. Light-shaded arrows show connections from the root node 0 to nodes n in the network, which are used to inject the flow into the network. Bold arrows in red show the flow injected into the habitat network; thin arrows in red show the flow through the selected connected nodes. Patches in red show the selected connected nodes



prescription i at n , that is $x_{ni} \sum_{m=1, \{0\}}^{N_n^-} w_{mn}$, so $z_{ni} = 1$ only if a prescription i is selected for node n and there is an incoming flow to n . Constraints (3)–(5) linearize the product of two binary variables as:

$$z_{ni} \leq \sum_{m=1, \{0\}}^{N_n^-} w_{mn} \quad \forall n \in N, i \in I \quad (3)$$

$$z_{ni} \leq x_{ni} \quad \forall n \in N, i \in I \quad (4)$$

$$z_{ni} \geq \sum_{m=1, \{0\}}^{N_n^-} w_{mn} + x_{ni} - 1 \quad \forall n \in N, i \in I \quad (5)$$

We formulate the habitat connectivity problem as selecting a subset(s) of fully connected nodes to maximize the total amount of habitat that is connected over T_{\min} continuous periods (or longer) in a landscape N over a planning horizon T , that is,

$$\max \sum_{t=1}^T \sum_{n=1}^N \sum_{i=1}^I (b_{nit} \lambda_{nit} z_{ni}) - f_1 P_1 \quad (6)$$

where the penalty decision variable P_1 , $P_1 \geq 0$, defines the number of nodes connected to the root node 0 above one node, and f_1 is the scaling factor, subject to constraints (3)–(5) and:

$$\sum_{m=1, \{0\}}^{N_n^-} y_{mn} - \sum_{m=1}^{N_n^+} y_{nm} = \sum_{m=1, \{0\}}^{N_n^-} w_{mn} \quad \forall n \in N \quad (7)$$

$$\sum_{m=1, \{0\}}^{N_n^-} w_{mn} \leq 1 \quad \forall n \in N \quad (8)$$

$$P_1 \geq \sum_{n=1}^N w_{0n} - 1 \quad (9)$$

$$y_{nm} \leq U w_{nm} \quad \forall n \in N, m \in N_m \quad (10)$$

$$w_{nm} \leq y_{nm} \quad \forall n \in N, m \in N_m \quad (11)$$



$$\sum_{m \in N_n} w_{mn} \leq \sum_{i=1}^I (x_{ni} \tau_{ni}) / T_{\min} \quad \forall \quad n \in 1, \dots, N, T_{\min} \leq T \tag{12}$$

For a selected node n , constraint (7) ensures that the amount of flow coming to the node is equal to the amount of flow outgoing from the node plus the fulfilled demand capacity at n . The demand capacity is 1 if a node is selected and zero otherwise. Term N_n^+ defines the set of nodes m that are connected to node n and can receive flow from n .

Constraint (7) ensures the flow balance through a node n and its connectivity with the other nodes. Constraint (8) helps avoid cyclic connections and ensures that the flow only comes to a node n from at most one source. Constraint (9) defines the penalty variable, which specifies the number of connections to the root node 0 exceeding one. Maximizing the objective value (6) with the penalty P_1 in place minimizes the number of connections receiving the flow from node 0 above one. The penalty in the objective function is required because each connection from the root node 0 creates a separate contiguous network. Compared to a formulation that sets a fixed number of connections to the root node (e.g., one), the penalty formulation makes it easier to find feasible solutions in fragmented landscapes where creation of a single contiguous habitat network is impossible. The coefficient f_1 defines the magnitude of the penalty term in the objective function equation. Setting the f_1 value sufficiently high yields a solution with a single fully connected network, after first finding a feasible solution with multiple connections to the root node.

Constraints (10) and (11) ensure agreement between the flow selection variable y_{nm} that defines the amount of flow through an arc nm and the arc selection binary variable w_{nm} . Constraint (10) ensures that the flow between nodes n and m is zero when the arc nm is not selected. Constraint (11) ensures that the arc selection variable w_{nm} is zero unless a positive flow is established from node n to node m . Constraint (12) ensures that the flow to a node n can only be established if the node retains suitable habitat over a continuous timespan T_{\min} or longer. The parameter τ_{ni} in Equation (12) defines the longest time span when suitable habitat is available in site n in prescription i and was derived as follows. Consider the following prescription example in site n :

10-year time periods, t :	1	2	3	4	5	6	7	8	9	10
Harvest events	-	-	1	-	-	-	-	-	-	-
Habitat availability, λ_{nit} :	1	1	0	0	0	0	1	1	1	1.

In this prescription, the longest continuous time span the habitat remained suitable over T periods is four periods, that is $\tau_{ni}=4$. The τ_{ni} values were calculated when generating the universe of harvest prescriptions I . Constraint (12) also relates the binary flow selection variable to patch n , w_{mn} to the timespan parameter τ_{ni} and allows the connections to node n if the node is assigned the harvest prescription i with the τ_{ni} value equal or above the minimum time span T_{\min} .

2.2 | Harvest scheduling problem

Forest patches (nodes) in the network can be harvested for timber. The allocation of harvest maximizes the net revenue, subject to a target volume of harvested timber in each period t , even harvest flow constraint in consecutive periods t and $t + 1$ and a constraint that maintains a minimum average age of forest stands in the area N at the end of the planning horizon. We adopt the harvest scheduling Model I formulation (Johnson & Scheurman, 1977; M. E. McDill &



Braze, 2000; M. McDill et al., 2002, 2016; Martin, Ruppert, Gunn, & Martell, 2017). The model considers an area of N forest patches over a planning horizon of T periods. For each patch n , a set of possible harvest prescriptions i , $i \in I$, defines the sequences of all harvest actions over T periods including a no-harvest scenario. As defined above, binary variable x_{ni} selects the harvest prescription i for a patch n . We only consider clear-cut harvest, which is the most common harvest type in boreal Canada (NFD, 2019). A forest stand can be harvested after it reaches a minimum harvest age of k years or older. Each patch includes only one stand characterized by age, tree species composition and a forested area, a_n , that could be harvested for timber. For patch n , prescription i defines a sequence of harvest times with volumes of harvested timber V_{nit} and a precomputed net revenue R_{ni} from harvesting that timber over period T minus harvest, hauling and mandatory postharvest regeneration costs.

We define Q_t as the volume of timber harvested in area N in period t and $Q_{t \min}$ and $Q_{t \max}$ as lower and upper bounds on the harvest volume in period t . We also define ρ_n as the unit price of timber harvested from a patch n net of harvest and hauling costs. Even harvest flow over consecutive planning periods t and $t + 1$ is enforced by a proportion ε that limits the change of the harvest volume proportion in consecutive periods t and $t + 1$ by $1 \pm \varepsilon$. We also add a minimum bound for the average age of forest stands in the managed area at the end of the planning horizon T , $E_{T \min}$, and define E_{ni} as the forest stand age in a patch n at the end of the planning horizon if prescription i is applied. The harvesting problem is defined as maximizing the net revenues, R_{ni} , associated with managing the forest over T periods, that is,

$$\max \sum_n \sum_i R_{ni} x_{ni} \tag{13}$$

s.t.:

$$\sum_{i=1}^I x_{ni} = 1 \quad \forall \quad n \in 1, \dots, N \tag{14}$$

$$Q_{t \min} \leq \sum_{n=1}^N \sum_{i=1}^I a_n V_{nit} x_{ni} \leq Q_{t \max} \quad \forall \quad t \in T \tag{15}$$

$$(1 - \varepsilon)Q_t \leq Q_{t+1} \leq (1 + \varepsilon)Q_t \quad \forall \quad t \leq T - 1 \tag{16}$$

$$\sum_{n=1}^N \left(\sum_{i=1}^I [(E_{ni} - E_{T \min}) a_n x_{ni}] \right) \geq 0 \tag{17}$$

The harvest revenue R_{ni} is calculated as the undiscounted net cash flow associated with harvesting forest in patch n over the entire planning horizon T in prescription i . In our formulation, the harvested volume is constrained by even harvest flow and target harvest volume constraints, so maximizing revenues minimizes the per-unit cost of harvesting a target volume of timber, subject to constraints (14)–(17). The revenue R_{ni} is calculated as the timber value net of harvest, hauling and postharvest regeneration costs, e_n :

$$R_{ni} = \sum_{t=1}^T (a_n \rho_n V_{nit} - e_n) \tag{18}$$



For each site n , the R_{ni} values were precomputed for every prescription i before optimization. Since our goal was to assess the impacts of long-term habitat protection, the use of undiscounted cash flows enabled similar handling of harvest allocation and habitat protection over the long term. The use of discounting would prioritize short-term harvest revenues over long-term cash flow, and so would misrepresent the long-term environmental sustainability of the harvest patterns and their costs.

Constraint (14) ensures that each patch with harvestable forest is assigned just one prescription. Note that the set of prescriptions I includes a no-harvest scenario with zero revenues. Constraint (15) ensures that the harvest volume for each period stays within a range $[Q_{t \min}; Q_{t \max}]$. Constraint (16) specifies that the harvest volumes in consecutive periods t and $t + 1$ do not deviate by more than upper and lower bounds $1 \pm \varepsilon$. Constraint (17) sets the average age of forest stands at the end of the planning horizon T to be greater or equal to the minimum age target $E_{T \min}$. This constraint ensures that a portion of the old-growth forest stands is left unharvested, which prevents overharvesting.

2.3 | Incorporating the Dynamic Caribou Habitat Scheduling (DCHS)

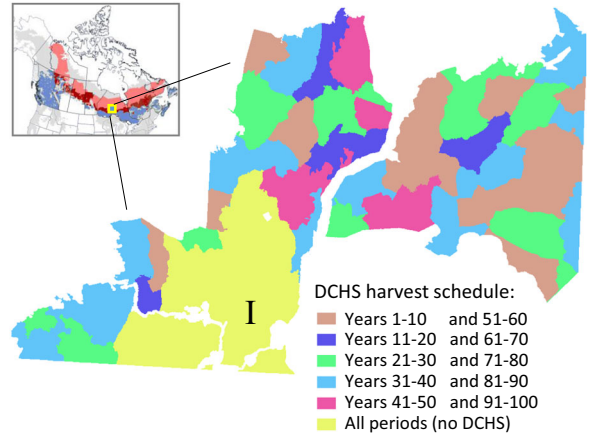
In 1996, the Ontario Ministry of Natural Resources and Forestry (OMNRF) adopted a new sustainable harvest approach in areas where caribou populations are present (FPAC, 2018; OMNR, 2009; Racey et al., 1999). The DCHS is a part of forest management plans approved by the Province of Ontario. For a 10-year planning period, a DCHS concentrates harvest areas and subsequently aggregates clear-cut disturbances, while minimizing densities of logging roads. Aggregating the harvest in a few relatively large regions helps to avoid creating a pattern of small cut blocks across large areas.

