Contents lists available at ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Overcoming challenges of sparse telemetry data to estimate caribou movement

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ABSTRACT

Spatially explicit individual-based models (SE-IBMs) can simulate species' movement behaviors. Although such models allow many applications to ecology and conservation biology and are useful for management purposes, they are difficult to parameterize directly from the kinds of observational data that are generally available. Coupled with pattern-oriented modeling strategy, SE-IBMs can be parameterized and assess alternate hypotheses on movement behaviors by comparing simulated to observed patterns of movement. We illustrated this with the endangered Atlantic-Gaspésie caribou population while using sparse Very High Frequency (VHF) telemetry data. We formulated alternative movement hypotheses built around proximate movement mechanisms and coded them into an SE-IBM to explain and predict caribou movement. These mechanisms were: a random walk, a biased correlated random walk, a foray loop to reproduce caribou extra-range movement patterns, and caribou fidelity during mating season. We combined these to test single- and two-behavior movement models regarding landscape quality. The best fitted model successfully reproduced most of the movement patterns derived from the VHF locations. We found that caribou movement in low quality habitat was better reproduced by a foray loop behavior than by a biased correlated random walk or a random walk. Adding an attraction to the individuals' mating area during the mating season also improved the model. We used the selected model to estimate and map potential landscape use by the Atlantic-Gaspésie caribou. We confirmed areas of high use seen in the VHF data and identified some potential areas where no caribou locations were recorded. We also found that large areas of moderate to high quality habitat were unused because they could not be reached by caribou. We conclude that sparse data sets, such as VHF collar locations, can be used to fit movement models whose parameters could not be estimated directly from the data. SE-IBMs coupled with pattern-oriented modeling can reveal new insights about landscape use beyond what can be defined with habitat selection models, and can identify habitat locations where management actions could be taken to facilitate species persistence or recovery of endangered populations.

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1. Introduction

Quantitative models of animal movement and landscape use can make important contributions to our understanding of animal fitness (Cagnacci et al., 2010). Individuals must move through their landscape to access food resources (Turner et al., 1994), to find a mate (Hooker et al., 2002), to reach suitable natal habitat (Richardson et al., 2005), or to escape predators (Forester et al., 2007). Understanding the mechanisms behind animal movement, quantifying how the landscape is used, and identifying potential movement corridors or barriers are therefore key understandings on how species interact with their environment (Gibeau et al., 2002; Marucco and McIntire, 2010). This information is crucial when land management is aimed at the protection or recovery of endangered

populations (Dyer et al., 2002; Gibeau et al., 2002). In this context, a deeper understanding of animal movement and spatial estimates of population landscape use, would allow managers to identify, more precisely or with greater certainty, areas in need of protection from human disturbances, or of restoration to enhance individual movement and thereby population viability. One way to gain such understanding is through movement models.

Individual-based models treat individuals as unique, autonomous entities with state-dependent behaviors, which interact with their environment and/or with each other. Population-level patterns emerge from these interactions (Railsback and Grimm, 2012). Spatially explicit individual-based models simulate individual movements over landscapes (Grosman et al., 2011; McIntire et al., 2007) and are particularly useful in forecasting landscape use (Gustafson, 2013). SE-IBMs are abstract representations of movement in terms of statistical processes governing the distances moved and the choice of direction between consecutive moves. These components need to be parameterized correctly. Usually, only some parameter values are known in advance, and others must be estimated from data (Marucco and McIntire, 2010; Wiegand et al., 2004).

For many animal populations, the data available are telemetry data obtained from transponders attached to the individuals (collars), with locations estimated by triangulation of the Very High Frequency radio signal or, more recently, from Global Positioning System fixes taken by the collars themselves. VHF location recording requires observers to find collared animals in the field (e.g., by aerial survey) which leads to several complications. Individuals outside the usual population range at the time of survey will rarely be detected because observers survey the commonly used areas for reasons of cost. Observers need to see the animals to record their position, but environmental conditions (e.g., landscape cover, weather, low light) can hide some of them. Then, because surveys are costly and time consuming, time lags between consecutive VHF locations are often long and irregular. For these reasons, VHF collar data are usually too sparse in time to permit direct estimation of movement parameters. That is, the frequency with which individual locations are obtained is too low compared to the rates of movement. Sparse data are problematic when used with some movement models. For example, step selection functions assume straight line steps between consecutive observed locations (Fortin et al., 2005) and state-space models require observed movement metrics like speeds or turning angles (Patterson et al., 2008). Such prerequisites cannot be fulfilled with such data. GPS collar data can have a much higher frequency of data capture but are still limited by relatively small sample sizes (Hebblewhite and Haydon, 2010). Despite their more advanced technology and greater capacity, GPS collars remain more expensive than VHF collars, and they have a shorter battery life (Latham et al., 2015). Also, not all studies require GPS locations; for some ecological questions, VHF locations are sufficient (Latham et al., 2015), so the method is expected to remain in use for some time. Finally, VHF technology is decades older than GPS technology. Thus, we have access to animal behavior for time periods before the advent of GPS collars (Hebblewhite and Haydon, 2010). Historical VHF data are available for many species (e.g., Arraut et al., 2010; Forero-Medina et al., 2011; Gibeau et al., 2002; Lewis et al., 2014; Weerakoon et al., 2004) and despite their above-mentioned limits, they represent an important resource for conservation applications. For example, they could be used to infer movement behaviors under historical landscape conditions less affected by human disturbances than today, provided that the challenges of estimating movement parameters from sparse data are overcome.

Pattern-oriented modeling is a strategy to estimate unknown model parameters that could not be directly measured, by adjusting a model to reproduce patterns which are features of the available data (Grimm and Railsback, 2012; Grimm et al., 2005). The first step

is to identify suitable patterns from the data. Large numbers of simulations are then run, sampling values from expected ranges of the unknown parameters. For each simulation, the selected patterns are derived from model outputs. Finally, best parameter values are identified by minimizing a measure of the difference between the simulated patterns and the patterns in the data. The POM strategy is particularly useful to parameterize SE-IBMs from sparse data when paired with a robust, hypothesis-driven methodology (McIntire and Fajardo, 2009). However, temporal or spatial resolution of the model, or sought in the results, should not be overwhelmingly different from the data.

We built SE-IBMs to understand the movements and to predict the potential landscape use of an animal population from sparse VHF telemetry data. Our case study was the Atlantic-Gaspésie caribou population, *Rangifer tarandus caribou*, in Québec, Canada. First, we proposed several movement hypotheses based on the literature, representing different movement mechanisms. We translated each hypothesis into a SE-IBM and calibrated each model with the VHF data using a POM strategy. We then selected the best model using a similar POM strategy, and validated the model against the VHF data. The model was then used to simulate individual movements from which we estimated and mapped the population's potential landscape use. Finally, we compared the estimated landscape use with a habitat selection study done for the same caribou population.

