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Assessing factors influencing the space use of a woodland caribou *Rangifer tarandus caribou* population using an individual-based model

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Similar to earlier studies, a population of woodland caribou *Rangifer tarandus caribou* in west-central Manitoba, Canada, showed preference for mature coniferous forests and fidelity to seasonal home ranges. However, because preferred forest types were common in the study area, these findings could not determine what would happen if these home ranges were disturbed because the relative importance of preference for these forest types and home-range fidelity in determining the space use of this population was not known. This question was explored using an individual-based space-use model that incorporates a random movement component, a habitat value function that considers these two factors individually or together, and a decision optimisation component. Four possible forms of the model were used to conduct Monte-Carlo simulations of space-use patterns, which were compared to true range-use patterns over an annual cycle. True range use could not be simulated without including a home-range fidelity factor in the model. This suggests that there is some factor about the selected home ranges that is not quantified by the forest type which is currently present that causes animals in this population to show fidelity to them. The explanation most consistent with the general understanding of the factors limiting this species is that these home ranges are refuges from predation. This suggests that the appropriate conservation action is to protect these ranges from disturbance unless the animals themselves demonstrate the presence of other suitable areas by dispersing to them.

Key words: habitat preference, home range, Manitoba, movement, Rangifer, Monte Carlo simulation, site fidelity

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Woodland caribou *Rangifer tarandus caribou* are presently a conservation priority in many parts of Canada. Past studies have shown that this species uses mature coniferous forests (e.g. Rettie & Messier 2000, Mahoney & Virgil 2003, Mosnier et al. 2003, Metsaranta & Mallory 2007), shows some fidelity to calving sites and makes small shifts in the areas which they use in winter though these areas can be broadly similar (e.g. Cumming & Beange 1987, Schaeffer et al. 2000, Rettie & Messier 2001, Wittmer et al. 2006, Metsaranta & Mallory 2007). In other words, both fidelity to seasonal ranges and preference for mature coniferous forests influence the space-use patterns of populations of this species. Evidence suggests that this species exhibits these behaviours in order to segregate themselves spatially from other ungulates and their primary predator, the wolf *Canis lupus* (Bergerud & Elliot 1986, Bergerud et al. 1990, Rettie & Messier 2000, Smith et al. 2000, James et al. 2004).

My study considers a population of woodland caribou in an area known as the Naosap range in west-central Manitoba, Canada (Fig. 1). The population is potentially affected by resource development activities, so it is considered to be of high conservation concern (Manitoba Conservation 2005). In a previous study, this population showed highly selective use of mature coniferous forests and fidelity

to seasonal home ranges (Metsaranta & Mallory 2007), and thus exhibited behaviour typical of this species. However, the effect of increased disturbance on this population could not be determined from these observations because most of the study area (68%) consisted of mature coniferous forest types, some of which were seemingly unoccupied. As a result, the importance of the selective use of these forests, relative to the importance of fidelity to seasonal home ranges, remained unknown. Typically, habitat selection studies examine only relative preference for different vegetation types. However, other factors in the home ranges to which animals in this population show fidelity may also be important, and may not be quantified by the type of forest currently present at those locations. Both selective use of mature coniferous forest and fidelity are components of habitat selection, but are rarely assessed concurrently. In my study, I used an individual-based model (IBM) to simulate the movement of individual animals in the population to test the relative importance of these two factors (preference for certain forest types and home-range fidelity) in determining its space-use pattern over the course of an annual cycle. Recent studies using simulation models to examine the ecology and management of woodland caribou (e.g. Bergman et al. 2000, Johnson et al. 2002, Franke et al. 2004, Weclaw &