During the planning process, the selection of DCHS regions is done for the entire harvest planning horizon. Periodically, a forest plan is updated after major disturbances when the current plan becomes no longer useful for harvesting or wildlife protection (Baskent & Keles, 2005; Martell, Gunn, & Weintraub, 1998). Currently, DCHS regions and their harvest times are delineated statically during the planning process and do not incorporate dynamic scheduling, which may be needed in response to changing landscape composition or timber demands. Regardless, aggregating the harvest within a DCHS region helps maintain connectivity between undisturbed habitats outside the harvested region but also offers some flexibility for reallocating cut blocks within the region.

We incorporated the DCHS principle into the harvest scheduling model by way of two scenarios. Our first scenario uses a static arrangement of DCHS regions and restricts the harvest schedule to fixed time periods and DCHS regions according to the provincial DCHS plan (Figure 3). Based on data received from OMNRF, we defined a set of static DCHS regions s , $s \in S$. Each region has a specified timeline (a 10-year period) when stands in that region can be harvested. We assume that fine-scale allocation of harvest within a particular DCHS region would maximize the net harvest revenues, as described above in the harvest planning problem (13). For each patch n and time period t , a binary parameter, δ_{nt} , defines whether a patch n can be harvested in period t according to a static DCHS plan ($\delta_{nt} = 1$) and $\delta_{nt} = 0$ otherwise. Constraint (19) forces the harvest in period t to regions as prescribed by the provincial DCHS plan, that is,

$$\sum_{i=1}^I x_{ni} V_{nit} = 0 \quad \forall \quad \delta_{nt} = 0, n \in 1, \dots, N, t \in T \quad (19)$$

FIGURE 3 An example of planned DCHS regions for Whitesand-Armstrong FMU. Region I contains a network of access roads. It is exempt from DCHS rules and can be harvested in any time period. DCHS, Dynamic Caribou Habitat Scheduling



2.4 | Dynamic allocation of harvesting in DCHS regions

Static delineation of DCHS regions and harvest schedules may not be sufficient to guarantee long-term connectivity of caribou habitat. One reason for implementing DCHS is to ensure that the regions harvested in a given time period are surrounded by an adequate area of undisturbed habitat. In short, DCHS aims to avoid situations when harvest occurs in adjacent DCHS regions at the same time. We capture this aspect with our dynamic DCHS scenario, which only uses the geographic boundaries of the DCHS regions but allows dynamic selection of harvestable DCHS regions over time. We introduce a set of constraints to penalize the allocation of harvest in adjacent DCHS regions in the same period t .

We introduce a binary decision variable, l_{st} , to define harvest in DCHS region s in period t . The l_{st} values are estimated via constraints (20) and (21), that is,

$$\sum_{n=1}^N \sum_{i=1}^I (x_{ni} V_{nit} \theta_{ns}) \leq l_{st} M \quad \forall s \in S, t \in T \quad (20)$$

$$l_{st} \leq M \sum_{n=1}^N \sum_{i=1}^I (x_{ni} V_{nit} \theta_{ns}) \quad \forall s \in S, t \in T \quad (21)$$

where θ_{ns} is a binary parameter that indicates whether a site n belongs to a DCHS region s ($\theta_{ns} = 1$ and $\theta_{ns} = 0$ otherwise) and M is a large integer value. For each time period t , we then define an $S \times S$ adjacency matrix of binary parameters, α_{sq} , where $\alpha_{sq} = 1$ if the neighboring DCHS regions s and q share a common boundary and $\alpha_{sq} = 0$ otherwise. We then introduce a binary decision variable L_{sqt} , $s, q \in S, t \in T$, to define the occurrence of harvest in a pair of neighboring regions s and q in period t (i.e., $L_{sqt} = 1$), and $L_{sqt} = 0$ otherwise. The L_{sqt} value is a product of decision variables l_{st} and l_{qt} , which indicate harvest in regions s and q in period t , and is linearized via constraints (22)–(24):

$$L_{sqt} \leq l_{st} \quad \forall s \in S, q \in S, t \in T \quad (22)$$

$$L_{sqt} \leq l_{qt} \quad \forall s \in S, q \in S, t \in T \quad (23)$$

$$L_{sqt} \geq l_{st} + l_{qt} - 1 \quad \forall s \in S, q \in S, t \in T \quad (24)$$



We then define a penalty decision variable associated with scheduling harvest in adjacent DCHS regions in the same period, P_2 , $P_2 \geq 0$ via constraint (25), that is,

$$P_2 \geq \sum_{t=1}^T \sum_{s=1}^S \sum_{q=1}^S L_{sqt} \alpha_{sq} \quad (25)$$

Constraints (20)–(25) create a harvest pattern that minimizes harvesting in adjacent DCHS regions in the same period.

A related goal of DCHS is to concentrate the harvest in a particular period in a few large regions while keeping the other regions intact. Thus, we need to ensure that the harvest is concentrated in as few DCHS regions as possible while avoiding harvest in adjacent regions in the same period. We add a decision variable P_3 , $P_3 \geq 0$, to the objective function equation to penalize the total number of DCHS regions harvested in the same time period t above one, that is,

$$P_3 \geq \sum_{t=1}^T \left[\sum_{s=1}^S l_{st} - 1 \right] \quad (26)$$

We also need to define a minimum threshold area, ϕ_{\min} , that can be harvested in DCHS region s if a decision is made to harvest that region in period t . We define the range of possible harvest areas in DCHS region s as $\{0, [\phi_{\min}; \phi_s]\}$, where ϕ_s is the total harvestable area in DCHS region s . This condition is established by introducing a binary decision variable, d_{st} , and a disjunction constraint (27), that is,

$$d_{st} \phi_{\min} \leq \sum_{n=1}^N \sum_{i=1}^I (A_n x_{ni} \theta_{ns} \mu_{nit}) \leq d_{st} \phi_s \quad \forall s \in S, t \in T \quad (27)$$

where μ_{nit} is a binary parameter, $\mu_{nit} \in \{0,1\}$, that indicates the presence of harvest in patch n in prescription i in period t ($\mu_{nit} = 1$) and $\mu_{nit} = 0$ otherwise. The μ_{nit} values are generated from the harvested volume data (i.e., $\mu_{nit} = 1$ when $V_{nit} > 0$ and $\mu_{nit} = 0$ otherwise).

The model also requires a masking constraint to ensure that no harvest occurs outside of the designated area, that is,

$$\sum_{i=1}^I \left(x_{ni} \sum_{t=1}^T V_{nit} \right) = 0 \quad \forall \quad \xi_n = 0, n \in 1, \dots, N \quad (28)$$

where ξ is a binary mask indicating that a patch n belongs to a harvestable area ($\xi = 1$) and $\xi = 0$ otherwise.

2.5 | Combining the harvest and habitat connectivity objectives

We combine the harvesting and habitat connectivity problems in a single objective via relative weights. Our full objective maximizes the weighted sum of the connected habitat amount in area N and the net harvest revenues over T planning periods, that is,

$$\max F \left[\sum_{t=1}^T \sum_{n=1}^N \sum_{i=1}^I (b_{nit} \lambda_{nit} z_{ni}) - f_1 P_1 \right] + \gamma (1 - F) \sum_n \sum_i R_{ni} x_{ni} - f_2 P_2 - f_3 P_3 \quad (29)$$

A normalizing factor γ rescales the harvest revenue term in Equation (29) to make it roughly the same order of magnitude as the amount of connected habitat. Scaling coefficients f_1 – f_3 adjust the relative weights of penalties P_1 – P_3 in the objective function equation. The scaling factor f_1 should be high enough to push the model to create a single (or minimum possible number of) contiguous subgraph(s) with the connected habitat.

Our Problem 1 (no DCHS hereafter) combines the harvest and habitat connectivity objectives without considering the DCHS rules, and maximizes the objective (29) without the penalty terms $f_2 P_2$ and $f_3 P_3$, subject to constraints (3)–(5), (7)–(12), (14)–(17), and (28). Problem 2 (static DCHS) enhances problem 1 by forcing the harvest to follow a static DCHS plan via constraint (19). The model maximizes the objective (29) without penalty term $f_2 P_2$, subject to constraints (3)–(5), (7)–(12), (14)–(17), (19), and (26)–(28). Problem 3 (dynamic DCHS) uses only the spatial boundaries of DCHS regions but enables dynamic selection of DCHS regions to harvest at a particular time. The model maximizes the full objective (29), subject to constraints (3)–(5), (7)–(12), (14)–(17), and (20)–(28).

Solving the objective functions (29)–(31) with different objective weights F enables exploration of the trade-off between maximizing the amount of protected habitat versus maximizing harvest revenues. The solutions for end-points of this trade-off when F values are set to 0 or close to 1 depict the most distinct policies when habitat protection or harvest revenues are prioritized, which we have further explored in our study. We composed the model in the General Algebraic Modeling System (GAMS, 2019) and solved it with the GUROBI linear programming solver (GUROBI, 2019). Table 1 lists the model parameters and variables. We ran the model on a HP Gen 10 workstation with dual Xeon Gold processors for 72 hr or until reaching a 0.5% optimality gap (whichever came first).

2.6 | Case study

We applied the model to examine harvesting and caribou protection strategies in the Whitesand-Armstrong Forest Management Unit (FMU) in northwestern Ontario, Canada (Figure 1). The area is adjacent to Wabikimi Provincial Park and includes portions of both the Nipigon and Brightsand caribou ranges (CPAWS, 2009; OMNR, 2012). The area has been moderately fragmented by logging, with timber delivered to mills in Thunder Bay, Ontario. Currently, a plan to build wood pellet and cogeneration plants in Armstrong, Ontario is under consideration by the provincial and federal governments as well as the Whitesand First Nation (Bieler, Trush, & Jakob, 2019). If established, a wood pellet plant and a cogen facility would ensure energy independence of local communities and create a sustainable market for fiber. However, large-scale harvest operations may increase forest fragmentation and cause the decline of local caribou populations. Protection of sensitive caribou habitat has been proposed as a management tool to help prevent further decline of caribou populations in the region (Neegan Burnside Ltd., 2014) but has to compete with forestry activities. Figure 4 depicts key spatial inputs including habitat intactness (Figure 4a), timber volume in current conditions (Figure 4b), hauling cost (Figure 4c,d), harvestable area and suitable habitat amounts (Figure 4f–h) and the distribution of high-use (category 1) and seasonal-use caribou habitat (category 2, Figure 4i).