2. Material and methods

2.1. Case study: the Atlantic-Gaspésie caribou population

Our study area was the Gaspésie peninsula in Quebec, Canada (Fig. 1), defined as the Gaspésie natural region (MDDEP, 2012). The area is mountainous and forms the northeastern limit of the Appalachian range. The study area falls within the boreal biome (Brandt, 2009) and, except for the coast, is part of the balsam fir-white birch bioclimatic domain (Saucier et al., 2003). The area is home to the small, relict Atlantic-Gaspésie caribou population ("caribou", hereafter), which is associated with alpine tundra habitats on high-elevation sites. The study area is surrounded by water on three sides while the western boundary adjoins a region highly modified by agriculture, industry and urban areas (Wildlife Conservation Society Canada, 2015) which we considered effectively impermeable to caribou movement. This caribou population is thus effectively isolated.

The caribou population belongs to the mountain ecotype (Hummel and Ray, 2008) of the woodland caribou subspecies (Banfield, 1961). When population surveys began in the 1980s, the population size was estimated to be around 200 (Fournier and Faubert, 2001). Numbers have declined steadily since that time, and, as of 2014, the estimated herd size was 94–100 individuals (Lalonde, 2015). The population was designated as endangered in 2000, a status re-examined and confirmed in 2002 and in 2014 (Environment Canada, 2014). The population was recently identified as a Designatable Unit for the caribou species in Canada, which is a "both discrete and significant unit that is an irreplaceable component of Canada's biodiversity" (COSEWIC, 2011). This status confers on the population priority for conservation action.

The proximate cause of the Atlantic-Gaspésie caribou decline is predation, mostly by coyotes (*Canis latrans*) and bears (*Ursus americanus*) (Crête and Desrosiers, 1995), but the ultimate cause is land-use changes, primarily due to forest harvesting. Forest harvesting increases the area of young forests, leading to increased abundances of alternate prey species such as moose (*Alces americanus*) and their predators (St-Laurent et al., 2009). Caribou telemetry locations suggest that individuals are mostly restricted to the Gaspésie National Park (Fig. 1). The population appears to be divided into three groups, gathered on Mts. Logan, Albert and
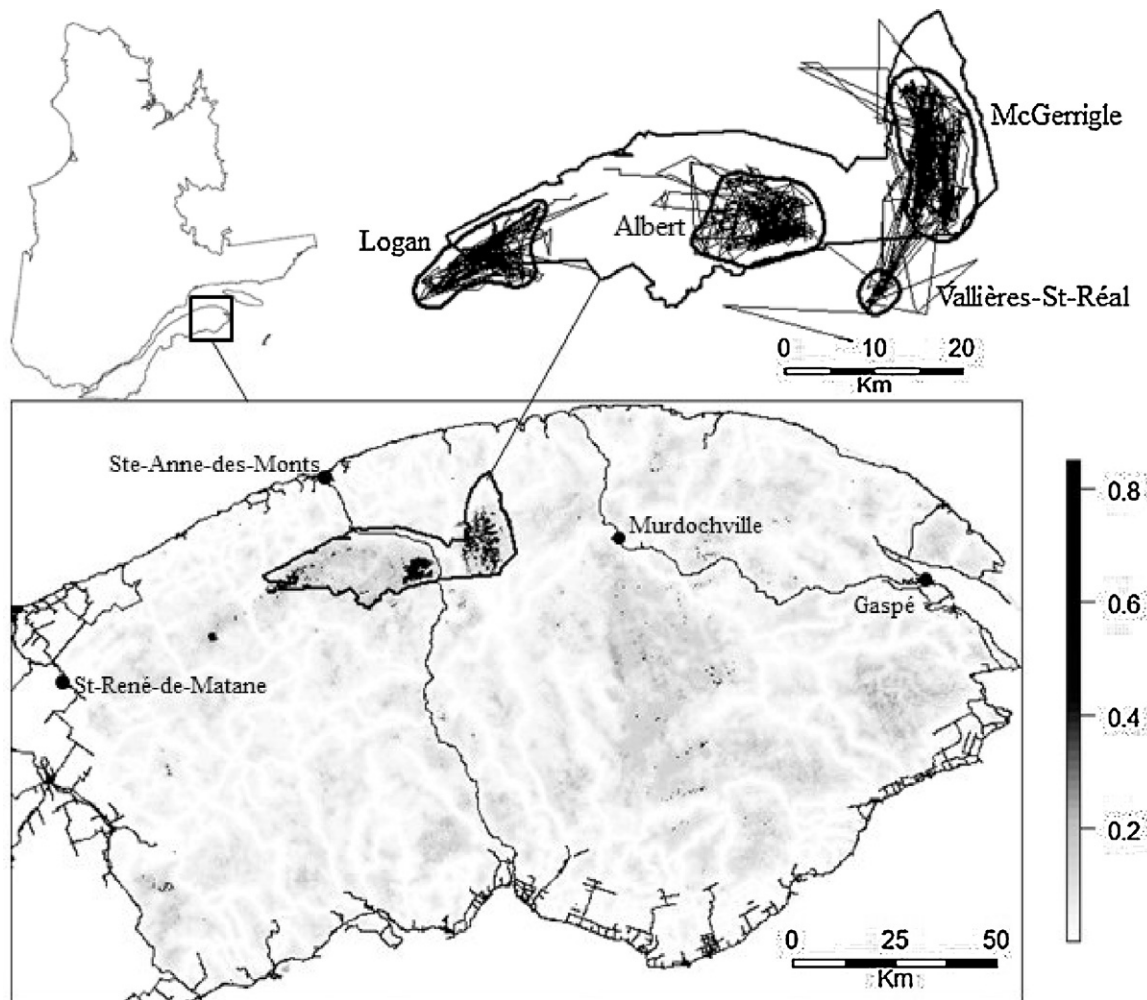
Fig. 1. Left inset: The province of Quebec (Canada), with study area, the Gaspésie natural region, outlined. Lower map: Summer resource selection function for the Atlantic-Gaspésie caribou (Gaudry, 2013) applied over our study area. Paved roads are shown in thin lines and the boundary of Gaspésie National Park is the thick outline. The four towns nearest to recent caribou sightings distant from the park are indicated (St-Laurent, unpublished data). Right inset: Caribou movement paths defined from consecutive VHF locations, with the park boundary and subpopulation ranges outlined.

McGerrigle (Mosnier et al., 2003) (Fig. 1), with very few individual exchanges. There is no evidence that the Atlantic-Gaspésie caribou is a metapopulation (sensu Hanski and Hanski, 1999) but, for the purpose of this study, we considered these groups as three subpopulations. We referred to them as the Logan, the Albert and the McGerrigle (caribou) subpopulations. Recent caribou sightings at unexpectedly distant locations (Fig. 1) and the 1997 colonization of Mt. Logan, probably by Albert caribou (Fournier and Faubert, 2001), show that long-distance movements and re-establishments are possible. A mechanistic understanding of caribou movements is essential to understand and facilitate colonization processes to secure the recovery of this population.

