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Trade-off between road avoidance and attraction by roadside salt pools in moose: An agent-based model to assess measures for reducing moose-vehicle collisions

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ABSTRACT

Moose-vehicle collisions are a frequent traffic-safety issue, particularly in northern regions where moose are attracted to the near-road areas because they can consume sodium from de-icing salts that accumulate in pools at snowmelt. Moose that find salt pools near roads tend to remember their location and to re-visit them to get the sodium they need in their diet. This study investigated the trade-off between road avoidance and salt pool spatial memory in the movement behaviour of moose using an agent-based model to determine how the interplay of these two factors influences the frequency of road crossings in the Laurentides Wildlife Reserve (Québec, Canada). Mitigation measures studied were the removal of roadside salt pools and the construction of compensatory salt pools away from the road shoulder. A GPS telemetry program of moose in the study area was used to validate our model. The model moose with both road avoidance and salt pool spatial memory activated produced the best results when comparing to the real moose data. Results show that both road avoidance and salt pool spatial memory significantly affect moose road crossings, but that road avoidance explains most of the variance. Road avoidance tended to decrease the number of moose crossings, but this decrease was partly compensated by the spatial memory of salt pools which typically increased the likelihood that moose will cross the road. The trade-off between road avoidance and salt pool memory was largest when original salt pools were maintained. In simulations where road avoidance and salt pool memory were both turned off, the impact of mitigation measures on the number of road crossings was lowest. For the most realistic moose behavior, the management scenarios resulted in reductions in road crossings between 22% and 79%, and the best scenario is to completely remove roadside salt pools. If compensation salt pools are used, they should be located as far as possible from the roads (beyond 500 m) to have an impact on moose road crossings.

1. Introduction

Roads and traffic fragment the habitat of many wildlife species, thereby decreasing habitat amount and quality, increasing mortality due to collisions with vehicles, reducing access to resources on the other side of the road, and subdividing animal populations into smaller and more vulnerable fractions (Jaeger et al., 2005; Fahrig and Rytwinski, 2009). For larger terrestrial mammals, wildlife-vehicle collisions (WVC) also pose a risk to human safety and vehicle integrity (Clevenger et al., 2001; Forman et al., 2003). It was estimated that, in North America and Europe, there are several millions of vehicle collisions with moose (*Alces alces*), elk (*Cervus canadensis*), caribou (*Rangifer tarandus*) and other members of the cervidae family each year (Groot Bruinderink and Hazebroek, 1996; Romin and Bissonette, 1996; Conover, 1997; Dussault et al., 2007).

Where large quantities of de-icing salt are used on roads in northern countries such as Canada, runoff leaches the road salt to the ditches and depressions beside the road in the spring snow melt. Moose need sodium in their diet (Jolicoeur and Crête, 1994), which they can either obtain by browsing on aquatic plants or by a quick trip to the roadside (potentially crossing the road to get to the salt pools on the other side). The latter is more "efficient" since sodium concentration is 2 or 3 times higher in the salt pools compared to aquatic plants (Leblond et al., 2007b), but it can increase the probability of moose-vehicle collisions (MVC) by 80% near roadside salt pools (Dussault et al., 2006a). The spatial memory of salt pools by moose has been demonstrated empirically by Miller and Litvaitis (1992) who showed that moose extended their summer home ranges to encompass the roadside salt pools at the edge of their home ranges (see also Laurian et al., 2008a). This implied that moose do not search for new salt pools all the time but remember their locations from year to year. To mitigate the risk of MVC, salt pools can be removed or drained, and compensatory salt pools can be maintained further away from the road to keep moose

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away from the roadway (Leblond et al., 2007b; Grosman et al., 2009).