**TABLE 1** Summary of the model variables and parameters

Symbol	Parameter/variable name	Description
Sets		
Θ	Arcs nm connecting adjacent nodes n and m in a landscape	$nm \in \Theta$
N	Nodes (forest patches) n in a landscape	$n \in N$
S	Harvest (DCHS) regions s and q in area N	$s, q \in S$
T	Planning time periods, t	$t \in T$
I	Harvest prescriptions, i	$i \in I$
Decision variables		
w_{nm}	Binary indicator of the species flow via an arc nm	$w_{nm} \in \{0,1\}$
y_{nm}	Amount of flow between the adjacent nodes n and m	$y_{nm} \geq 0$
x_{ni}	Binary selection of harvest schedule i in site n	$x_{ni} \in \{0,1\}$
z_{ni}	Product of the selection of flow to node n and harvest prescription i at site n	$z_{ni} \in \{0,1\}$
P_1	Penalty on the number of nodes connected to a root node 0 above one	$P_1 \geq 0$
P_2	Penalty on the total number of DCHS regions s harvested in the same period t above one	$P_2 \geq 0$
P_3	Penalty on harvesting in adjacent DCHS regions s and q in the same period t	$P_3 \geq 0$
d_{st}	Binary decision variable to enforce the disjunction $\{0, [\phi_{\min}; \phi_s]\}$	$d_{st} \in \{0,1\}$
l_{st}	Binary decision indicator of harvest in DCHS region s in period t	$l_{st} \in \{0,1\}$
L_{sqt}	Binary decision indicator of harvest in adjacent DCHS regions s and q in period t	$L_{sqt} \in \{0,1\}$
Parameters		
b_{nit}	Habitat amount in patch n in prescription i in period t	$b_{nit} \geq 0$
τ_{nt}	Longest continuous time span a patch n has suitable habitat in prescription i	$0 \leq \tau_{nt} \leq T$
T_{\min}	Minimum number of consecutive time period a connected node need to have suitable habitat	$0 \leq T_{\min} \leq T$
$Q_{t \min}, Q_{t \max}$	Lower and upper bounds on harvest volume over a period t	$Q_{t \min}, Q_{t \max} \geq 0$
a_n	Forest area in a node n	$a_n \geq 0$
V_{nit}	Volume of merchantable timber available for the harvest at a node n in period t in harvest prescription i	$V_{nit} \geq 0$
Q_t	Volume of timber harvested over a period t	$Q_t \geq 0$
R_{ni}	Net revenue associated with harvesting a node n according to prescription i	$R_{ni} \geq 0$
ε	Allowable increase or decrease in harvest volume in consecutive planning periods t and $t + 1$	0.02
$E_{T \min}$	Average target age of forest stands in the managed area at the end of the planning horizon T	65
E_{ni}	Forest stand age in a patch n at the end of the planning horizon if prescription i is applied	0–180
e_n	Postharvest regeneration costs	$e_n > 0$
d_n	Unit volume timber price net of harvest and hauling cost	$d_n > 0$

TABLE 1 (Continued)

Symbol	Parameter/variable name	Description
δ_{nt}	Binary indicator of that a patch n is harvestable in period t according to a static DCHS plan	$\delta_{nt} \in \{0,1\}$
ϕ_{\min}, ϕ_s	Minimum feasible and total harvestable areas in DCHS region s	$\phi_{\min}, \phi_s > 0$
α_{sq}	Binary indicator of the adjacent DCHS regions s and q sharing a common border	$\alpha_{sq} \in \{0,1\}$
θ_{ns}	Binary indicator whether a node n belongs to a DCHS region s	$\theta_{ns} \in \{0,1\}$
μ_{nit}	Binary indicator of harvest occurring in node n in prescription i in period t	$\mu_{nit} \in \{0,1\}$
λ_{nit}	Suitable habitat status for at a node n in prescription i in period t	$\lambda_{nit} \in \{0,1\}$
F	Objective weighting factor	$F \in [0;1]$
γ	Normalizing factor that rescales the harvest revenue term in Equation (29) to make it in the same order of magnitude as the amount of connected habitat	$\gamma = 1e-6$
f_1, f_2, f_3	Scaling factors for penalties P_1-P_3	$f_1-f_3 \in [0;1]$
U, M	Large positive values	$U > 0$

Abbreviation: DCHS, Dynamic Caribou Harvesting Scheduling.

2.7 | Data

We divided the study area landscape into 1×1 km patches (Table 2). For each patch, we estimated the potential amounts of suitable caribou habitat b_{nit} for each harvest prescription and forest age by combining two approaches. First, we modelled the current habitat distribution in the study area (Figure 4g) using a model of preferred caribou locations based on GPS tracking of collared animals undertaken by the Ontario Ministry of Natural Resources and Forests between 2009 and 2014 (Hornseth & Rempel, 2015). The location data were collected through two separate projects: the first was set up in 2009–2010 to help meet caribou monitoring and assessment commitments in Ontario's Woodland Caribou Conservation Plan (Avgar, Mosser, Brown, & Fryxell, 2013; COSEWIC, 2011; Pond, Brown, Wilson, & Schaefer, 2016), while the second collected caribou location data from 2010 to 2014 (OMNR, 2012). Suitable habitat amounts were calculated as a function of current forest composition, recent disturbances, esker and anthropogenic linear feature density and land cover type using resource-type selection coefficients developed by Hornseth and Rempel (2015) from the location data. Models were updated and extended to the lower boreal region, including the Brightsand Caribou Range (Rempel & Hornseth, 2018).

The future distribution of suitable caribou habitat was based on a boreal caribou habitat model for Ontario's Northwest Region (Elkie et al., 2018), from which we predicted amounts of suitable habitat based on a combination of land cover composition and forest age (Figure 4h and Table 3). For every 10-year forest age class, for each habitat type (such as useable, preferred, and refuge habitats), if present in patch n in period t , a score of 1 was assigned, and a total habitat suitability value was estimated as the sum of these scores. When forest patches included a mix of different land cover types, the total habitat suitability value was estimated as a weighted average of scores for individual cover types and their corresponding areas. We assumed that forest stands regain suitable habitat status 40 years after harvest. We then estimated

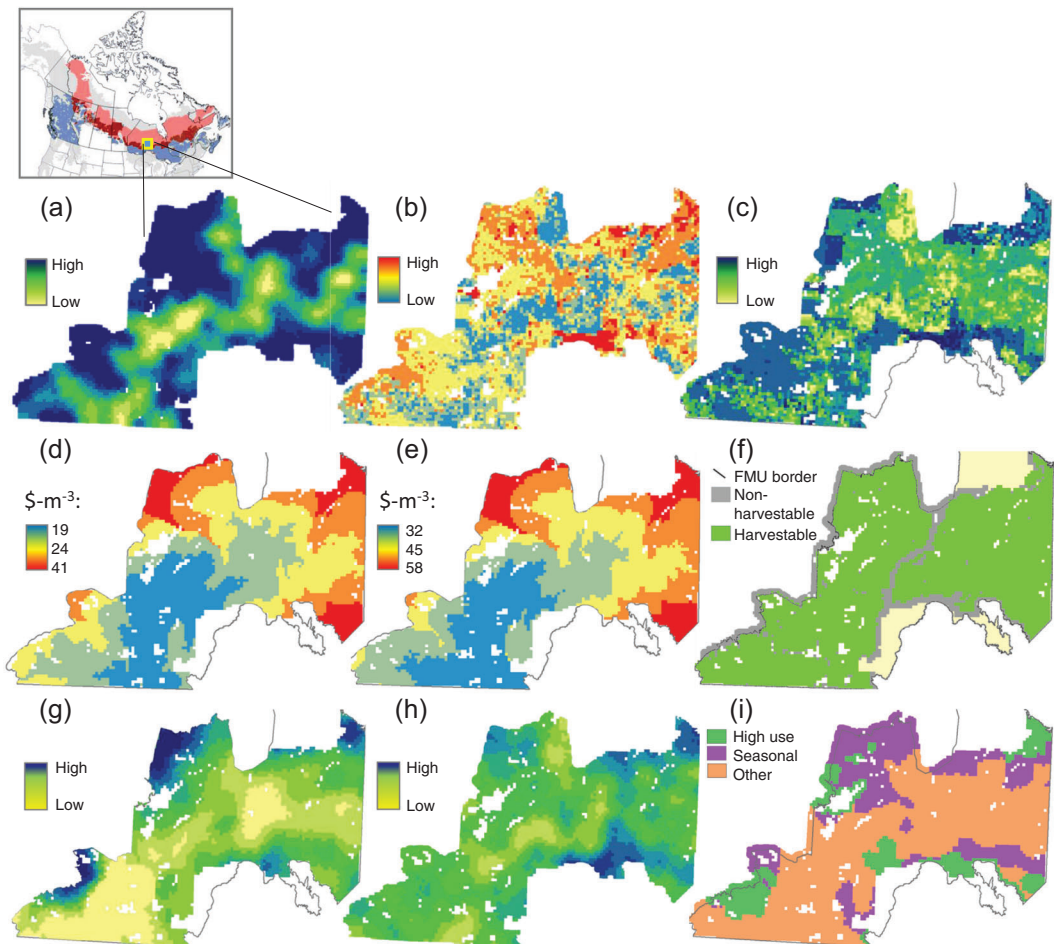


FIGURE 4 Model spatial inputs: (a) Map of habitat intactness at $t = 0$ (used to adjust the suitable habitat values b_{nit}); (b) stand age, years at $t = 0$; (c) timber volume, $\text{m}^3\text{-ha}^{-1}$ at $t = 0$; (d) timber hauling cost, $\text{\$-ha}^{-1}$ —hardwoods; (e) timber hauling cost, $\text{\$-ha}^{-1}$ —softwoods; (f) harvestable area; (g) suitable habitat amounts b_{nit} at $t = 0$ based on the model of Rempel and Hornseth (2018); (h) suitable habitat amounts b_{nit} at $t = 0$ based on the method of Elkie et al. (2018); (i) caribou habitat categories: 1, high-use habitat; 2, seasonal habitat; 3, other habitats potentially accessible by caribou

the habitat suitability values as a weighted average of the suitability values based on the current habitat distribution and the future land cover and age composition. The weighting factor for estimates based on the current distribution was set to 1 in time period 1, and linearly decreased over the planning horizon to 0 in period T . The sum of the weighting factors for the estimates based on the current distribution and future land cover/age was set to 1.