To develop movement models, we used VHF telemetry data from 35 caribou that were collared and followed from 1998 to 2001 (Mosnier et al., 2003). Periodic aerial surveys of the known population range located collared animals by their signal and recorded their position. Flights were conducted, on average, every two weeks (mean = 17 days, SD = 17 days). The mean number of locations per individual was 45 (SD = 20). We used a kernel density at 80% on the VHF locations to delineate subpopulation ranges (Fig. 1). Due to the low number of individuals per subpopulation, the value of 80% was the largest that identified three subpopulation ranges not biased by uncommon behavior from a single individual. Ranges for the Logan and Albert subpopulations are each represented by single contiguous areas, whereas the McGerrigle range is represented by

two areas, one centered on the McGerrigle mountains and a smaller, less frequently used one, around the Vallières-St-Réal (Fig. 1).

2.2. Spatially explicit individual-based model

To simulate caribou movement, we built SE-IBMs that incorporated temporally varying behavioral responses to spatially varying environmental conditions (Hanks et al., 2015, 2011). The models run on a grid of 75×75 m cells covering the study area. Model time steps are daily, indexed by calendar days; the large temporal scale of the telemetry dataset precluded finer resolution. Simulated individuals have a fixed name and mating area associated, two movement states, and a behavioral state. The movement states are the coordinates of the individual current positions on the landscape (i.e., the currently occupied cell) and a heading or direction of last movement. The behavioral state can change depending on time and location. All individuals move once per time step according to the current landscape conditions and their behavioral state. Alternate hypotheses on the processes governing movement in this population were expressed as alternate model formulations (McClintock et al., 2012) or spatial constraints on movement. A complete description of the SE-IBMs following the Overview, Design concepts, and Details protocol of Grimm et al. (2010, 2006) is available in Appendix A in Supplementary material. The model was written in R 3.1.0 (R Core Team, 2014).

Each landscape cell had three spatial characteristics that drive movement: the habitat quality, the presence or absence of paved roads and whether or not it is located within a seasonal mating area. Habitat quality was predicted using two seasonal resource selection function models (Manly et al., 2002) developed for the Atlantic-Gaspésie caribou (Gaudry, 2013) (Fig. 1). The RSF models were built with four habitat types (alpine tundra, mature fir stands, regenerating stands and other forest stands) and three linear anthropogenic features (paved roads, gravel/secondary roads, and hiking trails). One RSF was developed for the winter period (November 16th–April 30th) and the other RSF for the snow-free period, hereafter called "summer" (May 1st–November 15th). As in Gaudry (2013), we classified forest stands in our study area using the 1:20,000 digital ecoforestry map of the 3rd forest inventory program (source: Ministère des Forêts, de la Faune et des Parcs du Québec) updated in 2001 and the linear anthropogenic structure data published by the MFFP. Using the RSF models developed by Gaudry (2013), we obtained two seasonal maps of relative probabilities of caribou occurrence. We use these probabilities as surrogates for habitat quality (Hebblewhite et al., 2011). Roads are known to be significant barriers to caribou movement (Beauchesne et al., 2013; Dyer et al., 2002) so we defined the major paved roads (Fig. 1) as semi-permeable barriers to movement (Kramer-Schadt et al., 2004; Wiegand et al., 2004). The presence or absence of paved roads was determined at the cell level. Finally, many caribou populations exhibit fidelity to various sites, among which breeding and mating sites (Faille et al., 2010; Metsaranta, 2008; Schaefer and Mahoney, 2013). The mating season for the Atlantic-Gaspésie caribou is defined from September 15th to November 1st (Bergerud, 1973; Lalonde and Michaud, 2013). VHF data showed caribou clustering at high-elevation sites during the peak of the mating season. We defined three mating areas, using a 50% kernel density on subpopulation locations during the mating season.

Many ungulates exhibit at least two movement behaviors which can be distinguished as intra-patch or inter-patch movements (Johnson et al., 2002), possibly corresponding to "encamped" and "exploratory" behavioral states (Morales et al., 2004). We assumed these behaviors to be related to habitat quality and accordingly we distinguished "good habitat quality" movements from "low habitat quality" movements. Empirical kernel density functions of quality values at recorded VHF locations were bimodal within seasons (Fig. 2). We defined the minimum density between the two peaks as the quality threshold between the low-HQ and the good-HQ behaviors. The estimated summer and winter thresholds were 0.290 and 0.382, respectively (Fig. 2). During the simulation, at locations with quality value above or equal to the threshold, individuals followed a good-HQ movement behavior; otherwise individuals follow a low-HQ movement behavior. Above-threshold quality habitat is mostly found within the subpopulation ranges (around 67% of it), although it does exist elsewhere in the area.

We created 35 individuals to represent the VHF-collared caribou and randomly placed them inside their own mating area. A complete simulation lasted four years of 365 days. In each time step, Julian date was incremented and landscape quality values were updated if the season changed. Individuals were then assigned a movement model according to their location, and the hypothesis under test (see Section 2.3). Then, a step length was sampled independently for each individual from a lognormal distribution with state-dependent parameters; the parameter for mean step length varied with habitat quality (Table 1). In order to minimize the number of parameters to be estimated, we assumed that standard deviation for step lengths did not vary with habitat quality (Table 1). To avoid unrealistically large daily movements, step lengths were truncated at 20 km. Each individual identified all unique locations at the selected step length from its current position (Fig. 3a), and thus the potential straight-line pathways it could follow (Fig. 3b).

Each pathway was evaluated with respect to each characteristic (Table 2) of the model being evaluated (see Section 2.3) and assigned a numeric value (Table 2). For each characteristic, the values were rescaled across all pathways to sum to 1 (see Appendix A in Supplementary material for more details). These rescaled values were interpreted as the probabilities that the individual would choose a given pathway with respect to the given characteristic (e.g., habitat quality, paved road presence). The product of the rescaled values was then calculated for each path, and rescaled again to sum to 1 over all paths. The results were finally interpreted as per-pathway movement probabilities, assuming that each characteristic was assessed independently. Finally, one pathway was randomly drawn based on these probabilities (Fig. 3c) and the individual moved to the pathway endpoint (Fig. 3d). This straight line was not intended to represent an exact caribou trajectory at fine scale, but rather an emergent net displacement over a day with habitats that caribou potentially went through (Fortin et al., 2005). At the end of a run, we produced a map of landscape use as the number of caribou visits per cell over the last three years of the simulation. The maps were created by counting all cells intersecting the straight-line pathways of each movement. The first year of movement was not included in the map generation so as to limit the effect of initial conditions.