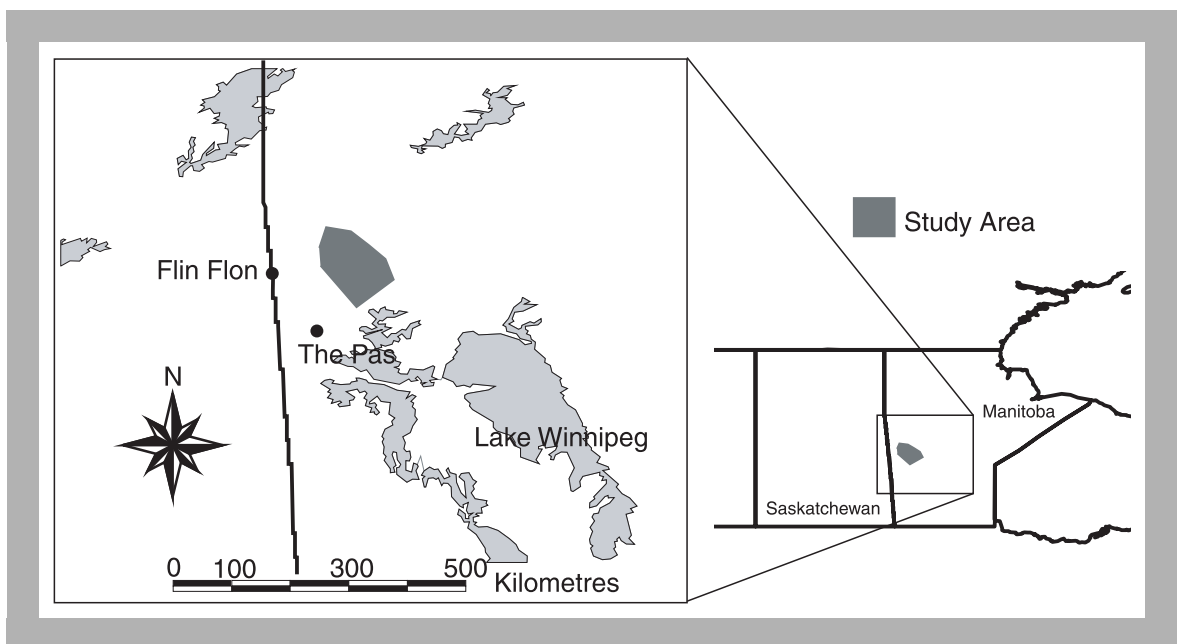


Figure 1. Location of the study area which straddles the boundary of the boreal shield and boreal plains ecozones in west-central Manitoba, Canada.

Hudson 2004, McNay et al. 2006, McCutchen 2007) have not addressed this type of question explicitly. IBMs describe the behaviour of individual organisms, and thus operate at the lowest level of the biological hierarchy considered in ecology (Breckling et al. 2006, Grimm et al. 2006). Several recent studies have applied IBMs to study the ecology a number of different species (e.g. Railsback et al. 1999, Railsback & Harvey 2002, Willis et al. 2006).

Determining the relative importance of preference for certain forest types and fidelity to home ranges is important because their relative ranking has different conservation implications for the population. If selective use of mature coniferous forest is more important, then this suggests that disturbing the home ranges currently used would have a negligible effect as long as sufficient suitable forest remains in the larger region to which animals could disperse. For example, Rettie & Messier (2001) suggested that female caribou in Saskatchewan (ca 400 km to the west of my study area) did not exhibit calving site fidelity because many similar unoccupied areas were available. In this case, the appropriate conservation action would be to ensure that enough forest in the greater study region is in a suitable condition. Previous assessments have shown that it will take at least 40 years after disturbance for forests in the region to return to this condition (Metsaranta 2007). Thus, determining what constitutes a sufficient level of suitable habitat and what condition it must remain in is a non-trivial problem (Racey & Arsenault 2007). On the other hand, if home-range fidelity is more important, then this implies that some important characteristic of the home ranges currently used is not described simply by the forest type that is currently present. Cumming (1996) suggests that seasonal ranges represent implicit refuges from predation. In this case, the appropriate conservation action would be to ensure that the home ranges which these animals presently choose to use should be protected from changes to their floral, but more particularly to their faunal (e.g. Bergerud 2007) composition.

Material and methods

Study area

My study area is in west-central Manitoba, Canada, northeast of the towns of Flin Flon and The Pas (see Fig. 1). The northern part of the study area is in the Churchill River upland ecoregion of the boreal

shield ecozone, consisting of bedrock outcrops interspersed with lowlands and lakes, with low topographic relief. The southern part is in the mid-boreal lowland ecoregion of the boreal plains ecozone, consisting of lacustrine or organic parent materials and level topography. Tree species include black spruce *Picea mariana*, white spruce *Picea glauca*, jack pine *Pinus banksiana*, tamarack *Larix laricina*, trembling aspen *Populus tremuloides* and white birch *Betula papyrifera*. Mean daily temperatures range from +17.7°C in July to -21.4°C in January, mean annual rainfall and snowfall from 323.3 mm and 170.2 cm in The Pas to 345.3 mm and 143.9 cm in Flin Flon. Snow is present from mid-November to early April, with maximum depths in January and February. A large part of the study area burned in 1989 (Hirsch 1991).