The study area may also experience other anthropogenic disturbances that are undesirable for caribou populations. We adjusted the suitable habitat amounts b_{nit} using a habitat intactness coefficient that accounted for human-mediated disturbances in the area of interest. For each patch n , we calculated habitat intactness values for all combinations of harvest prescriptions i and time periods t . We estimated intactness by averaging the three criteria which negatively affect the amount of suitable habitat: the area proportion of nonlinear anthropogenic

TABLE 2 Summary of data assumptions

Assumption	Description
Data spatial resolution (sites n)	1×1 km
Temporal resolution	10-year planning periods
Planning horizon	100 years
Initial forest composition and age and land cover at $t = 1$	OMNRF's Forest Resource Inventory (FRI) spatial database (OMNRF, 2019)
Caribou habitat suitability model	Elkie et al. (2018)—based on forest stand age and species/land cover composition
Caribou habitat suitability	Score 1.0 is assigned for each habitat type present at a site (i.e., useable, preferred or refuge); the total habitat value is the average of scores for all habitat types for a given forest age/tree species/land cover composition
Caribou habitat value in site n	A weighted average based on the proportion of each habitat type (useable, preferred, refuge) within each age/species/land cover combination in a map cell
Spatial resolution of habitat estimates	5,000 ha interpolated to a grid of 1×1 -km map cells
Minimum forest age when site n achieves a suitable habitat status	>40 years after harvest
Habitat intactness	Averaging the area % of nonlinear human disturbances, linear features density and the area % of forest stands younger than 30 years
Hauling distances	Based on CanVec road network data (NRcan, 2019)
Hauling rate	$\$90 \text{ hr}^{-1}$, 1-hr waiting time and $\$4 \text{ m}^{-3}$ overhead cost for a 40 m^3 truckload
On-site timber harvest cost	$\$15 \text{ m}^{-3}$
Range of assessed area-wide harvest volumes	$0.05\text{--}0.3 \text{ M m}^3\text{-ha-yr.}^{-1}$
Projected yield assumptions	Growth and yield data from McKenney et al. (2016)
Future forest area loss due to fire	Fire regime zones and fire return intervals from Boulanger et al. (2014)
Minimum harvest age	70 years
Area-wide mean forest age at the end of the planning horizon	≥ 80 years
Even harvest flow range	$\pm 2\%$

disturbances, the density of anthropogenic linear disturbances (seismic lines, roads, pipelines, and transmission lines) and the area proportion of post-disturbance forest stands younger than 30 years (Figure 4a and Table 2).

Previous assessments of long-term caribou movement patterns in northern Ontario suggested that caribou tend to select habitat at broad scales (i.e., in the 5,000–10,000 ha range) rather than finer scales (Hornseth & Rempel, 2015). Therefore, we estimated the presence of

**TABLE 3** Minimum age at which a stand attains suitable caribou habitat status

Land cover type	Habitat type		
	Useable	Preferred	Refuge
Lowland spruce			61
Mixedwood conifers			71
Other lowland conifers	51		41 ^a
Jack pine dominant	41	61	41 ^a
Jack pine mixedwood	41	61	41
Black spruce dominant or black spruce mixedwood	61		41
Black spruce lowland	41	101	41 ^a
Treed bog and fen	Permanent		Permanent

^aWe assumed that harvested forest for this land cover type would require 40 years to regain suitable habitat status.

suitable habitat at coarse scales using a grid of 5,000-ha hexagon cells and then interpolated the habitat values to a grid of 1 × 1-km map cells. For the current caribou distribution, the habitat selection and resource utilization were modelled using the approach presented in Hornseth and Rempel (2015). This methodology is consistent with the general habitat description for caribou (OMNRF, 2015). Similarly, the suitable habitat estimates based on future land cover composition and age were aggregated from the spatial resolution of individual land cover polygons in Forest Resource Inventory data at the same 5,000-ha resolution (Figure 4g).

We used road network data from the CanVec database (NRCan, 2019) to estimate hauling costs, assuming an on-site harvest cost of \$15 m⁻³ and delivery of hardwood timber to Armstrong, Ontario (the closest market, which has a proposed pellet plant) and softwood to the Resolute Forest Products mill in Thunder Bay, Ontario (Figure 4d,e). The hauling costs were based on typical estimates for northern Ontario conditions (Maure, 2013) and included the delivery cost with a hauling rate of \$90 hr⁻¹, assuming a 40 m³ truckload, 1 hr waiting time and an overhead cost of \$4 m⁻³ (Table 2). The cost of accessing remote sites was incorporated by increasing the per-unit hauling cost value from sites without road access in direct proportion to the distance to the nearest road. Based on discussions with specialists from the Ontario Ministry of Natural Resources and Forests, we adjusted the hauling cost value so the area-wide timber cost per unit is approximately 25% higher than the unit cost value without accounting for road access.

The starting values for stand age, merchantable timber volume and land cover composition were estimated from Ontario's Forest Resource Inventory database (OMNRF, 2018). To estimate the future timber volume in the harvest prescriptions, we used yield curves for northwestern Ontario from a recent timber supply study (McKenney et al., 2016). These yield values were adjusted by the projected annual losses of forested area due to fire disturbances using fire regime zones from Boulanger, Gauthier, and Burton (2014). The minimum age of harvest k was set to 70 years. We assumed that the area-wide mean forest age at the end of the planning horizon must be equal to or greater than the current mean age (i.e., approx. 80 years). We set the even harvest flow bounds to $\pm 2\%$ and the harvest planning horizon T to 100 years with 10 × 10-year time steps. Table 2 summarizes key data assumptions.



2.8 | Forest management and habitat protection scenarios

We evaluated six harvest and caribou protection policies for a set of harvest targets between 0.05 and $0.3 \text{ M m}^3\text{-yr}^{-1}$. Two management policies were represented by groups of “harvest priority” and “habitat protection priority” scenarios. “Harvest priority” scenarios maximize the net harvest revenues without prioritizing the protection of caribou habitat and have the scaling factor F in the objective function set to zero. “Habitat protection priority” scenarios set the scaling factor to 0.99 and maximize the amount of caribou habitat that can be kept connected over T_{\min} periods or longer, while giving low priority (0.01) to maximizing the revenues from harvest. Both scenario groups meet the harvest target $[Q_{t \min}; Q_{t \max}]$. Each scenario group included “no DCHS,” “static DCHS,” and “dynamic DCHS” scenarios for problems 1–3, as defined earlier (Figure 3). We also examined optimal solutions assuming long-term (i.e., $T_{\min} = 100$ years) and medium-term ($T_{\min} = 60+$ years) protection of caribou habitat. To estimate the total amount of connected habitat in the absence of harvest, we solved the connectivity objective (6) without harvest and then used this estimate to calculate the proportion of connected area in the solutions with harvest using objective Equations (29)–(31).

3 | RESULTS

3.1 | General connectivity patterns

We compared the optimal solutions for two distinct sets of scenarios that prioritized harvest and habitat protection. The original problem included 5,322 forest sites, 25.3 K continuous and 208 K binary variables, but the size of the MIP model was reduced significantly after presolve. The no DCHS problem included 21.3 K continuous and 78.7 K binary variables after presolve and reached an optimality gap below 0.5% in less than 6 hr. The static DCHS problem included 21.3 K continuous and 47.4 K binary variables after presolve and reached an optimality gap of 0.5% within 18–24 hr. The dynamic DCHS problem included 21.3 K continuous and 80 K binary variables after presolve and reached an optimality gap of 0.12%–0.25% after 72 hr.

The maximum level of sustainable harvest with given assumptions and constraints approached $0.31 \text{ M m}^3\text{-yr}^{-1}$ in no DCHS scenarios. At this level, suitable habitat can be connected in a long-term network that covers approximately 56% of the Whitesand-Armstrong FMU area. Both harvest priority and habitat protection priority solutions show the bulk of the harvest allocated in close proximity to a network of logging roads in the south-central portion of the FMU (Figure 5a,b). Prioritizing habitat connectivity increases the area of connected habitat by 5.0%–9.5% (Table 4). The habitat protection solutions show unharvested corridors connecting habitat areas on the northern shores of Lake Nipigon and habitats in the undeveloped northern parts of the FMU (Figure 5b). These solutions also avoid allocating harvest in areas with the most suitable category 1 habitat and seasonal use category 2 habitat, instead allocating much of the harvest to eastern parts of the FMU (Figure 5). Although the harvest allocations in the habitat protection solutions keep more habitat connected than the harvest priority solutions, they increase the mill gate timber cost per unit by as much as $\$5.4 \text{ m}^{-3}$ (Figure 6). The average timber cost increase was $\$3.3 \text{ m}^{-3}$, which is comparable with the size of royalties paid by forest companies for harvesting timber on Crown lands in Ontario. Figure 6b also indicates that the impact of caribou habitat protection on timber supply costs is appreciable even at relatively low harvest levels ($0.1 \text{ M m}^3\text{-yr}^{-1}$ and above). This is because the sites with the most productive

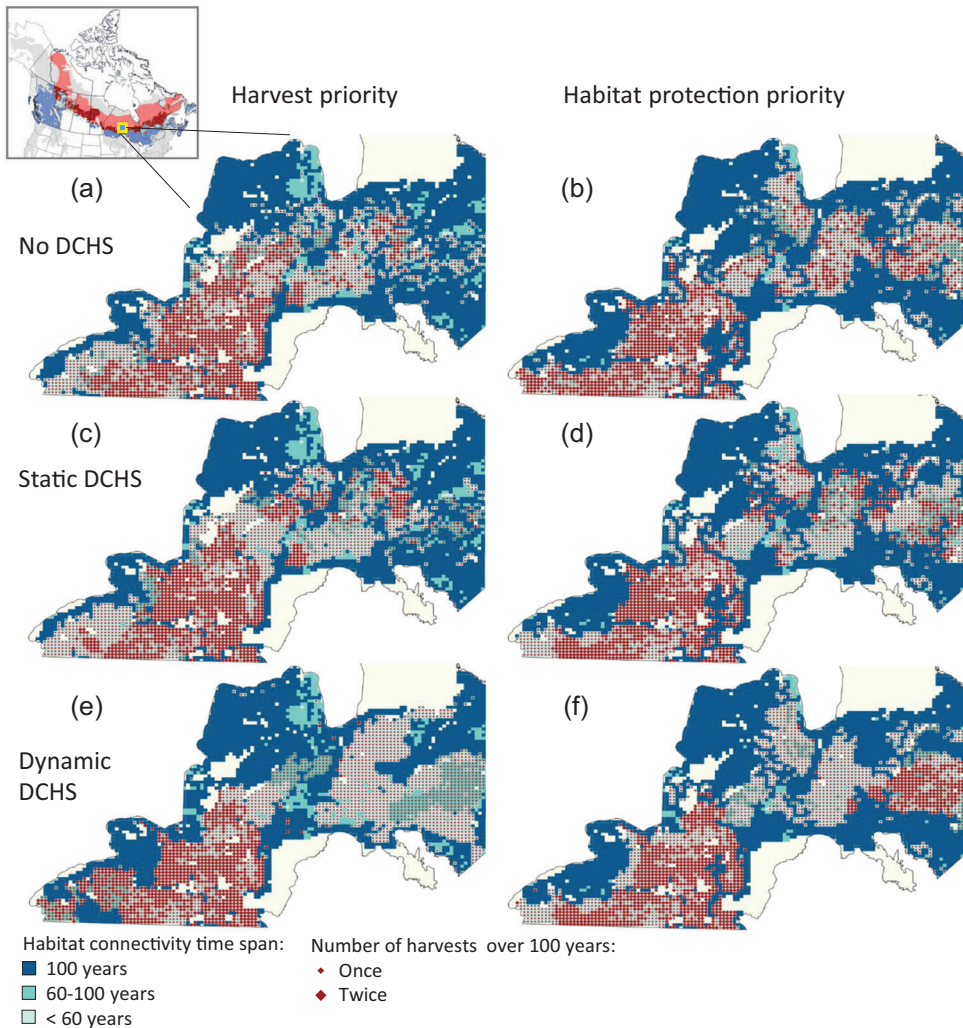


FIGURE 5 Examples of optimal harvest selection and habitat connectivity patterns. Example solutions with a harvest volume target of $0.3 \text{ million m}^3\text{-yr}^{-1}$ are shown. No-DCHS scenarios: (a) harvest priority; (b) habitat protection priority. Static DCHS scenarios: (c) harvest priority; (d) habitat protection priority. Dynamic DCHS scenarios: (e) harvest priority; (f) habitat protection priority. Shaded regions indicate the number of consecutive periods the habitat retained its suitable status over the planning horizon T . Dark-shaded areas indicate habitats connected over 100 years, medium-shaded areas indicate habitats connected between 60 and 99 years and light-shaded areas indicate habitats connected for less than 60 years. Small and large dot symbols show patches with one or two harvests, respectively, over the planning horizon T . DCHS, Dynamic Caribou Harvesting Scheduling

mature coniferous stands represent both a desirable source of timber and highly preferred caribou habitat. Their protection moves harvest to lower-productivity sites that are more geographically remote, which increases the timber unit cost.