2.3. Movement models

We simulated good-HQ movement behavior using a habitat-mediated random walk model to represent low correlation movements (e.g., foraging; Morales et al., 2004). To explain the caribou low-HQ movement behavior we tested three alternative movement hypotheses: a hm-RW, the same as the good-HQ movement to represent a single-behavior movement strategy; a habitat-mediated biased correlated random walk (Van Moorter et al., 2009); and a habitat-mediated foray loop (Conradt et al., 2003). To test these as alternative models, one of the three low-HQ movement behaviors was chosen to apply to all individuals throughout a simulation run.

To test which mechanism best represents the caribou movement displayed in our telemetry data, we created six different SE-IBMs (M1–M6). M1 was a single movement-behavior model where individuals followed a hm-RW for the good-HQ and low-HQ movement behaviors. M3 and M5 were two-behavior movement models; individuals followed a hm-RW for the good-HQ movement behavior and either a hm-BCRW (M3) or a hm-FL (M5) for the low-HW movement behavior. M2, M4 and M6 were respectively the same as M1, M3 and M5 where we added the mating area attraction. Pathway characteristics (Table 2) used in the alternate movement models were as follows:

- M1 $\sim$ habitat quality + paved road presence
- M2 $\sim$ M1 + mating area attraction
- M3$_{good}$ $\sim$ M1;

M3$_{low}$ $\sim$ habitat quality + paved road presence + correlation + bias

- M4$_{good}$ $\sim$ M3$_{good}$ + mating area attraction;

M4$_{low}$ $\sim$ M3$_{low}$ + mating area attraction

- M5$_{good}$ $\sim$ M1;

M5$_{low}$ $\sim$ habitat quality + paved road presence + foray loop

- M6$_{good}$ $\sim$ M5$_{good}$ + mating area attraction;
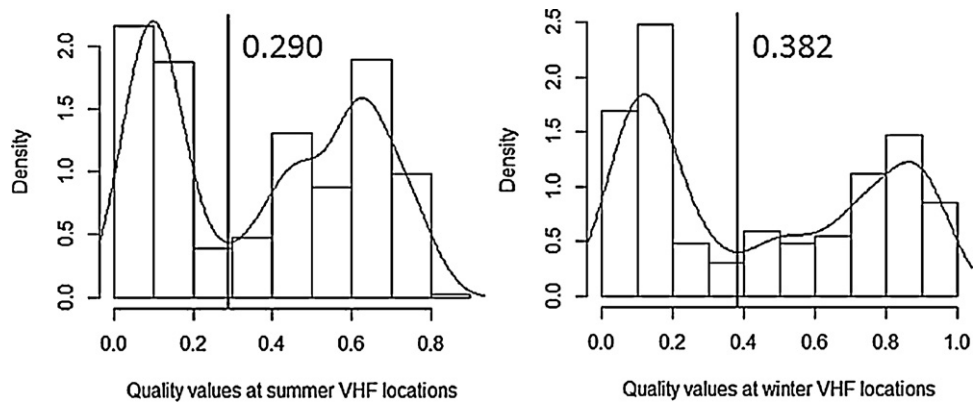
Fig. 2. Kernel density estimates of habitat quality values at VHF locations for summer (800 locations) and winter (770 locations). The thresholds separating good and low habitat quality behaviors are shown.

Table 1
Model parameters to be estimated with the range of values tested within the POM strategy and their unit.

Parameter to be estimated		Range tested	Unit
$\mu_{sl.good}$	Mean of the lognormal distribution for the step length simulation in good quality habitat	[3;8]	Log(m)
$\mu_{sl.low}$	Mean of the lognormal distribution for the step length simulation in low quality habitat	[3;8]	Log(m)
σ_{sl}	Standard deviation of the lognormal distribution for the step length simulation	[0.5;1.5]	Log(m)
p_{cross}	Probability for a caribou to cross a paved road	[0;1]	
σ_{ma}	Standard deviation of the truncated Normal distribution for the mating area attraction	[0;180]	Degree
σ_c	Standard deviation of the truncated Normal distribution for the correlation movement	[0;180]	Degree
$\max_{dist.bias}$	Maximum distance for the bias to occurs between the individual position and the closest area of good quality	[0;50]	Km
σ_b	Standard deviation of the truncated Normal distribution for the biased movement	[0;180]	Degree
$\max_{steps.loop}$	Maximum step length of the outward portion of the foray loop	[0;20]	Step
σ_{fl}	Standard deviation of the truncated Normal distribution for the foray loop movement	[0;180]	Degree
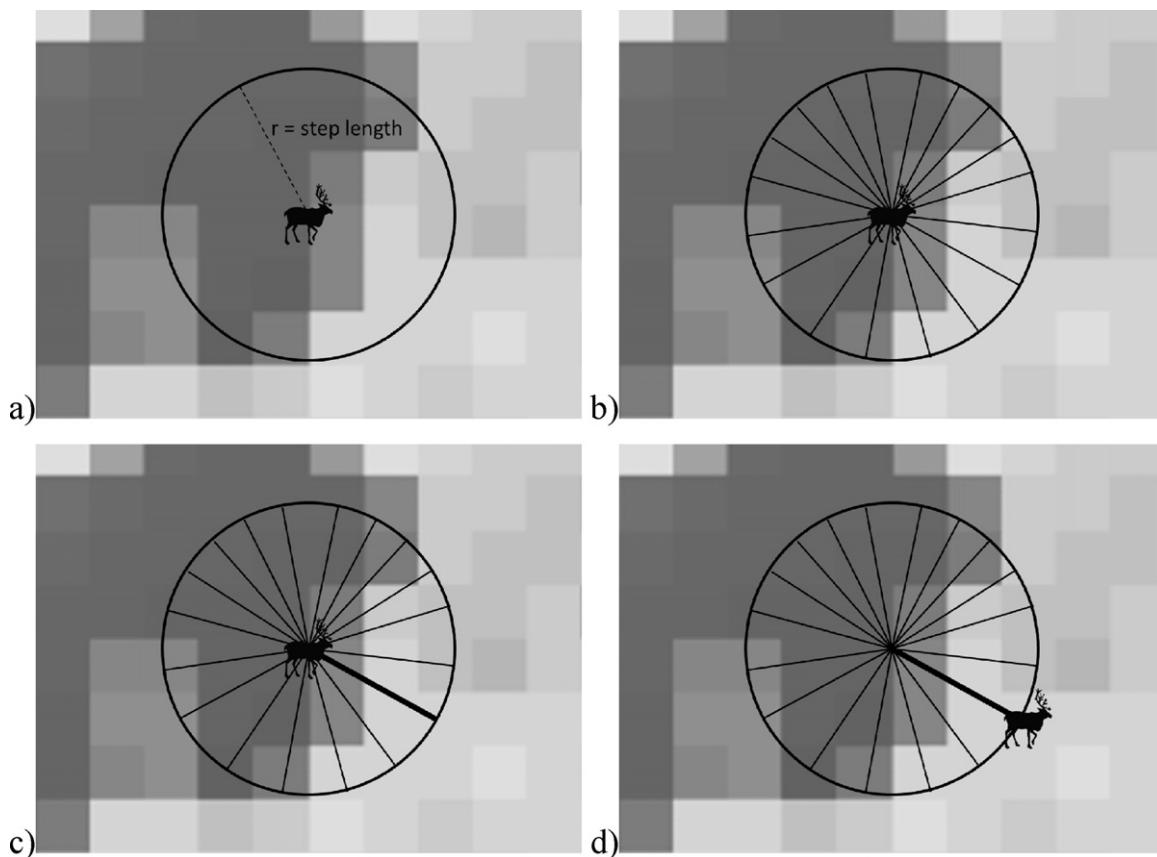
Fig. 3. Movement illustrations of one daily time step for one individual. (a) A step length is sampled. (b) All unique pathways are identified, going from the individual current position to every unique cell of the gridded landscape at the sampled distance. (c) One pathway is selected (thick line) based on probabilities derived from the pathway characteristics of the movement model followed by the individual. (d) The individual moves to the end of the selected pathway.