Agent-based modelling (ABM) considers the resource use and other behaviours of individuals as well as the variability in their activities, and this approach is increasingly used to simulate animal movement (Tang and Bennett, 2010). Identifying the key external environmental factors, internal states, motion abilities and navigation capacities of the animal remains the primary challenge in applying a movement ecology approach to a particular system (Nathan et al., 2008; Tang and Bennett, 2010). Grosman et al. (2009) used ABM to explore whether the removal of roadside salt pools and their replacement by compensatory salt pools could reduce the number of moose road crossings. This model (hereafter referred to as the G2009 model) predicted a significant reduction in road crossings when the roadside salt pools were either completely or partly removed, with or without the creation of compensatory salt pools. However, in the original version of this model, moose agents did not have spatial memory of roadside salt pools they had previously visited. Furthermore, an assessment of moose movement obtained from telemetry data revealed that most, but not all, moose avoid roads (Laurian et al., 2008b). Thus, a more realistic road avoidance behaviour scheme than the one in the G2009 model was required to adequately represent individual moose behaviour near roads.

The main objective of this paper was to assess whether the inclusion of road avoidance behaviour and of salt pool spatial memory for moose agents can provide a better representation of real moose behaviour in the landscape, and can thus generate a more reliable predictive modelling tool to examine various mitigation measures for reducing MVC. It is known that moose are not maximising their energy (or mineral) intake at all cost, but they try to consume a reasonable amount of resources while minimising other risks like mortality on the road (Dussault et al., 2005; Laurian et al., 2008b). This trade-off between avoidance of risks associated with roads and attraction by roadside salt pools for sodium acquisition is essential for understanding moose movement behaviour in landscapes that contain roads. However, since moose exhibit some variability in their behaviour including high or low levels of road avoidance (Laurian et al., 2008b), we also wanted to compare the independent and combined influences of road avoidance and salt pool memory on moose movement patterns near roads. Furthermore, we applied the model to assess the effect of road avoidance behaviour and salt pool memory on the reductions of road crossing frequencies in different scenarios of salt pool removal and displacement to assess the potential influence of inter-individual variation. This will provide highway managers with an estimate of the range of the effectiveness of mitigation measures.

The trade-off between the effects of road avoidance and memory of salt pool locations makes it difficult to predict how the number of road crossings and the effect of salt pool removal and replacement would change following the implementation of these two types of behaviour in the G2009 model. This paper investigates the interplay and relative importance of these two behaviours on moose reactions to roads and management of salt pools as a mitigation measure of MVC. The new model represents major scientific advances over the previous (G2009) model as it also uses home range enforcement and a more realistic method of distance selection to produce a more realistic representation of moose movement.

2. Methods

2.1. Study area and available datasets

The study area was the northern portion of the Laurentides Wildlife Reserve (LWR) situated between Québec City and Ville de Saguenay, Canada (Fig. 1). The LWR is a 7861 km^2 forested region (Dussault et al., 2006a) with two provincial highways (HW 175 and 169) crossing its territory. Winters are severe in this reserve with annual snowfalls greater than 550 cm in some areas. Snow starts to accumulate in early November and lasts until early June under forest cover. De-icing efforts in the LWR apply >100 metric tons of road salt/km/yr (Jolicoeur and Crête, 1994).