Imposing habitat connectivity constraints increases the proportion of the study area where forests are harvested a single time over the planning horizon (Table 4). This stems from the allocation of harvest to less productive locations to protect prime caribou habitat. When



TABLE 4 Net revenues, delivered timber prices, and the total area harvested either once or twice over the planning period *T* for solutions prioritizing harvest versus solutions prioritizing habitat protection

Harvest scenario	Harvest target (million m ³ ·year ⁻¹)	Connected habitat area increase in connectivity vs. harvest priority solutions (%)	Revenues over <i>T</i> periods (million \$)			Mill gate timber price (\$ m ⁻³)			Area harvested over <i>T</i> periods (ha)				
			Scenarios:		Habitat protection priority	Harvest		Habitat protection priority	Once		Habitat protection priority	Twice	
			Harvest priority	Habitat protection priority		Harvest priority	Habitat protection priority		Harvest priority	Habitat protection priority			
No DCHS*	0.05	5.7	189.8	166.4	27.18	32.19	20,090	28,196	15,146	11,347			
	0.1	8.5	365.8	320.2	28.63	33.71	40,293	48,025	30,305	28,421			
	0.2	8.8	690.5	608.8	30.92	34.73	81,814	84,213	60,924	60,673			
	0.3	9.5	978.4	887.9	33.07	35.47	123,567	122,562	92,199	91,898			
Static DCHS*	0.05	5.3	189.2	169.5	27.29	31.36	20,152	24,136	15,161	13,120			
	0.1	8.4	364.6	319.2	28.75	34.19	40,440	51,066	30,241	26,548			
	0.2	8.9	686.6	616.0	31.09	34.41	82,716	86,014	60,988	60,300			
	0.3	8.1	968.1	891.6	33.32	35.41	126,162	126,276	92,213	91,856			
Dynamic DCHS*	0.05	5.0	189.2	172.2	27.34	30.75	20,502	25,557	15,088	12,424			
	0.1	6.3	363.3	328.2	28.92	32.83	40,701	45,026	30,139	28,942			
	0.2	7.0	653.8	604.3	33.3	34.82	84,256	86,542	60,157	61,850			
	0.3	7.4	902.2	894.5	35.66	35.28	150,157	127,268	76,191	91,508			

Abbreviation: DCHS, Dynamic Caribou Harvesting Scheduling.

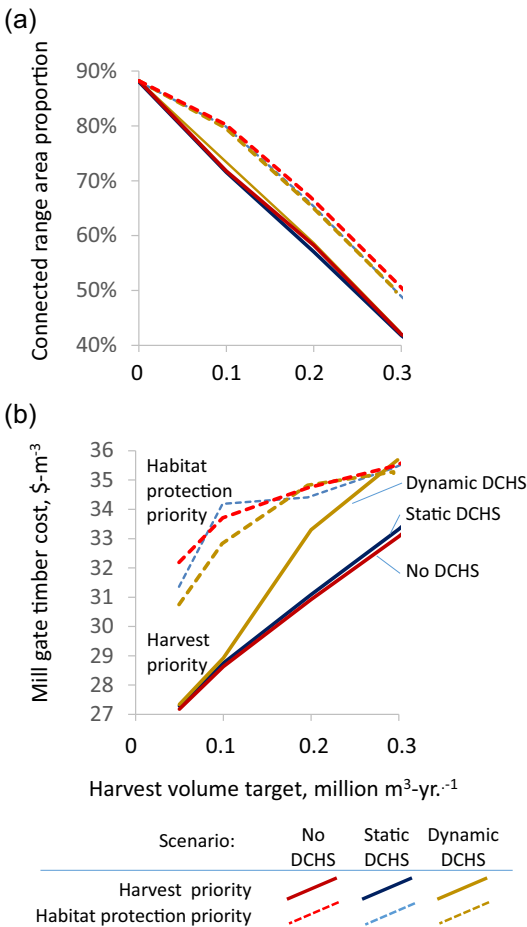


FIGURE 6 Impact of the timber harvest target on the area of connected habitat and the timber cost: (a) connected proportion of the total range area, %, vs. timber volume harvest target, million $\text{m}^3\text{-year}^{-1}$; (b) mill gate timber price, $\text{\$ m}^{-3}$, vs. timber volume harvest target, million $\text{m}^3\text{-year}^{-1}$. Solid lines depict harvest priority scenarios and dotted/dashed lines depict habitat connectivity priority scenarios. DCHS, Dynamic Caribou Harvesting Scheduling

connectivity constraints are in place, increasing the harvest volume target requires harvesting larger numbers of these low-productivity sites in addition to the intensively managed area in the south-central part of the FMU, nearly all of which is harvested twice over the planning horizon, regardless of scenario. Overall, an efficient habitat protection strategy is to protect areas with high-use caribou habitat near the northern, southwestern and eastern FMU borders while increasing harvest intensity in the south-central region, which has the lowest hauling costs.

3.2 | Impact of DCHS policies

Imposing DCHS rules concentrates harvest within a set of regions that guarantees a sufficient area of undisturbed habitat around these regions. The impact of DCHS is most noticeable in harvest priority scenarios, in particular in the dynamic DCHS scenario (Figure 5e), which imposes a strict penalty on harvesting in neighbouring DCHS regions during the same period. The impact of DCHS is less distinguishable in habitat priority solutions (Figures 5d and 5f) because the creation of large contiguous regions of connected habitat must be offset by allocating harvest to much of the remaining FMU area, regardless of the DCHS rules.

With respect to the harvest priority scenarios, applying the static DCHS rules leads to only a small increase of the timber costs compared to no DCHS solutions (Figure 6 and Table 4). This



is because a significant portion of timber harvest occurs in the south-central part of the FMU, which is exempt from the DCHS rules (Figure 3, callout I) and therefore provides flexibility when allocating harvest. However, in the dynamic DCHS scenarios, which feature a strict penalty on harvesting in adjacent DCHS regions, the cost of timber supply increases sharply and approaches the timber costs in the habitat protection solutions. Still, long-term habitat protection (i.e., $T_{\min} = 100$) imposes a higher premium on the timber supply cost than in harvest priority scenarios with dynamic DCHS because it requires more substantial spatial reallocations of harvest to protect a sufficient amount of prime caribou habitat (see the connected habitat patterns in Figure 5e vs. Figure 5b,d,f).

Primarily, the impact of DCHS in habitat priority solutions is captured as changes in the harvest patterns. Harvest tends to be concentrated in DCHS regions proximal to the network of access roads, similarly to the scenario without DCHS, so the coarse-scale harvest pattern, including the total area harvested, remains relatively stable. At low harvest levels, in habitat priority solutions, the cost of timber in the dynamic DCHS scenario is lower than in the static and no DCHS scenarios (Table 4). As mentioned earlier, this is because the stringent constraints of the dynamic DCHS scenario on harvesting in DCHS regions force the model to locate as much harvest as possible in the exempt south-central region (Figure 3, callout I). Doing so allows the most flexible harvesting and decreases the timber cost. While this behavior persists at high harvest levels, the larger volume of harvest cannot be allocated completely to the south-central region, so a sizeable share of the harvest must be apportioned among other DCHS regions. The net result is that, at the highest harvest target ($0.3 \text{ M m}^3\text{-year}^{-1}$), the timber costs converge at just over $\$35 \text{ m}^{-3}$ for the habitat priority scenarios with static, dynamic or no DCHS rules. In fact, the costs converge between these scenarios and the harvest priority scenario with dynamic DCHS.

Our results also confirm that the DCHS rules are effective in creating undisturbed habitat space around the harvested regions. For example, in static DCHS solutions the number of adjacent DCHS regions harvested in the same time period is reduced significantly compared to no DCHS solutions, and is further reduced to minimum adjacency levels in the dynamic DCHS solutions (Figure 7a). Habitat priority solutions impose stricter spatial constraints on harvest and usually have slightly more harvest in adjacent regions than the harvest priority solutions (Figure 7a).

In our optimal solutions, the protection of high-use habitat is mandatory but the protection of seasonal habitat is optional. Figure 7b indicates that the habitat priority solutions protect significantly more areas of seasonal habitat than the harvest priority solutions. With respect to the DCHS scenarios, a notable reduction in the area of protected seasonal habitat only occurred in the dynamic DCHS scenarios (Figure 7b). The dynamic DCHS rules have a big impact when the harvest volume target is high and approaches the maximum sustainable harvest limit, otherwise the choice of the objective (i.e., harvest vs. habitat protection priority) has a bigger impact on the area of the protected seasonal habitat than the implementation of DCHS rules.