Table 2
Pathway characteristics and index values used to assign pathway probabilities (see Appendix A in Supplementary material for more details).

Pathway characteristic	Index value
Habitat quality	Mean quality value for the cells composing the pathway
Paved road presence	Probability p_{cross} of crossing a paved road for a caribou raised to the number of road crossing the pathway
Mating area attraction	Probability from a truncated Normal distribution ($-180°$ and $180°$) with mean equal 0 and standard deviation σ_{ma} of the angle between the pathway direction and the direction towards the individual mating area
Correlation	Probability from a truncated Normal distribution ($-180°$ and $180°$) with mean equal 0 and standard deviation σ_c of the angle between the pathway direction and the individual current heading
Bias	Probability from a truncated Normal distribution ($-180°$ and $180°$) with mean equal 0 and standard deviation σ_b of the angle between the pathway direction and the direction towards the closest area of good quality
Foray loop	Probability from a truncated Normal distribution ($-180°$ and $180°$) with mean equal 0 and standard deviation σ_{fl} of the angle between the pathway direction and the direction away or towards the last visited habitat of good quality

$M6_{low} \sim M5_{low} +$ mating area attraction

As explained in the previous section, all pathway characteristics included in a given model were considered to be independent. Using these models, we tested three different mechanisms to explain caribou range fidelity and extra-range movement: an attraction to a mating area during mating season, a bias toward close areas of good quality and a foray loop movement. If mating area attraction occurred (M2, M4 and M6), we assumed that individuals favored pathways leading towards their mating area during mating season. Under the bias models (M3 and M4), pathways leading individuals towards the closest area of good quality were preferred. The bias relies on some combination of habitat sensing at shorter ranges and of memory at longer ranges. Because the biases are implemented as probability distributions on movement angles, there is no supposition that sensing is necessarily of high accuracy or that recall is total. We included a parameter $max_{dist.bias}$ for the maximum distance from good habitat for which bias occurred (Schultz and Crone, 2001). We further included a correlation in the biased movement; individuals should also tend to continue moving in the same direction by favoring pathways minimizing rotation of their current heading. Under the foray loop models (M5 and M6), individuals explore their surroundings by orienting away from their last visited good habitat. If a good habitat is not found on the outward path within the maximum number of steps, $max_{steps.loop}$, individuals close the loop by reorienting subsequent steps towards their last known good habitat location.

2.4. Model parameterization

We estimated the unknown parameters for each model (Table 1) with a POM strategy. POM requires the identification of emergent patterns produced by the model which can be compared to the observed data. We identified three such patterns: emergence of subpopulations, frequency of road crossings, and distributions of distances moved. These three patterns were not spatial per se. We considered them pseudo-spatial as they represented specific features of the Atlantic-Gaspésie caribou movement, derived from the spatial VHF telemetry data in combination with the location of tundra habitats and roads. They are considered primary patterns as they represent important characteristics of the caribou movement that we sought to reproduce (Latombe et al., 2011). Simulated caribou locations were extracted at time steps corresponding to the dates of VHF locations for each individual to define the patterns for the simulation runs.

Each simulated caribou had a mating area associated and therefore belonged to the subpopulation which had its range containing the individual mating area. For each subpopulation range, we counted the number of simulated locations from individuals belonging to that subpopulation which occurred inside the associated range. These were compared with the corresponding values from the observational VHF data by taking the absolute deviations (ADs $= |x - y|$) We obtained four ADs for this pattern, one for the Logan caribou, one for the Albert caribou and two for the two parts

McGerrigle range (Fig. 1). Similarly, we calculated three ADs of the number of road crossings events, one for each subpopulation. A crossing was defined when consecutive locations were on opposite sides of a paved road (Fig. 1). As an AD statistic approached zero, the pattern emerging from the simulation approached the pattern in the observed data. Finally, we compared the distributions of distances between consecutive locations for each subpopulation, as follows. We first calculated the POMDEV statistics between the distributions of simulated and observed distances. A POMDEV statistic indicates a relative deviance between two distributions "[corresponding] to twice the sum of the log of an approximate likelihood given by the approximating function of density from the simulation results applied on the field data" (Piou et al., 2009). We then calculated null indices by comparing the distributions of observed movement distances with distributions obtained by drawing random points inside the 100% minimum convex polygon of the telemetry data. To allow model comparisons, we calculated three McFadden's R^2 as 1 minus the ratio of simulated and null deviance statistics (McFadden, 1974), one for each subpopulation. As McFadden's R^2 statistic approached 1, the pattern of distances in the simulation approached the equivalent pattern in the observed data.

We used a best-fit calibration method (Railsback and Grimm, 2012) to estimate model parameters (Table 1). We ran 100,000 simulations for each model using a HTCondor cluster (Thain et al., 2005). While more simulations may have resulted in more precise parameter estimates, ours appeared adequate to obtain parameter estimates with reasonable confidence intervals regarding computation time. For each simulation, parameter values were sampled independently from uniform distributions (Table 1). For each model, we selected a subset of the runs whose outputs best reproduced all the patterns simultaneously. We used thresholds to define that a pattern was reproduced. We created a quantile value Q which we incremented from 0 to 1 by 0.01. At each Q value tested, we identified, independently for each pattern, the Q-ile simulation run and its pattern statistic associated which stood for the pattern threshold. For example, at $Q = 0.01$, the threshold for the Logan subpopulation emergence pattern is equal to the AD statistic of that pattern for the ($Q \times 100,000$) 1000th simulation when ranked for this particular statistic from low to high. For a simulation to be selected, the AD statistic for each subpopulation range patterns ($n = 4$) and for each road crossing patterns ($n = 3$) must be lower than the defined thresholds and the McFadden's R^2 statistics for each distance moved patterns ($n = 3$) must be above the thresholds. We increased Q until at most 500 of the 100,000 simulations were selected. The number of simulations selected was a trade-off between too few simulations to obtain reliable parameter estimates and too many that included noise. From this selection, we removed simulations where individuals were stuck on a single landscape cell, an infrequent occurrence. We identified these situations from the output maps of landscape use. We defined a cell in a map as an outlier when its number of visits was greater than 10 times the 0.975 quantile number of visits for that map. We removed simula-

Table 3
Parameter estimates with 95% confidence intervals for each model.