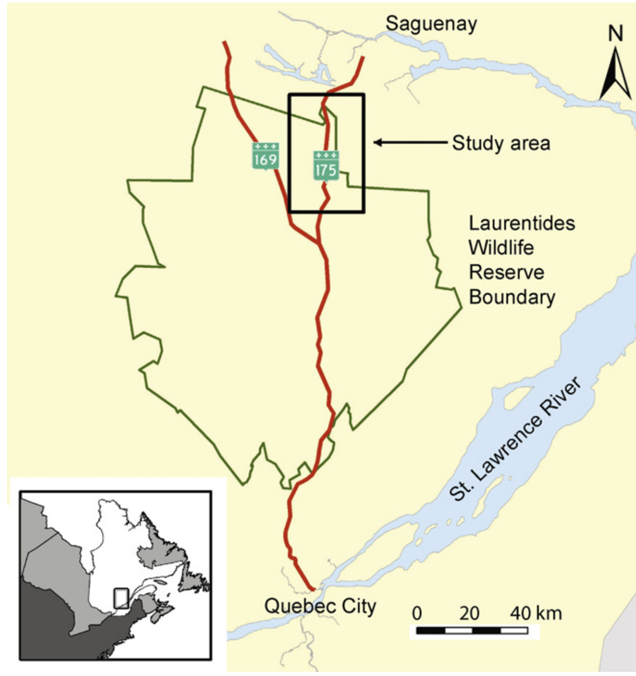

Fig. 1. The study area is indicated by the black rectangle centered on the upper portion of HW 175 above the junction with HW 169. The boundary of the Laurentides Wildlife Reserve (LWR) is outlined in green. The LWR is situated between Québec City and Saguenay in the Province of Québec, Canada. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

We used moose locations obtained through a GPS telemetry program of moose in the study area to validate our models. The moose movement dataset consisted of GPS telemetry locations for 47 moose, recorded every 2 h for 3 years (∼200,000 locations). Other datasets available allowed us to map forest stands available within the study area (∼10,000 polygons), ecoforest maps provided by the Ministère des Ressources naturelles et de la Faune du Québec (MRNF), highways, water bodies and streams, topography, and roadside and compensatory salt pool locations. The forest polygon vegetation dataset included slope, tree species composition and age, disturbance type and time, habitat type for moose with food and cover quality based on the Habitat Quality Indicators developed by Dussault et al. (2006b) (Table 1). The other environmental factors such as salt pool locations and forest polygons remained constant during the 3-year period where moose movement data were collected. Thus our data adequately reflected the targeted spatial configurations. These datasets and several scientific papers that investigated moose behaviour in the LWR (Dussault et al., 2004, 2005, 2006a,b, 2007; Leblond et al., 2007a,b; Laurian et al., 2008a,b) provided the solid background knowledge needed to model moose behaviour with confidence in the LWR. More detailed information on the datasets is provided in Grosman et al. (2009).

2.2. Salt pool management scenarios

Five scenarios were studied with the model in order to cover a range of salt pool management options (Table 2):

Table 1
Habitat types and corresponding food and cover quality attributes along roads in the Laurentides Wildlife Reserve. Habitat types were based on the vegetation available in each forest polygon as indicated on forest maps of the study area. Based on the MRNF habitat quality indicators.

Habitat type	Description	Food quality	Cover quality
Other	Lakes islands other	2	1
Fi50	Deciduous intolerant hardwoods up to 50 years old	4	2
Ft50	Deciduous tolerant hardwoods up to 50 years old	5	2
IMP	Buildings urban area fens bogs alder stands	2	1
Mi10	Mixed and intolerant hardwoods 10 years old	5	1
Mi30	Mixed and intolerant hardwoods 30 years old	4	3
Mi50	Mixed and intolerant hardwoods 50 years old	3	3
Mt50	Mixed and tolerant hardwoods 50 years old	5	3
R10	Conifers regenerating	3	1
RE30	Conifers with black spruce 30 years old	1	4
RS30	Conifers with balsam fir or white spruce 30 years old	2	4

Source: Dussault et al. (2006b).

Scenario #1: current situation;
Scenario #2: 100% salt pool removal, no compensation salt pools;
Scenario #3: 100% salt pool removal, 100% compensation salt pools, 8 of which were less than 500 m from the road. Note that only 18 compensation salt pools were needed to replace the 36 roadside salt pools since the latter were clustered in groups;
Scenario #4: 2/3 salt pool removal, no compensation salt pools;
Scenario #5: 2/3 salt pool removal, 2/3 compensation salt pools, 4 of which were less than 500 m from the road.