3.3 | Long-term versus medium-term habitat protection

We compared long-term protection solutions, where the minimum habitat protection period T_{\min} was 100 years, with solutions emphasizing medium-term protection, with T_{\min} set to 60 years or longer. Relaxing the long-term habitat protection requirement allows harvest to extend over a larger area. In general, medium-term habitat protection solutions increased the area of forest stands harvested only once (Figure 8 and Table 5). The total area harvested over the planning horizon T increased, but the hotspots where stands were harvested twice remained the

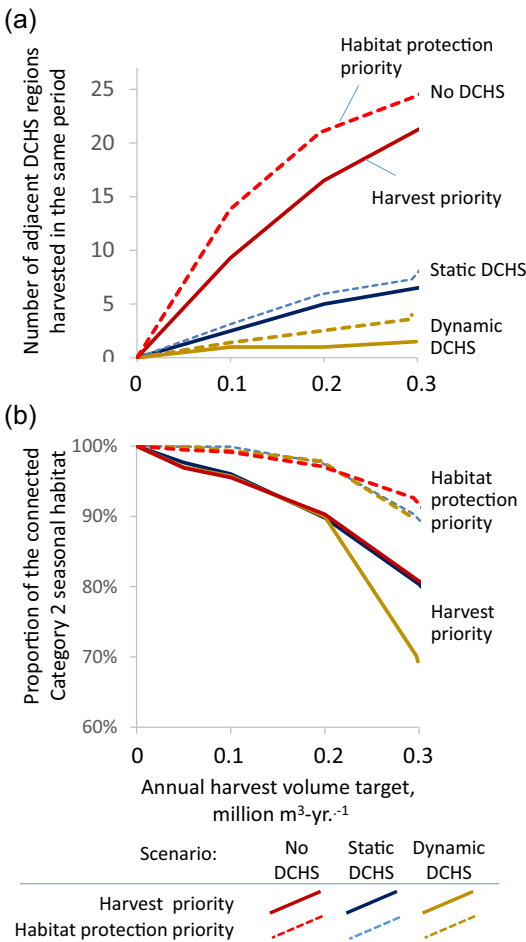


FIGURE 7 (a) Mean number of adjacent DCHS regions harvested in the same time period; (b) the proportion of the connected category 2 habitat vs. the harvest volume target. Solid lines depict the harvest priority scenarios and dotted/dashed lines depict the habitat connectivity priority scenarios. DCHS, Dynamic Caribou Harvesting Scheduling

same (Figure 9). Scenarios with the medium-term habitat protection objective connected less habitat area over the long term than scenarios with the long-term habitat protection objective (Table 5). Overall, the solutions with the long-term habitat protection objective ($T_{\min} = 100$ years) enabled protection of, on average, 11.7% more habitat area over the long term while giving up the medium-term (60 year) protection of only 5.4% habitat area (Table 5).

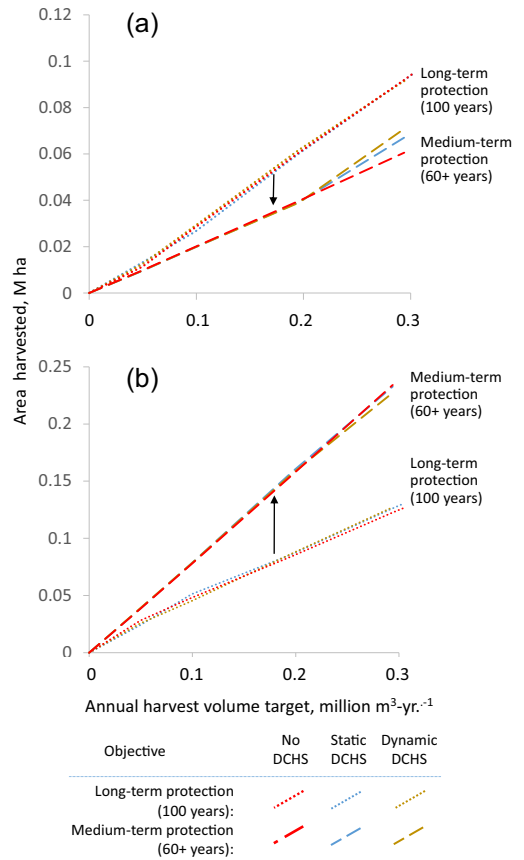
Relatively small geographical differences between the solutions with the long-term and medium-term habitat protection targets can be attributed to constraint (12), which maintains the minimum *uninterrupted* habitat protection period T_{\min} . Possible habitat protection options to maintain a 60-year protection period are limited to deferral of harvest to 40 years or immediate harvest at $t = 0$ in sites which can regain suitable habitat status in 40 years. This significantly reduces the potential number of sites where such measures could be implemented, and so does not change the location of major habitat protection hotspots (Figure 9).

4 | DISCUSSION

Incorporating the concept of long-term habitat connectivity into forest planning can help reduce the negative impacts of harvest activities on caribou populations. In our study, the main



FIGURE 8 Area with one and two harvests over the planning horizon T vs. the harvest volume target: (a) area with two consecutive harvests; (b) area harvested once over T periods. Dotted lines show the scenarios with the long-term habitat connectivity objective ($T_{\min} = 100$ years) and dashed lines show the scenarios with the medium-term connectivity objective ($T_{\min} = 60+$ years). DCHS, Dynamic Caribou Harvesting Scheduling



regions where long-term protection of habitat was cost-effective included prime habitat areas near the borders of the FMU, including along the north shore of Lake Nipigon. Habitat protection in these regions can be achieved by relocating harvest to the south-central region with a dense network of access roads, and by using more intensive harvest regimes over the planning period. Prioritizing habitat connectivity leads to a small increase in the overall harvest area because harvest has to be allocated to less productive sites to protect prime caribou habitat containing old conifer stands.

Our results indicate that the implementation of DCHS, which is the current harvesting policy in Ontario’s boreal forests when caribou populations are present, causes only a minor increase of the timber supply cost in our study area. The low impact of DCHS on the timber price is a result of the decision to exclude the south-central portion of the FMU from the DCHS rules (Figure 3, callout I). Notably, several other FMUs in northern Ontario (such as Black Spruce Forest, English River Forest, Kenogami Forest, and Whiskey Jack Forest) are similar in that respect and have DCHS regions delineated in the northern parts, while southern portions are exempt from DCHS harvesting. The impact of DCHS on the timber supply cost would be more significant if the entire FMU area was subject to DCHS. Strict enforcement of DCHS with the control of harvesting in adjacent DCHS regions increases the cost of timber, but the cost increase does not exceed the cost premiums in the solutions prioritizing protection of caribou habitat. In our study area, the complex configuration of the access road network amidst caribou habitat areas, some of which are high-use, translates to strict harvest limitations when prioritizing the protection



TABLE 5 The proportion of the habitat area that remains connected over the long term (100 years) and the medium term (60 years) in solutions that prioritize long-term and medium-term habitat connectivity

Harvest scenario	Habitat protection period, T_{min}	Proportion of the habitat area that remains connected (%)		Proportion of the seasonal habitat that remains connected (%)		Area harvested over T periods (ha)		
		Over 100 years	Over 60 years	Over 100 years	Over 60 years	One harvest	Two harvests	Total
No DCHS*	60 (medium-term)	44.8	67.6	62.4	97.0	173,591	60,534	234,125
	100 (long-term)	58.4	62.2	86.7	91.7	122,562	91,898	214,460
Static DCHS*	60 (medium-term)	45.8	66.0	68.5	93.2	165,672	67,073	232,745
	100 (long-term)	56.5	60.6	84.1	88.3	126,276	91,856	218,132
Dynamic DCHS*	60 (medium-term)	45.9	65.2	62.5	96.3	156,632	70,833	227,465
	100 (long-term)	56.7	59.7	84.0	87.8	127,268	91,508	218,776

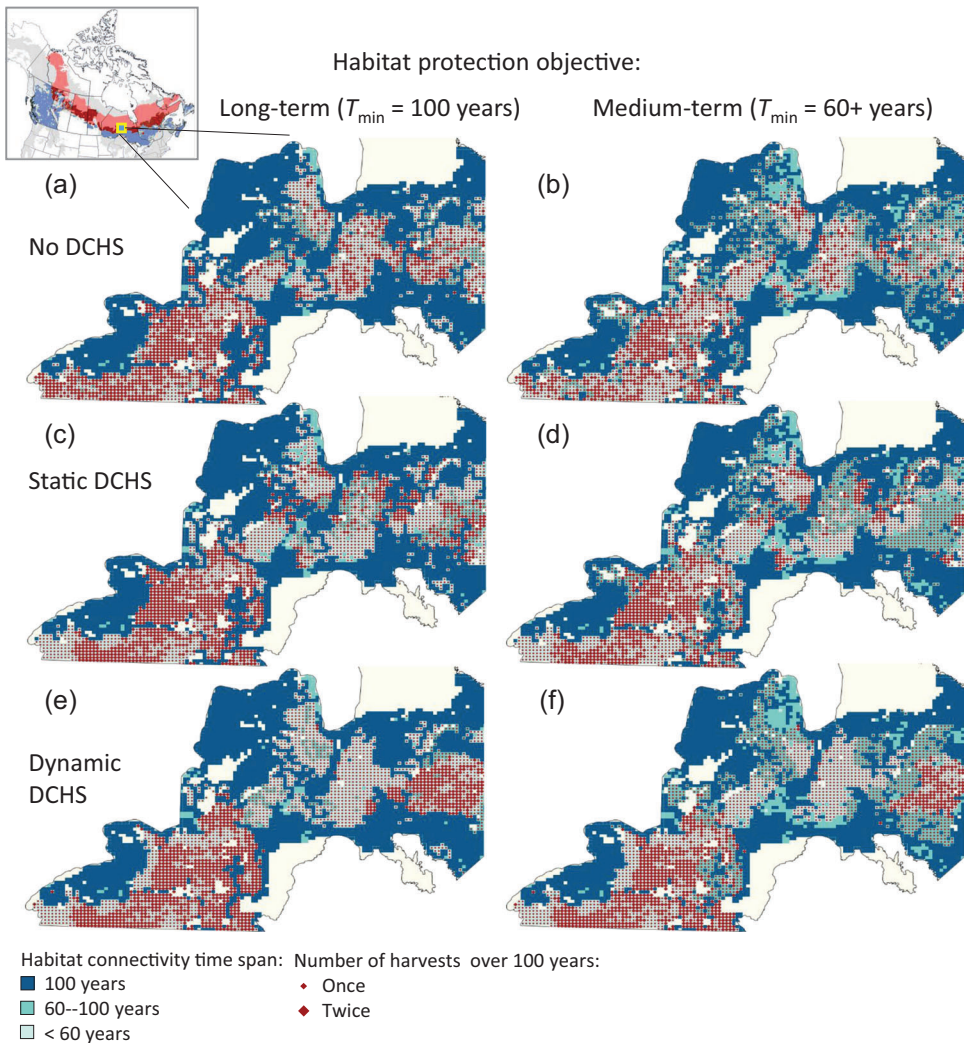


FIGURE 9 Examples of harvest and habitat connectivity patterns for the scenarios with the long-term ($T_{\min} = 100$ years) and medium-term ($T_{\min} = 60+$ years) habitat protection objectives. The maps show the habitat protection priority solutions with the harvest volume target $0.3 \text{ million m}^3\text{-yr}^{-1}$. No-DCHS scenarios: (a) Long-term habitat protection ($T_{\min} = 100$ years); (b) Medium-term habitat protection ($T_{\min} = 60+$ years). Static DCHS scenarios: (c) Long-term habitat protection ($T_{\min} = 100$ years); (d) Medium-term habitat protection ($T_{\min} = 60+$ years). Dynamic DCHS scenarios: (e) Long-term habitat protection ($T_{\min} = 100$ years); (f) Medium-term habitat protection ($T_{\min} = 100$ years). Dark-shaded areas indicate the habitats connected over 100 years, medium-shaded areas—the habitats connected over 60—less than 100 years and light-shaded areas indicate the habitats connected over less than 60 years. Small and large dot symbols show the forest sites with one and two consecutive harvests over the planning horizon T . DCHS, Dynamic Caribou Harvesting Scheduling

of habitat. The impact of these spatial restrictions on harvest patterns is greater than the impact of DCHS rules currently planned for the FMU. This translates to a higher cost of timber supply, but enables protecting, on average, 7.4% more of the total range area and 12.1% more area with seasonal habitat than in the harvest priority scenarios. In our case, adopting a DCHS strategy in conjunction with the habitat protection objective achieves a



reasonable balance between the goals of meeting a desired harvest target and long-term habitat protection, despite the increase in timber supply cost.