Data collection

Radio-telemetry data were collected from February of 1998 to April of 2001. Animals were captured by net gunning and outfitted with standard VHF radio collars (Lotek Wireless Inc, Newmarket, Ontario, Canada). Between 14 and 25 female woodland caribou were located every two weeks using standard aerial radio-tracking methods. A total of 1,358 locations were obtained. Methods are further described in Metsaranta (2002) and Metsaranta & Mallory (2007).

Model simulations

A complete description of the individual-based model (IBM) used to conduct the simulations can be found in Appendix I. For this paper, I evaluated four possible versions of the IBM which differed as to whether or not the movement of individuals is random or non-random, and also the factors that cause movement to be non-random. The four models were: a random movement model (Model 1), a model in which movements are governed only by habitat preference (Model 2), a model in which movements are governed only by home-range fidelity (Model 3), and a model governed by both habitat preference and home-range fidelity (Model 4). The models are further described in Table 1. These four models have been chosen for several reasons. Model 1 is included because it represents a basic null-model where simulated animals move randomly without preference. Model 2 and Model 3 are meant to test the two hypotheses outlined in the introduction, each of which has different management implications. If the portion of the study area

Table 1 . Habitat types present in the study area, proportion of the study area which the habitat types represent (in %), third order habitat preferences determined by compositional analysis, and the habitat value assigned to each of those types in the movement model.

Habitat type	% of study area	Summer habitat quality	Model value	Winter habitat quality	Model value
Upland conifer pine	9.3	High	100	High	100
Upland conifer spruce	11.0	High	100	High	100
Lowland conifer	6.7	Neutral	50	Neutral	50
Upland hardwood	2.1	Low	0	Neutral	50
Treed muskeg	30.5	High	100	High	100
Open wetland	6.1	Neutral	50	Neutral	50
Water	16.7	High	100	Neutral	50
Immature conifer	14.7	Neutral	50	Neutral	50
Immature hardwood	1.2	Low	0	Low	0
Open hardwood	2.1	Low	0	Low	0
Open conifer	1.2	Neutral	50	Neutral	50
Non-vegetated	0.1	Low	0	Neutral	50

that consisted of preferred forest types (68%) coincided with the home ranges to which the study animals exhibited fidelity, then Model 2 should be sufficient to simulate space-use patterns. If, on the other hand, there is something else in the home ranges which causes the animals in this population to show fidelity to them that is not quantified by the type of vegetation present, then Model 3 would be required. Model 4 is relevant in as far as it tests the additional predictive capability of a complex model that includes both factors, relative to more simple models that include only one factor.

Model initialisation

For the simulations, biological years began on 16 April of one year and ended on 15 April of the following year. Each simulation began with the true locations (N = 22 animals) at the beginning of the biological year of 1999. The annual simulation period was divided into two seasons with a different

Table 2. Parameters of each of the four possible individual-based models (1-4) that were used in attempting to explain the space use of woodland caribou in the Naosap area of west-central Manitoba.

Model	Name	Chances to optimise (N)	Forest type preference weight (H _w)	Home-range fidelity weight (S _w)
1	Random	1	0	0
2	Forest type preference only	25	1	0
3	Home-range fidelity only	25	0	1
4	Both	25	1	1

home-range centre and preference for different forest types: summer (16 April-15 October), and winter (16 October-15 April). The home-range centre was defined as the mean x-coordinate and mean y-coordinate of the locations for that animal during that season. I defined 12 forest types (Table 2) from a vector-based Forest Resource Inventory (FRI) database that was converted to a 1 km² grid. Seasonal preference values for each forest type were