	$\mu_{sl.good}$	$\mu_{sl.low}$	σ_{sl}	p_{cross}	σ_{ma}	σ_c	$max_{dist.bias}$	σ_b	$max_{steps.loop}$	σ_{fl}
M1	5.00	4.11	1.31	0.14						
	[4.68;6.09]	[3.92;4.27]	[1.03;1.36]	[0.10;0.79]						
M2	5.66	4.09	1.10	0.51	31.00					
	[5.39;6.35]	[3.90;5.27]	[0.89;1.31]	[0.09;0.57]	[21.49;51.43]					
M3	5.48	4.41	1.14	0.20		86.65	25.64	87.01		
	[5.29;6.20]	[4.23;4.59]	[0.78;1.37]	[0.12;0.51]		[79.96;98.28]	[11.84;41.39]	[58.47;143.37]		
M4	5.97	4.59	1.34	0.17	85.95	113.42	20.45	121.53		
	[5.17;6.38]	[3.68;5.25]	[0.96;1.37]	[0.13;0.35]	[20.08;105.68]	[91.94;139.14]	[18.30;43.54]	[97.93;153.94]		
M5	5.53	3.85	1.26	0.14					3.53	124.70
	[5.26;6.72]	[3.54;5.19]	[1.05;1.33]	[0.10;0.20]					[2.82;14.09]	[76.09;141.25]
M6	5.98	4.92	1.36	0.12	144.77				5.68	134.91
	[5.81;6.39]	[3.87;5.17]	[1.02;1.39]	[0.09;0.18]	[26.42;150.76]				[4.64;16.80]	[74.32;151.12]

tions from the previous selection where their output map contained such outlier cells. We used kernel density estimators to determine the mode of the parameter values from the selected simulations. We interpreted these modes, which are values close to the ones most commonly used in the selected simulations, as the parameter estimates. We estimated 95% confidence intervals of the parameter estimates with an Efron bootstrapping method. We re-sampled with replacement the parameter values from the selected simulations and defined the new mode. We iterated this step 10,000 times for each parameter. The 2.5th and 97.5th percentiles of the mode distributions obtained by bootstrap defined the confidence intervals of the parameters.

2.5. Movement hypothesis testing

Using the six fitted models, we assessed which model, and which corresponding hypothesis was best supported by the observational data, again using a POM strategy (Railsback and Grimm, 2012). We ran each model 10,000 times, sampling parameters from the empirical density functions defined over the 95% confidence intervals of the bootstrapped estimates. Fewer simulations were needed than for model parameterization. We used the same 10 comparison statistics described above and we calculated the mean statistic values across the 10,000 runs for each model. Then, we summed the statistic means for each global pattern. We selected the model with the lowest MAD sum for the emergence of subpopulations, the lowest MAD sum for road crossing frequency and the highest sum of McFadden's R^2 means for the distances moved as the model best supported by the data.

2.6. Model validation

We conducted an internal validation to test the ability of the best model to reproduce the data with which it was parameterized. We ran the model 10,000 times and, for each simulation, recorded the values for the subpopulation emergence and road crossing patterns. That is, we recorded the actual pattern values (e.g., number of location inside a range), not the AD statistics. AD statistics were useful to compare models but cannot be used to test for the robustness of a single model. We tested if the empirical pattern values fell within the pattern's simulated 95% coverage (Kramer-Schadt et al., 2007; Wiegand et al., 2004). The distances moved recorded per simulation were distributions, not single values. We could not apply the coverage test used for the other two patterns, and so did not use the distances moved pattern in model validation.

2.7. Landscape use estimate and comparison with habitat selection model

Using the selected best movement model, we ran 10,000 simulations, with 20 individuals created in each subpopulation to reduce

dependency on the current population distribution. We summed the resultant landscape use maps to represent the potential landscape use by caribou during the period of the VHF surveys. A seasonally averaged map of relative occurrence probabilities from the two RSF models was constructed as an alternate estimate of potential landscape use. To summarize the differences between the two measures, we calculated the mean landscape use as a function of distance from the nearest subpopulation range (results within the ranges were not included). We rescaled values to the range [0,1] to facilitate comparisons.

3. Results

3.1. Model parameterizations and selection

The Q values used to select the simulations best reproducing the data were: 0.43, 0.45, 0.46, 0.48, 0.47, and 0.46 for models M1–M6, respectively. For all six models, estimates of mean step length were higher in good habitats than in low quality habitats (Table 3). In good habitats, mean daily net distance moved ranged from 350.0 m to 997.1 m whereas in low quality habitats, estimates ranged from 103.9 m to 345.4 m. Estimated road crossing probabilities were low for all models, ranged from 0.12 to 0.51 (Table 3).

Model M6, with a foray loop behavior in low quality habitat and a mating area attraction was the most consistent with the caribou VHF data. M6 yielded the lowest MAD sum for the subpopulation range pattern, the second lowest MAD sum for road crossings, and the highest McFadden's R^2 mean sum for the distribution of distances moved (Table 4). M5, with the foray loop behavior as in M6, but without mating area attraction, also performed well (Table 4). It was the best model with respect to road crossings and the second best for the subpopulation range pattern.

3.2. Model validation

The best model (M6) was consistent with the data, according to our internal validation tests. For six out of the seven patterns tested, values derived from the VHF data fell within the 95% coverages of the simulation output values (Table 5). The presence of McGerrigle caribou in the Vallières-St-Réal part of the subpopulation range was under-represented by the simulations; simulated 95% coverage of [0;34] did not include the total of 56 occurrences in the VHF survey data (Table 5). However, some of the 10,000 simulations did reproduce or exceed this indicator; the maximum number of McGerrigle caribou locations simulated in the Vallières-St-Réal area was 93.