Notably, the proposed model was not designed to maintain connectivity corridors between core habitat areas. While the optimal solutions established some corridors between areas with high-use habitat, this was unintentional. Potentially, a set of corridor connectivity constraints could be added to maintain corridor space between high-use habitat areas in different parts of the range, like in the models of St. John et al. (2016) and Conrad et al. (2012). Such a formulation could be useful for planning harvest in areas with isolated caribou ranges, which would require maintaining corridors to facilitate the movement of the animals between the ranges. Habitat connectivity criteria and corridor design are likely to become more important in the future, as the total amount of intact forest suitable to support caribou populations in the Canadian boreal region is likely to decline (EC, 2011).

4.1 | Potential model extensions

The current model formulation did not track costs of constructing logging roads, but instead factored such costs into the total tree-to-mill delivery cost value from a particular forest site. Potentially, the location and timing of road construction could be incorporated via a network flow model similar to the formulation presented in Yoshimoto and Asante (2018). This may increase the cost of moving the harvest to remote DCHS regions, which currently have no access roads.

Our model did not impose limits on the minimum width of the corridors connecting the sites with large amounts of habitat. While the optimal solutions delineated sufficiently large contiguous clusters of suitable habitat, some corridors connecting these large areas had a width of a single map cell. In our study, the minimum width of the habitat corridor was set by our chosen spatial data resolution. The choice of a 1-km resolution followed caribou recovery guidelines from Environment Canada (2011) which calls for a minimum 500-m buffer between protected sites and human disturbances (so a point surrounded by a 500-m buffer suggests a minimum 1-km spatial resolution to model habitat connectivity). Commonly, harvest scheduling is performed at finer spatial scales, but for the sake of practicality, it may be necessary, as in our case, to coarsen the resolution of harvest planning while maintaining the minimum width of the established corridors. Potentially, an approach similar to that presented in St. John et al. (2018) could ensure the minimum width of habitat corridors, but is likely to increase the size of the optimization problem substantially.

ACKNOWLEDGMENTS

The funding for this study was provided by Natural Resource Canada's Cumulative Effects Program. Our sincere thanks to Josie Hughes for advice on the caribou habitat model and DCHS and John Pedlar for useful comments on an early version of the manuscript.

AUTHOR CONTRIBUTIONS

Conceptualization: D. Y., R. G. H., R. R., F. H. K. Data curation: D. Y., N. L., R. R., F. H. K. MIP model development: D. Y. and R. G. H. Funding acquisition: D. Y. Methodology: D. Y., R. G. H., N. L., F. H. K., R. R. Visualization: N.L. Writing: D. Y., R. G. H., R. R., and F. H. K.

ORCID

Denys Yemshanov <http://orcid.org/0000-0002-6992-9614>



REFERENCES

- Avgar, T., Mosser, A., Brown, G. S., & Fryxell, J. M. (2013). Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *Journal of Animal Ecology*, *82*, 96–106.
- Baskent, E. Z., & Keles, S. (2005). Spatial forest planning: A review. *Ecological Modelling*, *188*(2-4), 145–173.
- Bettinger, P., Sessions, J., & Boston, K. (1997). Using Tabu search to schedule timber harvests subject to spatial wildlife goals for big game. *Ecological Modelling*, *94*, 111–123.
- Bieler, A., Trush, M., & Jakob, J. B. (2019). Whitesand's BioEnergy Project. Ontario Centre for Workforce Innovation. Retrieved from <https://ocwi-coie.ca/wp-content/uploads/2019/02/01-017-01-Whitesand-First-Nation-Final-Report-1.pdf>
- Boulanger, Y., Gauthier, S., & Burton, P. J. (2014). A refinement of models projecting future Canadian fire regimes using homogeneous fire regime zones. *Canadian Journal of Forest Research*, *44*, 365–376.
- Brandt, J. P., Flannigan, M. D., Maynard, D. G., Thompson, I. D., & Volney, W. J. A. (2013). An introduction to Canada's boreal zone: Ecosystem processes, health, sustainability, and environmental issues. *Environmental Reviews*, *21*(4), 207–226.
- Canadian Parks and Wilderness Society, Wildland League (CPAWS). (2009). *A snapshot of caribou range condition in Ontario*. Special Report. Retrieved from <https://wildlandsleague.org/media/Caribou-Range-Condition-in-Ontario-WL2009-HIGH-RES.pdf>
- Cordeira, J., Gaston, K., & Pinto, L. (2005). Connectivity in priority area selection for conservation. *Environmental Modeling & Assessment*, *10*(3), 183–192.
- Committee on the Status of Endangered Wildlife in Canada (COSEWIC). (2011). *Designatable units for caribou (Rangifer tarandus) in Canada*. Committee on the status of endangered wildlife in Canada. Ottawa, ON: Environment Canada. Retrieved from http://www.cosewic.gc.ca/4E5136BF-F3EF-4B7A-9A79-6D70BA15440F/COSEWIC_Caribou_DU_Report_23Dec2011.pdf
- Conrad, J., Gomes, C. P., van Hove, W.-J., Sabharwal, A., & Suter, J. (2012). Wildlife corridors as a connected subgraph problem. *Journal of Environmental Economics and Management*, *63*(1), 1–18.
- Constantino, M., Martins, I., & Borges, J. (2008). A new mixed-integer programming model for harvest scheduling subject to maximum area restrictions. *Operations Research*, *56*(3), 542–551.
- Crowe, K., Nelson, J., & Boyland, M. (2003). Solving the area-restricted harvest scheduling model using the branch and bound algorithm. *Canadian Journal of Forest Research*, *33*(9), 1804–1814.
- Dilkina, B., Houtman, R., Gomes, C., Montgomery, C., McKelvey, K., Kendall, K., ... Schwartz, M. (2017). Trade-offs and efficiencies in optimal budget-constrained multispecies corridor networks. *Conservation Biology*, *31*, 192–202. <https://doi.org/10.1111/cobi.12814>
- Elkie, P., Green, K., Racey, G., Gluck, M., Elliott, J., Hooper, G., ... Rempel, R. (2018). *Science and information in support of policies that address the conservation of Woodland Caribou in Ontario: Occupancy, habitat and disturbance models, estimates of natural variation and range level summaries*. Electronic Document. Version 2018. Ontario Ministry of Natural Resources, Forests Branch.
- Environment and Climate Change Canada (ECCC) (2017). *Report on the progress of recovery strategy implementation for the woodland caribou (Rangifer tarandus caribou), boreal population in Canada for the period 2012-2017. Species at Risk Act Recovery Strategy Series*. Ottawa, ON. Retrieved from http://registrelep-sararegistry.gc.ca/virtual_sara/files/Rs%2DReportOnImplementationBorealCaribou%2Dv00%2D2017Oct31%2DEng%2Epdf
- Environment Canada (EC). (2011). *Scientific assessment to support the identification of critical habitat for woodland caribou Rangifer tarandus caribou), boreal population, in Canada* (p. 115). Ottawa, ON.
- Environment Canada (EC). (2012). *Recovery Strategy for the woodland Caribou (Rangifer tarandus caribou), boreal population, in Canada. Species at risk act recovery strategy series*. Ottawa, ON: Environment Canada. Retrieved from http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/plans/rs%5Fcaribou%5Fboreal%5Fcaribou%5F0912%5Fe1%2Epdf
- Felton, A., Ranius, T., Roberge, J.-M., Öhman, K., Lämås, T., Hynynen, J., ... Nordin, A. (2017). Projecting biodiversity and wood production in future forest landscapes: 15 key modeling considerations. *Journal of Environmental Management*, *197*, 404–414.
- Ferguson, S. H., & Elkie, P. C. (2004a). Habitat requirements of boreal forest caribou during the travel seasons. *Basic and Applied Ecology*, *5*, 465–474.



- Ferguson, S. H., & Elkie, P. C. (2004b). Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). *Journal of Zoology*, 262, 125–134.
- Festa-Bianchet, M., Ray, J. C., Boutin, S., Cote, S. D., & Gunn, A. (2011). Conservation of caribou (*Rangifer tarandus*) in Canada: An uncertain future. *Canadian Journal of Zoology*, 89(50), 419–434.
- Forest Products Association of Canada (FPAC). (2018). *Forest sector contributions to woodland caribou recovery. September 2018*. Retrieved from https://www.fpac.ca/wp-content/uploads/FPAC04_CaribouReport_F5_en-web_Compressed.pdf
- GAMS Development Corporation (GAMS) (2019). General algebraic modeling system (GAMS). Washington, DC. Retrieved from <http://www.gams.com>
- Gurobi Optimization Inc. (GUROBI). (2019). *GUROBI optimizer reference manual. Version 8.1*. Retrieved from <http://www.gurobi.com>
- Hebblewhite, M. (2017). Billion dollar boreal woodland caribou and the biodiversity impacts of the global oil and gas industry. *Biological Conservation*, 206, 102–111.
- Hebblewhite, M., & Fortin, D. (2017). Canada fails to protect its caribou. *Science*, 358(6364), 730–731.
- Hornseth, M. L., & Rempel, R. S. (2015). Seasonal resource selection of woodland caribou (*Rangifer tarandus caribou*) across a gradient of anthropogenic disturbance. *Canadian Journal of Zoology*, 94, 79–93.
- Jafari, N., & Hearne, J. (2013). A new method to solve the fully connected reserve network design problem. *European Journal of Operational Research*, 231(1), 202–209.
- Jafari, N., Nuse, B. L., Moore, C. T., Dilkina, B., & Hepinstall-Cymerman, J. (2017). Achieving full connectivity of sites in the multiperiod reserve network design problem. *Computers & Operations Research*, 81, 119–127.
- James, A. R. C., Boutin, S., Hebert, D. M., & Rippin, A. B. (2004). Spatial separation of caribou from moose and its relation to predation by wolves. *Journal of Wildlife Management*, 68(4), 799–809.
- James, A. R. C., & Stuart-Smith, A. K. (2000). Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management*, 64, 154–159.
- Johnson, C. J., Parker, K. L., Heard, D. C., & Gillingham, M. P. (2002). A multiscale behavioural approach to understanding the movements of woodland caribou. *Ecological Applications*, 12, 1840–1860.
- Johnson, K. N., & Scheurman, H. L. (1977). Techniques for prescribing optimal timber harvest and investment under different objectives discussion and synthesis. *Forest Science*, 23, a0001–z0001.
- Latham, A. D. M., Latham, C., McCutchen, N. A., & Boutin, S. (2011). Invading white-tailed deer change wolf-caribou dynamics in northeastern Alberta. *Journal of Wildlife Management*, 75(1), 204–212.
- Martell, D. L., Gunn, E. A., & Weintraub, A. (1998). Forest management challenges for operational researchers. *European Journal of Operations Research*, 104(1), 1–17.
- Martin, A. B., Richards, E., & Gunn, E. (2016). Comparing the efficacy of linear programming models I and II for spatial strategic forest management. *Canadian Journal of Forest Research*, 47, 16–27.
- Martin, A. B., Ruppert, J. L. W., Gunn, E. A., & Martell, D. L. (2017). A replanning approach for maximizing woodland caribou habitat alongside timber production. *Canadian Journal of Forest Research*, 47, 901–909.
- Maure, J. (2013). *Ontario forest biofibre*. Presentation made at Cleantech Biofuels Workshop, February 13, 2013. Retrieved from https://www.sault-canada.com/en/aboutus/resources/Supporting_Doc_2_-_Available_biomass.pdf
- McDill, M., Rebain, S., & Braze, J. (2002). Harvest scheduling with area-based adjacency constraints. *Forest Science*, 48(4), 631–642.
- McDill, M. E., & Braze, J. (2000). Comparing adjacency constraint formulations for randomly generated forest planning problems with four age-class distributions. *Forest Science*, 46(3), 423–436.
- McDill, M. E., Tóth, S. F., John, R. T., Braze, J., & Rebain, S. A. (2016). Comparing model I and model II formulations of spatially explicit harvest scheduling models with maximum area restrictions. *Forest Science*, 62(1), 28–37.
- McKenney, D. W., Mussell, A., & Fox, G. (2004). An economic perspective on emulation forestry and a case study on woodland caribou-wood production trade-offs in northern Ontario. In A. Perera, L. Buse & M. Weber (Eds.), *Emulating natural forest landscape disturbances: Concepts and applications* (pp. 209–218). Columbia University Press. Chapter 17.
- McKenney, D. W., Nippers, B., Racey, G., & Davis, R. (1997). Trade-offs between wood supply and caribou habitat in northwestern Ontario. *Rangifer*, 10, 149–156.