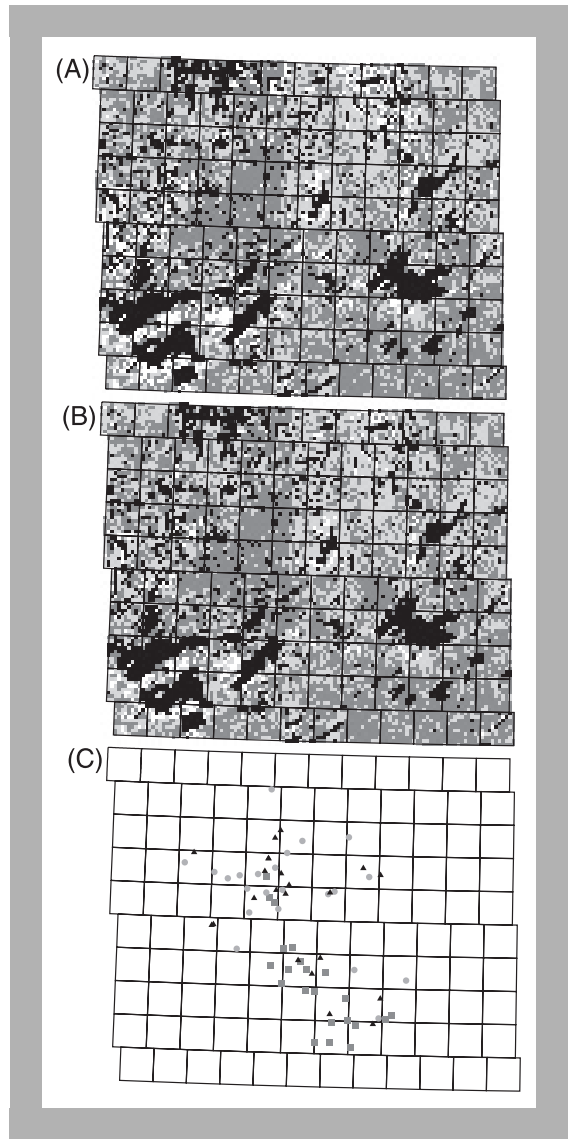
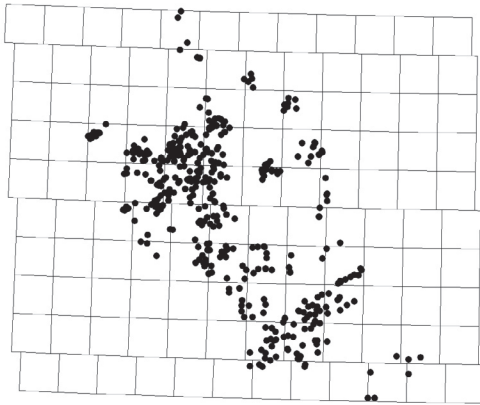
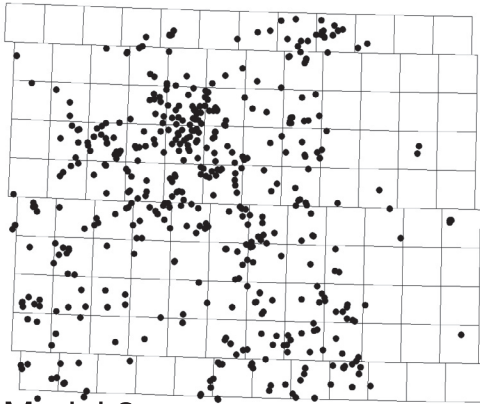


Figure 2. Some initial conditions in the model showing A) summer habitat preference, and B) winter habitat preference with darker grey tones indicating preferred habitats; black areas are water. C) shows the start locations (▲), summer home ranges (●) and winter home ranges (■) for each animal. The large grid cells are 100 km² townships, and each habitat grid cell is 1 km².