3.3. Landscape use estimate

The highest simulated landscape use rates were concentrated in the center of each subpopulation range, with a very low potential landscape use outside these ranges (Fig. 4). Potential landscape

Table 4
Pattern statistics for the model selection process. White columns are the statistic means over the 10,000 simulations and grey columns are the sum of these statistic means over each of the three global patterns. Bold values highlight the model which performed the best for that statistic.

|	MAD SR_L	MAD SR_A	MAD SR_{McG}	MAD SR_{Vall}	Sum MADs SR.	MAD $Xing_L$	MAD $Xing_A$	MAD $Xing_{McG}$	Sum MADs Xing	McF.$R^2{}_L$ mean	McF.$R^2{}_A$ mean	McF.$R^2{}_{McG}$ mean	Sum means McF.R^2
M1	134.99	71.48	85.85	49.82	342.14	0.04	2.36	0.35	2.75	0.55	0.58	0.49	1.62
M2	81.11	54.49	84.70	52.53	272.83	0.08	2.27	0.55	2.90	0.58	0.62	0.52	1.72
M3	84.48	95.16	115.32	47.96	342.92	0.04	2.15	0.88	3.07	0.57	0.61	0.51	1.69
M4	**74.22**	70.87	98.87	**47.60**	291.56	0.04	2.10	0.82	2.96	0.59	**0.63**	0.53	1.75
M5	77.46	60.06	72.04	50.16	259.72	**0.02**	2.14	**0.20**	**2.36**	0.59	0.62	0.53	1.74
M6	80.07	**53.09**	**60.69**	48.86	**242.71**	0.04	**2.04**	0.30	2.38	**0.60**	**0.63**	**0.54**	**1.77**

SR = subpopulation range pattern, L = Logan, A = Albert, McG = McGerrigle, Vall = Vallières-St-Réal, Xing = road crossing pattern, McF.R^2 = McFadden's R^2.

Table 5
Pattern values from the VHF data and 95% coverages from 10,000 simulations with the best model.

	SR_L	SR_A	SR_{McG}	SR_{Vall}	$Xing_L$	$Xing_A$	$Xing_{McG}$
VHF data	266	279	357	56	0	3	0
95% range	[77;334]	[139;430]	[236;592]	[0;34]	[0;1]	[0;8]	[0;4]

SR = subpopulation range pattern, L = Logan, A = Albert, McG = McGerrigle, Vall = Vallières-St-Réal, Xings = road crossing pattern.
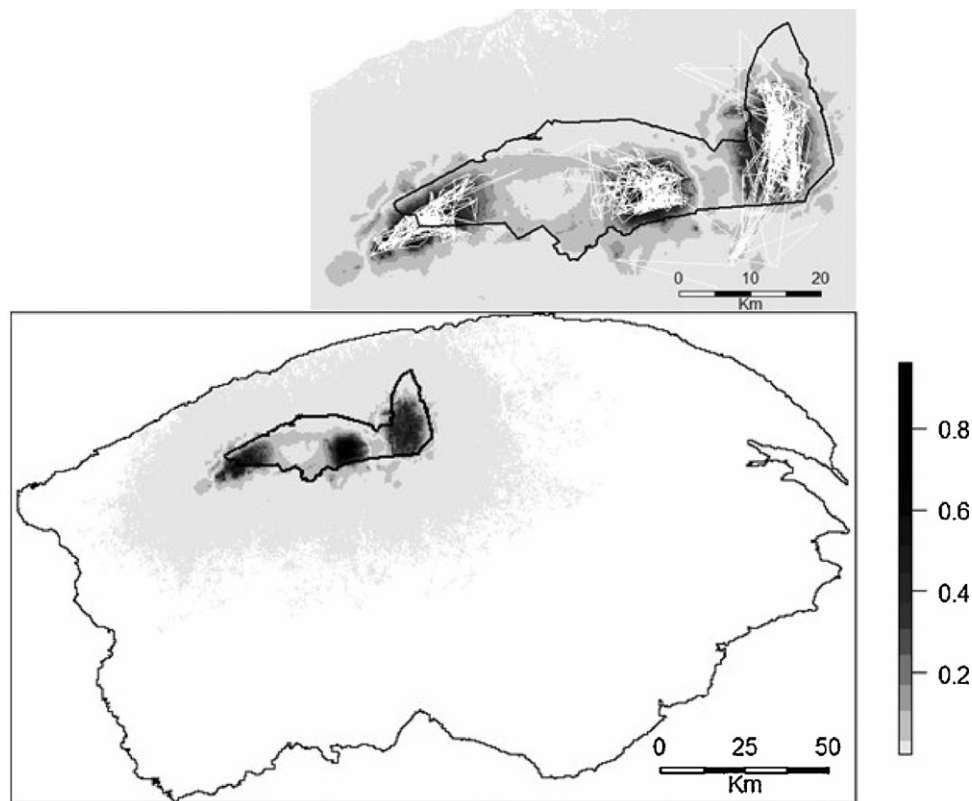
Fig. 4. Lower map: Atlantic-Gaspésie caribou predicted landscape use for the time period of the VHF surveys, with the Gaspésie National Park boundary overlaid. Inset: landscape use in the vicinity of the park with caribou paths inferred from VHF data (Fig. 1) shown as thin white lines.

use outside the Gaspésie National Park was also low. These results were expected and were already displayed by the VHF locations themselves. However, there was the suggestion of two corridors between the Logan and Albert subpopulation ranges, indicating possible movements of individuals between the two subpopulations (Fig. 4). This was not revealed by the VHF data. The model also identified areas of high potential use south of the Albert subpopulation range, where one VHF location was recorded, and to the west and north of the Logan subpopulation range where no locations were recorded (Fig. 4).

3.4. Comparison of SE-IBM and RSF landscape use estimates

According to both movement and RSF models, caribou landscape use decreased sharply with distance from the nearest subpopulation ranges (Fig. 5). The models behaved similarly for distances up to 3 or 4 km. At greater distances, SE-IBM landscape use rates decreased rapidly, approaching 0 at a distance of 15 km. In contrast, RSF landscape use estimates remained relatively high, between 0.18 and 0.53, at distances of up to 100 km from the subpopulation ranges.
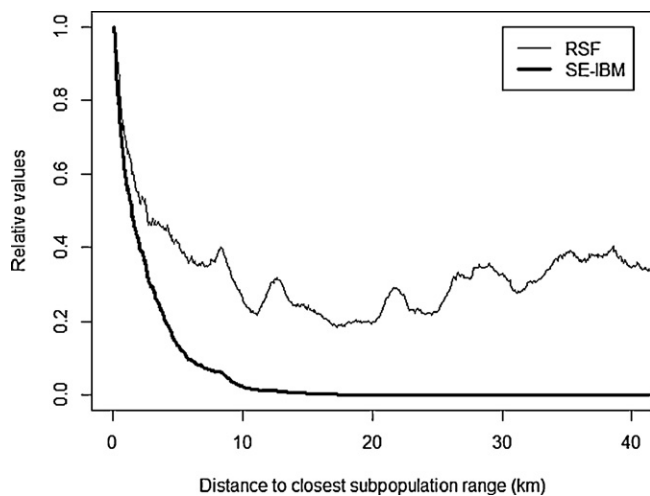
Fig. 5. Atlantic-Gaspésie caribou relative landscape use as a function of distance to the nearest subpopulation range, calculated from RSF and SE-IBM models.