- McKenney, D. W., Yemshanov, D., Pedlar, J., Allen, D., Lawrence, K., Hope, E., ... Eddy, B. (2016). Canada's timber supply: Current status and future prospects under a changing climate. Natural Resources Canada, Canadian Forest Service. Great Lakes Forestry Centre, Sault Ste. Marie, Ontario. 75p. Information Report GLC-X-15.
- Meneghin, B. J., Kirby, M. W., & Jones, J. G. (1988). An algorithm for writing adjacency constraints efficiently in linear programming models. In B. Kent & L. Davis (Eds.), *The 1988 Symposium on Systems Analysis in Forest Resources* (pp. 46–53). USDA Forest Service Rocky Mountain For. Range Exp. Stn. Gen. Tech. Mar. 29-Apr. 1, 1988.
- National Forestry Database (NFD). (2019). *Harvest. 5.2 Area harvested by jurisdiction, tenure, management and harvesting method*. Retrieved from <http://nfdp.ccfm.org/en/data/harvest.php>
- Natural Resources Canada (NRCan). (2019). *Topographic data of Canada—CanVec Series*. Retrieved from <https://open.canada.ca/data/en/dataset/8ba2aa2a-7bb9-4448-b4d7-f164409fe056>
- Neegan Burnside Ltd. (2014). *Witesand First Nation Cogeneration and Pellet Mill Project Design and Operations Report*. Prepared by Neegan Burnside Ltd. for Sagatay Cogeneration LP, with its General Partner, Sagatay Cogeneration Ltd., and Whitesand First Nation as agent. October 2014. Retrieved from https://www.whitesandfirstnation.com/assets/files/REA/final/030895_8_Design_and_Operations_Report.pdf
- Öhman, K. (2000). Creating continuous areas of old forest in long term forest planning. *Canadian Journal of Forest Research*, 30, 1817–1823.
- Öhman, K., Edenius, L., & Mikusiński, G. (2011). Optimizing spatial habitat suitability and timber revenue in long-term forest planning. *Canadian Journal of Forest Research*, 41, 543–551.
- Önal, H., & Briers, R. A. (2006). Optimal selection of a connected reserve network. *Operations Research*, 54(2), 379–388.
- Ontario Ministry of Natural Resources and Forestry (OMNRF). (2015). *General habitat description for the forest-dwelling woodland caribou (Rangifer tarandus caribou)*. Retrieved from <http://govdocs.ourontario.ca/node/29324>
- Ontario Ministry of Natural Resources and Forestry (OMNRF). (2018). *Forest Resources Inventory (FIM v 2.2D) Packaged Product*. Available at <https://geohub.lio.gov.on.ca/datasets/forest-resources-inventory-fim-v2-2d-packaged-product>
- Ontario Ministry of Natural Resources (OMNR). (2009). *Ontario's Woodland Caribou Conservation Plan*. Toronto, ON: Queen's Printer for Ontario.
- Ontario Ministry of Natural Resources (OMNR). (2012). *Ontario's Woodland Caribou Conservation Plan progress report winter 2012*. Toronto, ON: Ontario Ministry of Natural Resources. Retrieved from <https://www.porcupininspectors.com/wp-content/uploads/Woodland-Caribou.pdf>
- Ontario Ministry of Natural Resources (OMNR). (2014). *Forest Management Guide for Boreal Landscapes*. Toronto, ON: Queen's Printer for Ontario.
- Pond, B. A., Brown, G. S., Wilson, K. S., & Schaefer, J. A. (2016). Drawing lines: Spatial behaviours reveal two ecotypes of woodland caribou. *Biological Conservation*, 194, 139–148.
- Racey, G., Harris, A., Gerrish, L., E. Armstrong, E., McNicol, J., & Baker, J. (1999). *Forest management guidelines for the conservation of woodland caribou: A landscape approach*. Thunder Bay, ON: Ontario Ministry of Natural Resources.
- Rempel, R. S., & Hornseth, M. L. (2018). *Range-specific seasonal resource selection probability functions for 13 caribou ranges in Northern Ontario* (p. 42). Peterborough, ON: Ontario Ministry of Natural Resources and Forestry, Science and Research Branch. Science and Research Internal File Report IFR-01.
- Ruppert, J. L. W., Fortin, M.-J., Gunn, E. A., & Martell, D. L. (2016). Conserving woodland caribou habitat while maintaining timber yield: A graph theory approach. *Canadian Journal of Forest Research*, 46, 914–923.
- Sessions, J. (1992). Solving for habitat connections as a Steiner network problem. *Forest Science*, 38(1), 203–207.
- Snyder, S., & ReVelle, C. (1996). Temporal and spatial harvesting of irregular systems of parcels. *Canadian Journal of Forest Research*, 26(6), 1079–1088.
- Snyder, S., & ReVelle, C. (1997). Dynamic selection of harvests with adjacency restrictions: The SHARe model. *Forest Science*, 43(2), 213–222.
- Snyder, S. A., Haight, R. G., & ReVelle, C. S. (2004). Scenario optimization model for dynamic reserve site selection. *Environmental Modelling & Assessment*, 9(3), 179–187.



- Species at Risk Act (SARA). (2002). *Bill C-5, An act respecting the protection of wildlife species at risk in Canada*. 25 August 2010. Retrieved from <http://laws.justice.gc.ca/PDF/Statute/S/S-15.3.pdf>
- St. John, R., Tóth, S. F., & Zabinsky, Z. (2018). Optimizing the geometry of wildlife corridors in conservation reserve design. *Operations Research*, 66, 1471–1485. <https://doi.org/10.1287/opre.2018.1758>.
- St. John, R., Öhman, K., Tóth, S. F., Sandström, P., Korosuo, A., & Eriksson, L. O. (2016). Combining spatiotemporal corridor design for reindeer migration with harvest scheduling in northern Sweden. *Scandinavian Journal of Forest Research*, 37(1), 655–663.
- Tóth, S. F., Haight, R. G., & Rogers, L. W. (2011). Dynamic reserve selection: Optimal land retention with land-price feedbacks. *Operations Research*, 59(5), 1059–1078.
- Tóth, S. F., Haight, R. G., Snyder, S., George, S., Miller, J., Gregory, M., & Skibbe, A. (2009). Reserve selection with minimum contiguous area restrictions: An application to open space protection planning in suburban Chicago. *Biological Conservation*, 142(8), 1617–1627.
- Venier, L. A., Thompson, I. D., Fleming, R., Malcolm, J., Aubin, I., Trofymow, J. A., ... Brandt, J. P. (2014). Effects of natural resource development on the terrestrial biodiversity of Canadian boreal forests. *Environmental Reviews*, 22(4), 457–490.
- Weintraub, A., Barahona, F., & Epsten, R. (1994). A column generation algorithm for solving general forest planning problems with adjacency constraints. *Forest Science*, 40(1), 142–161.
- Williams, J. C., ReVelle, C. S., & Levin, S. A. (2004). Using mathematical optimization models to design nature reserves. *Frontier in Ecology and Environment*, 2(2), 98–105.
- Williams, J. C., ReVelle, C. S., & Levin, S. A. (2005). Spatial attributes and reserve design models: A review. *Environmental Modeling and Assessment*, 10(3), 163–181.
- Williams, J. C., & Snyder, S. A. (2005). Restoring habitat corridors in fragmented landscapes using optimization and percolation models. *Environmental Modeling and Assessment*, 10, 239–250.
- Wittmer, H. U., Sinclair, A. R. E., & McLellan, B. N. (2005). The role of predation in the decline and extirpation of woodland caribou. *Oecologia*, 144, 257–267.
- Yemshanov, D., Haight, R. G., Koch, F. H., Parisien, M.-A., Swystun, T., Barber, Q., ... Liu, N. (2019). Prioritizing restoration of fragmented landscapes for wildlife conservation: A graph theoretic approach. *Biological Conservation*, 232, 173–186.
- Yemshanov, D., Haight, R. G., Liu, N., Parisien, M.-A., Barber, Q., Koch, F. H., ... Choudhury, S. (2020). Assessing the trade-offs between timber supply and wildlife protection goals in boreal landscapes. *Canadian Journal of Forest Research*, 50, 243–258.
- Yoshimoto, A., & Asante, P. (2018). A new optimization model for spatially constrained harvest scheduling under area restrictions through maximum flow problem. *Forest Science*, 64(4), 392–406.

How to cite this article: Yemshanov D, Haight RG, Rempel R, Liu N, Koch FH. Protecting wildlife habitat in managed forest landscapes—How can network connectivity models help? *Natural Resource Modeling*. 2021;34:e12286. <https://doi.org/10.1111/nrm.12286>