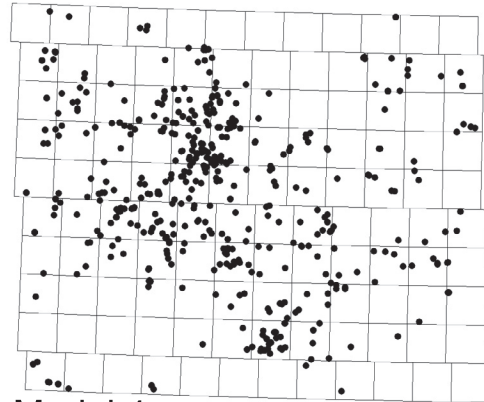
Observed



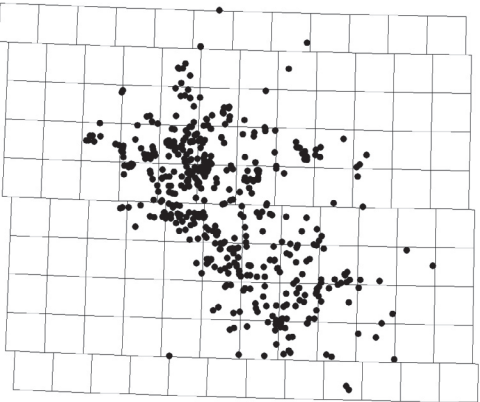
Model 1



Model 2



Model 3



Model 4

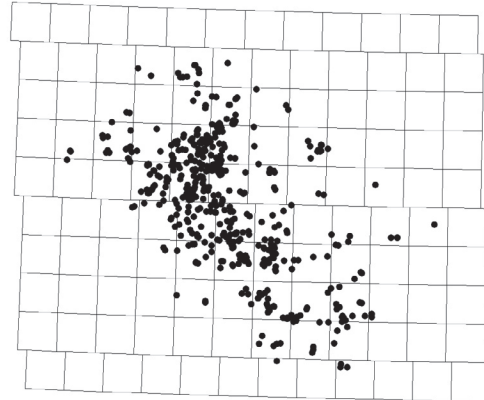


Figure 3. The true locations of animals for the biological year of 1999, and a realisation of simulated locations from each of the four models.

determined by compositional analysis (Aebischer et al. 1993) and represent third order selection (Johnson 1980). High-value forests were defined as those that were not significantly preferred over the

highest ranked forest type and were given a value of 100. Low-value forests were defined as those that were not significantly preferred over the lowest ranked forest type, and were given a value of 0. All

other forest types were considered neutral and were given a value of 50. More details on telemetry data collection, habitat selection analysis and how habitat types were defined from the FRI data can be found in Metsaranta & Mallory (2007) and Metsaranta (2002). The distribution of different forest quality classes in each season, the centre of each animal's home range in each season, and the location of each animal at the beginning of the biological year of 1999, are presented in Figure 2.

Model evaluation

For each of the four models, 100 Monte Carlo simulations of annual cycles were generated, and the coordinates imported into ArcView GIS. True locations during the biological year of 1999 and simulated locations from one realization of each model, are presented in Figure 3. Fixed kernel home-range estimates were calculated at four probability isopleths (95, 75, 50 and 25%) for the true locations and each Monte Carlo repetition of each model using the animal movement extension for ArcView

(Hooge & Eichenlaub 1999). The resulting polygon of each probability isopleth for each Monte Carlo repetition of each model was intersected with the corresponding isopleth for the true locations. From this, a spatial version of the Dice similarity coefficient (Dice 1945) was calculated as:

$$D = \frac{2(P_t \cap P_s)}{2(P_t \cap P_s) + P_t \not\subset P_s + P_s \not\subset P_t} \quad (1),$$

where P_t is the polygon representing the true distribution of locations, P_s is the polygon representing the simulated location, $P_t \cap P_s$ is the area covered by both the true and simulated polygons, $P_t \not\subset P_s$ is the area of the true polygon not contained within the simulated polygon, and $P_s \not\subset P_t$ is the area of the simulated polygon not contained within the true polygon. The Dice coefficient does not depend upon which polygon is considered to overlap the other, approaches 1 when the two polygons overlap perfectly in space and have the same area, and approaches 0 either as the area over which the polygons overlap becomes small or when the difference in area