4. Discussion

By using spatially explicit individual-based models coupled with a pattern-oriented modeling strategy and spatially and temporally sparse data obtained from VHF surveys, we were able to build a robust movement model for the Atlantic-Gaspésie caribou population and estimate its landscape use. All the movement patterns defined with the telemetry data, except one, were commonly reproduced by simulations. The one exception, namely the number of individual occurrences in a small, disjunct component of one the three subpopulation ranges, was reproduced by the best supported model, but with low probability. The patterns used for model parameterization and selection represented three distinct and characteristic features of the observed movements of the Atlantic-Gaspésie caribou: distinct subpopulation ranges associated with site fidelity, road avoidance, and daily movement distances. They also seemed the most informative that could be derived from the VHF locations. Using multiple independent patterns ensured a strong filtering of the different model parameterizations and movement hypotheses when selecting our best model (Grimm and Railsback, 2012; Latombe et al., 2011).

The VHF location data contained enough information to clearly identify habitat-specific movement behaviors. The best supported models (M4, M5 and M6) all included distinct behaviors in low and high quality habitats, as have been found (based on GPS data) in another caribou population (Johnson et al., 2002) and for elk (Morales et al., 2004). The VHF data was further able to discriminate between two hypotheses on movement behavior in low quality habitats. Foray loop behavior better reproduced characteristics of the data than did a biased correlated random walk. This suggests that caribou voluntarily moved away from good quality habitats to explore their surroundings, possibly in search of new resources (e.g., food, space, shelter, other individuals, etc.) embedded within relatively hostile or low quality habitats (Conradt et al., 2003). When such forays were unsuccessful, individuals returned to the good quality areas, which were mostly located inside the subpopulation ranges. The estimated number of daily time steps per foray loop was six steps (Table 3). Thus, the transit returning to high quality habitat, the second phase of an unsuccessful foray loop, would be better explained by memory rather than a perceptual process leading to directional bias (Fagan et al., 2013; Van Moorter et al., 2009). The VHF data also sufficed to identify a temporal component to the caribou behavior. Adding mating season range attraction improved the model ability to replicate patterns in the data. The model mechanisms suggested that Atlantic-Gaspésie caribou fidelity to their range was based at least in part on intrinsic behavior and not solely on responses to spatially varying habitat quality (Faille et al., 2010). Finally, the VHF data led to low estimates of paved road crossing probabilities which is consistent with known road avoidance behavior for this species (Beauchesne et al., 2013; Dyer et al., 2002; Leblond et al., 2013), as well for this population (Gaudry, 2013).

Estimated mean step lengths were larger in good quality than in low quality habitats, which was counter-intuitive. Indeed, several sources have shown the opposite pattern; animals remain for shorter times, and thus to travel faster, within in low quality habitats, and remain longer in good quality habitats to benefit from better environmental conditions (Johnson et al., 2002; Morales et al., 2004). However, our findings may reflect characteristics of the Gaspésie landscape. The tops of the mountains, where much of the good quality, safer habitats for caribou are found, have very low tree cover (i.e., alpine tundra) and moving around is easy. Valley bottoms, which are considered low quality habitats, have dense tree covers of balsam fir and other tree and shrub species (Nadeau Fortin, 2015), potentially slowing or inhibiting caribou movement.

The landscape use map derived from the movement simulations provides a spatial understanding of where the population potentially moved through and interacted with its landscape, over the survey period. High landscape use was predicted, as expected, for the areas where VHF locations were recorded; in this case, at high elevation sites where we defined the subpopulations ranges (Mosnier et al., 2003). But the more interesting results were where high landscape use was predicted from environmental conditions and individual movement behavior in areas where no caribou were observed (Marucco and McIntire, 2010). Such predictions can only be obtained by simulations. Our models seemed to reveal movement corridors between the Logan and the Albert ranges, even though no individual exchange was recorded between the two subpopulations in these data. Clearly, because the current Logan population was established by recolonization from the Albert population during the late 1990s, such connections exist. A better connectivity analysis would be needed to explore if individual exchanges were likely or, even though these areas were likely used, individuals were still faithful to their subpopulation (Lookingbill et al., 2010). Some areas outside the Gaspésie National Park, where no VHF locations were recorded, nevertheless showed a high potential for landscape use; these areas were reachable by the caribou. These regions could indicate specific opportunities for expanding the park or at least for adding some measures of habitat protection outside the park to improve caribou conservation (as suggested in St-Laurent et al., 2009).

Defining good quality areas that individuals can actually access is one of the main differences between the outputs from the spatially explicit individual-based model and the results from the empirical habitat selection model (i.e., RSF). The RSF model suggested large areas of usable, but sub-optimal, habitats distant from the current subpopulation ranges. The spatial constraints added by the individual-based model as well as the spatial and temporal components of individual movement behavior had the effect of making it extremely improbable that members of the existing population would reach these more distant areas (Grosman et al., 2011; Marucco and McIntire, 2010). Movement simulations therefore showed very low potential landscape use at distance above a few kilometers from the subpopulation ranges. This will be further exacerbated because we found two behavioral reasons for this limitation, namely return to mating area and foray loops. In other words, they may be compelled to return even if good habitat were found outside. The movement model, if tied to a demographic population model (Marucco and McIntire, 2010; Wiegand et al., 2004), could be used on a longer time scale to identify stepping stones that enable the population to reach more distant, high quality, habitats within the peninsula.

5. Conclusions

Identifying mechanisms of animal movement and estimating potential landscape use does not necessarily require large amounts of high resolution telemetry data, provided some basics of species habitat preferences are known. Using spatially explicit individual-based models and pattern-oriented modeling techniques could overcome the limitations of other movement models with such data (e.g., step selection functions). We were able to identify and quantify drivers of individual movement behaviors, and thus simulated spatial landscape use at the population level, using only relatively few locations obtained by VHF telemetry. These models can identify for managers landscape features that could be modified to improve population movement (e.g., paved roads), as well as intrinsic behavioral characteristics that must be accommodated (e.g., mating site fidelity). Estimating potential landscape use of the animal population gives managers a spatial reference of where movement is facilitated or impeded, defining priority areas to work on for the protection or recovery of endangered populations. For example it can help to define areas to apply new protection rules or to design movement corridors for the studied species. Despite the above-mentioned limits of the VHF data, they represent an important resource for conservation applications, especially when immediate actions are needed. The methods used in this study could be applied on other populations or species, facilitating conservation studies when observational data are few.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2016.05.004.

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