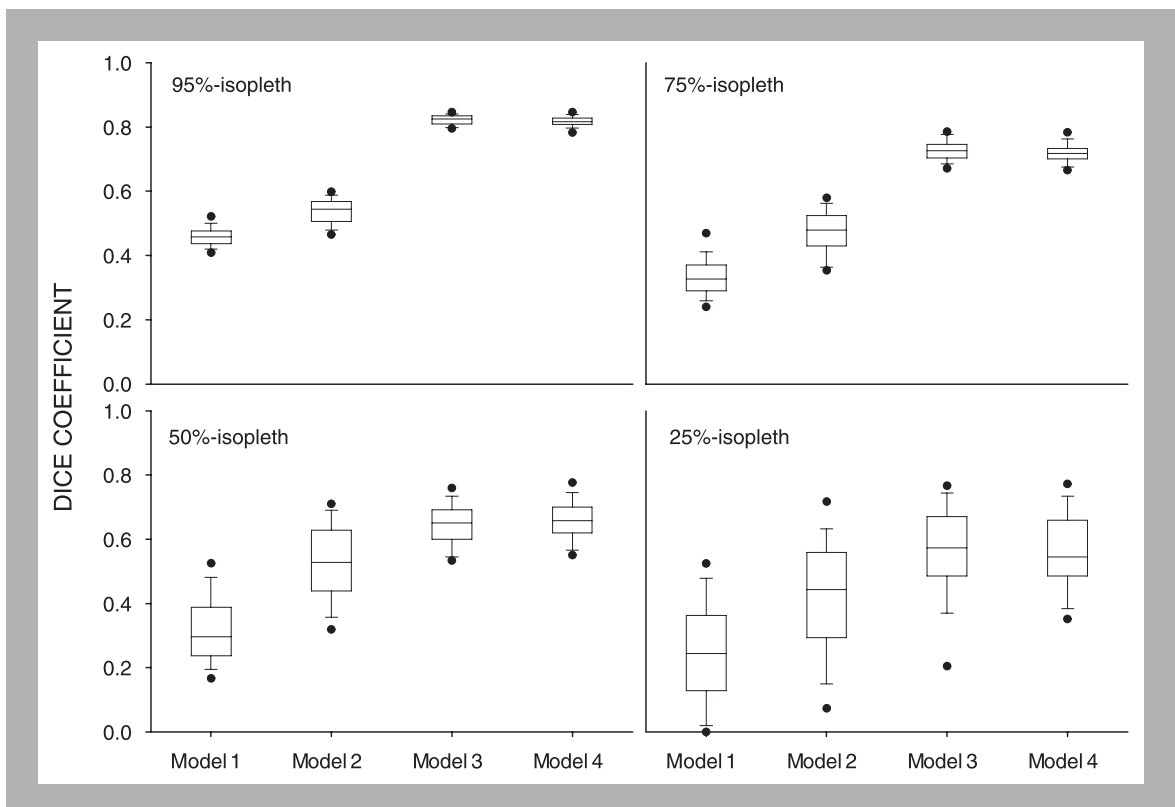


Figure 4. Box and whisker plots depicting the distribution of the spatial Dice coefficient values for 100 Monte Carlo repetitions for each of the four models at each probability isopleth tested. The ends of the box represent the lower and upper quartiles, the line in the box represents the median, the whiskers represent the 10th and 90th percentiles, and the dots represent the 5th and 95th percentiles.

between them becomes very large (Zijdenbos et al. 1994). Models better able to simulate space use have values closer to 1. The Dice coefficient values were logit transformed, and a one-way analysis of variance was used to determine if there were significant differences in the Dice coefficient among the four models at each of the four probability isopleths tested.

Results

The distribution of Dice coefficient values obtained from the 100 Monte Carlo simulations for each model for each of the four probability isopleths tested (Fig. 4), showed that for all isopleths, there were significant differences in the Dice coefficient values among the four models ($F_{3,396} = 3952.4$, $P < 0.001$ for the 95%-isopleth; $F_{3,396} = 1158.6$, $P < 0.001$ for the 75%-isopleth; $F_{3,396} = 212.3$, $P < 0.001$ for the 50%-isopleth; $F_{3,396} = 60.3$, $P < 0.001$ for the 25%-isopleth). Post-hoc tests (Scheffe) showed that the values for all of the non-random models (Models 2, 3 and 4) were significantly higher than the values for the random model (Model 1), that the values for the models incorporating home-range fidelity (Models 3 and 4) were significantly higher than the values for the model incorporating only preference for different forest types (Model 2), and that the values for the model incorporating preference for different forest types (Model 2) were significantly larger than the values for the random model (Model 1). The values for the two models that incorporated home-range fidelity (Models 3 and 4) were not significantly different.

Discussion

The true space use of this population was best described by Model 3 and Model 4, in which simulated animals considered home-range fidelity in their movement decisions. The model that was least able to do so was Model 1, in which simulated animals moved at random. A home-range model that considers only a simple directional bias towards a centre was first described by Holgate (1971), and has been used as a null model for the basis of evaluating other possible mechanistic home-range models for other species, including wolves (Lewis & Murray 1993) and coyotes *Canis latrans* (Moorcroft et al. 1999). These studies found that a model incorporating

aversion to the scent marks of adjacent packs improved the ability to model range dynamics relative to the simple directional bias model. In contrast, my study showed that a simple directional bias was sufficient to adequately model the range use of this woodland caribou population. Although the model incorporating preference for different forest types (Model 2) was significantly better at modelling space use than a random model (Model 1), it was not as good as models incorporating home-range fidelity (Models 3 and 4). Incorporating information about preference for different forest types into a model that already included home-range fidelity did not improve upon its ability to simulate space use, as there was no significant difference between Model 3 (in which animals made decisions based only on home-range fidelity) and Model 4 (in which animals made decisions based on both home-range fidelity and preference for different forest types). Model 4 requires detailed information about which forest types are preferentially used, and therefore Model 3 is more parsimonious. In other words, a model that included more information did not improve the ability to simulate the space use of this population, in contrast to a simple model that includes only a directional bias towards the centre of a home range. However, extrapolating this finding to other populations may require caution as the models were not tested on independent data not used for model parameterisation.

It may be possible that incorporation of additional factors into the habitat value function would result in simulated space-use patterns which match the true space-use patterns equally well or better than a simple model that takes into account only home-range fidelity. For example, female woodland caribou may avoid other caribou during the spring and summer calving and post-calving periods as a spacing out strategy to remain hidden from predators (Bergerud 1996). The value function could be modified in such a way that individuals move about the environment at this time of year to maximise their distance from other caribou. In addition, since caribou are known to shift their winter distribution in relation to snow conditions (Stardom 1975, Darby & Pruitt 1984), it would be possible to incorporate preference for shallow snow depths into the model, if a spatial database of snow depths was available for the study area. Alternately, since caribou tend to occur in small groups during winter (Darby & Pruitt 1984, Stuart-Smith et al. 1997, Rettie & Messier 1998, Brown et al. 2000, Metsaranta & Mallory

2007), the model could incorporate attraction to other caribou during this period. Similarly, if simulated moose *Alces alces* were added to the model, the value function could be modified in such a way that individual caribou attempt to maximise their distance from alternate prey, since this would conceivably simultaneously maximise their distance from wolves (Rettie & Messier 2000). Finally, since several studies demonstrate that woodland caribou tend to avoid the area around linear features such as roads and seismic lines (James & Stuart-Smith 2000, Dyer et al. 2001, Dyer et al. 2002), the value function could be modified to account for this avoidance. Individual-based movement models incorporating some of these factors are being evaluated in other woodland caribou populations (McCutchen 2007).

The description of preference for certain forest types over others used in my study was rather simplistic. Several recent studies have applied more complex, resource selection function-based (Boyce & McDonald 1999, Boyce et al. 2005) approaches to assessing habitat (e.g. Johnson et al. 2004, Gustine et al. 2006) and management options (e.g. Brown et al. 2007) for this species. However, movement dynamics are not exclusively driven by the characteristics of vegetation, but also by the concurrent movement of other ungulate species, attraction or repulsion from conspecifics during different times of year, attempted avoidance of predators and transient environmental factors such as depth of snow, which all vary both temporally and spatially. Whether models incorporating these factors improve the ability to simulate space use, relative to the simple model used here which used only home-range fidelity, would require further testing and validation against independent data sets. Data for parameterising some of these relationships would be easier to obtain than for others. In any case, individual-based modelling approaches, such as those outlined in this paper, represent a framework into which all of these factors could be integrated and tested (e.g. Breckling et al. 2006).

As noted in previous studies (Bergerud & Elliot 1986, Bergerud et al. 1990, Rettie & Messier 2000, Smith et al. 2000, James et al. 2004), it is likely that these home ranges represent areas which allow caribou to undertake a spatial segregation strategy to avoid moose and therefore wolves. This would be consistent with spatial segregation between moose and caribou noted by Cumming et al. (1996) and James et al. (2004). It would also be consistent with

the mechanistic models of wolf home-range patterns which predict that buffer areas of low wolf density occur in the area between the territories of wolf packs as a result of aversion to the scent marks of adjacent packs (Lewis & Moorcroft 2001, Briscoe et al. 2002). The models also predict that ungulate densities are highest in these buffer areas (Lewis & Murray 1993, White et al. 1996). It is possible that the implicit refuges proposed by Cumming (1996) represent these buffer areas of low wolf density. Overall, my results suggest that there is some factor about the home ranges to which this population exhibits fidelity which is not quantified when only the type of forest currently present there is considered. Therefore, it is likely that disturbing the home ranges used by this population would have negative consequences for its persistence, primarily through the subsequent changes in the regional faunal composition which increase susceptibility to predation. However, the mechanism explaining why this susceptibility increases after these post-disturbance shifts in faunal composition still requires further elucidation (Wittmer et al. 2005, Brown et al. 2007). From a conservation perspective, this suggests that the appropriate action to take would be to ensure that the home ranges which these animals presently choose to use should be protected from changes to both its floral and faunal composition, unless the animal's themselves demonstrate the presence of other suitable areas by dispersing to them.

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Appendix I

The basic algorithm for the model is as follows:
For each of N animals

- a) From its location, determine the distance to its home-range centre and its current habitat type. Calculate the initial location value (V);
- b) loop through an annual cycle until $t = 365$ days;
- c) loop through a decision cycle until $m = M$, where M is the maximum number of chances to find a higher value location in each decision cycle;
- i) Add 1 to m, draw a random daily distance moved, multiply the distance by 14, draw a random direction and then calculate the value of the new location (v) based on this distance and direction;

- ii) if v is $\geq V$ then update the location, set the current value of V to v , add 14 to t , reset m to 0 and exit decision cycle. This represents the animal finding a higher value location;
- iii) if $m=M$ then update the location, set the current value V to v , add 14 to t , reset m to 1 and exit decision cycle. This represents the animal giving up and choosing a random location.

The model was coded using Visual Basic for Applications in Microsoft Excel. Random numbers were generated by the Mersenne Twister algorithm in PopTools 2.6.6 (Hood 2005). The model generates random locations every 14 days in order to match the resolution of the radio-telemetry data used to parameterise and evaluate the model, which were collected on a 10-18 day interval. An alternate algorithm for generating locations (step ii) would draw a daily distance and direction travelled for 14 days, and then only show the location on the 14th day. This algorithm was tested during model development, and was shown not to materially affect the simulation results.

Movement distance and direction

Daily movement distance was modeled as a random deviate drawn from a Weibull distribution:

$$f(x) = \frac{\alpha x^{\alpha-1}}{\beta^\alpha} e^{-\left(\frac{x}{\beta}\right)^\alpha}, \quad \alpha > 0, \quad \beta > 0 \quad (1).$$

From data for all animals and study years, the parameters for summer were $\alpha_s=0.904$ and $\beta_s=351.36$. The parameters for winter were $\alpha_w=1.03$ and $\beta_w=764.37$. The direction was modeled as a geographic azimuth relative to grid north using a random deviate from a uniform distribution on the unit circle.

Habitat value function

The habitat value function governs the decisions made by simulated animals. It can consider preference for different forest types and site fidelity together, or each factor individually, and simulated animals move about the environment in an attempt to maximise its value. The value of any particular

location in space is determined by the type of forest at that location and the distance that the location is from the centre of the individual animal's seasonal home range, and was defined by:

$$V = \frac{(S_{\max} \times H_w \times H_{\text{val}}) + (H_{\max} \times S_w \times S_{\text{hr}})}{H_{\max} \times S_{\max} \times (H_w + S_w)} \quad (2),$$

where S_w is the relative weight assigned to the importance of home-range fidelity, S_{hr} is the distance of current location to the home-range centre, S_{\max} is the maximum distance that can be perceived, H_w is the relative weight assigned to the importance of preference for different forest types, H_{\max} is the maximum value of any forest type, and H_{val} is the value of forest type at the respective location. The habitat value function increases as the animal gets closer to the centre of its home range and as the value of the forest type at a location approaches the maximum value. Setting either of the weights (S_w or H_w) to 0 eliminates that factor from consideration. The present analysis only considers the possibility that S_w and H_w are either 0 or 1. The value of S_{\max} was set to 100 km so that simulated animals can perceive their home range from anywhere within the study area (locations were constrained to remain within its boundaries), and to constrain the function to be between 0 and 1.

Decision optimisation

Animals have imperfect knowledge of their environment. This is incorporated into the model algorithm with the number of opportunities (M) each simulated animal is given to find a higher value location. A simulated animal finding a better location moves there. If a better location is not found in M tries, the M th location is chosen. This conceptually represents the information an animal can perceive and the time it has to process it. If $M=1$, it represents either: no information, no processing time or random movement without preference. Increasing M represents increasing information, more processing time, or stronger preferences. Further exploration of the implications of this parameter is considered outside the scope of this analysis. My simulations use $M=1$ for random movement and $M=25$ for models in which decisions are based on the value function.