In order to study road avoidance behaviour and salt pool spatial memory separately and together, the five scenarios were run for four combinations of behaviour resulting in twenty different configurations overall. The four combinations of moose behaviour were:

A. Road avoidance behaviour and salt pool spatial memory both on;
B. Road avoidance behaviour on and salt pool spatial memory off;
C. Road avoidance behaviour off and salt pool spatial memory on;
D. Road avoidance behaviour and salt pool spatial memory both off.

2.3. ABM model

The model was programmed using the open-source Recursive Porous Agent Simulation Toolkit, Repast Simphony from the Argonne National Laboratory, U.S. Dept. of Energy (Repast Simphony, 2008). It is considered a mature and flexible platform written in Java with many users in the scientific community and has good development support (Railsback et al., 2006; Tesfatsion, 2008). Repast Simphony includes the GeoTools and the Java Topology Suite toolkits. GeoTools can read and write ArcGIS vector datasets which were imperative for this ABM since all GIS datasets are vector-based. The Java Topology Suite was used to create and process geometric objects such as new target moose locations, and on-the-fly buffering in the model. GeoDa (Anselin, 2004) was used to create a list that identified all the neighbouring polygons of each forest polygon that was loaded in the model initialization. The GIS analysis was done using ArcGIS 9.3 (ESRI, 2009). The model description followed the ODD (Overview, Design concepts, Details) protocol for describing individual- and agent-based models (Grimm et al., 2006, 2010).

Table 2
The five salt pool management scenarios with the number of roadside and compensation salt pools in each case.

Scenario	# Roadside salt pools	# Compensation salt pools
Current situation	36	0
100% Salt pool removal, no comp. salt pools	0	0
100% Salt pool removal, 100% comp. salt pools	0	18
2/3 Salt pool removal, no comp. salt pools	12	0
2/3 Salt pool removal, 2/3 comp. salt pools	12	12

2.3.1. Purpose

The agent-based model investigates how the interplay of two opposing factors: road avoidance and salt pool spatial memory, affected 40 model moose in the Laurentides Wildlife Reserve. We are simulating the behaviour of moose that we assume are using roads and salt pools.

2.3.2. Entities, state variables, and scales

MooseGISModel was the controller of the ABM which verified that the various input parameters were valid, for example, that the sum of weights was 1, the number of years was between 1 and 4, etc. (Fig. 2). It then read the vector GIS datasets (all in the same MTM projection) and created all of the entities described below as well as the daily schedule.

There was one active entity in the model: moose ($n=40$); and a number of passive ones: forest stands ($n=10{,}575$), home ranges ($n=40$), salt pools (by scenario: 1: 36 roadside; 2: 0 salt pools; 3: 18 compensatory; 4: 12 roadside; and 5: 24, 12 roadside and 12 compensatory; see Table 2), road ($n=1$), East study area ($n=1$; the portion of the study area east of highway 175) and west study area ($n=1$; the portion of the study area west of highway 175).

The active agent, moose, had the following state variables: its current forest polygon, its current habitat type, its previous forest polygon, its forest polygon before the previous one, the distance travelled today in meters; the total distance travelled that year and its current x and y location in meters. These 40 model moose were implemented as a point GIS data set in ArcGIS.

The first passive agent, the forest stand, had 10,575 forest polygons extracted from the forest maps from the MRNF. These agents had the following state variables: number of salt pools within the forest polygon, whether or not the highway 175 was within 500 m of the forest polygon, proximity to water bodies, proximity to salt pools, habitat type, food quality and cover quality (Dussault et al., 2006b), slope, adjacent forest polygons as determined by the GeoDa program, and whether or not it was within 75 m of the highway 175. These variables determined the movement of the model moose. The 10,575 forest polygons were implemented as a polygon GIS data set in ArcGIS.

The 40 home-range agents had one state variable, a buffer in meters which was set to 625 m. The 40 home ranges that corresponded to 40 real annual moose home ranges, constructed using the Minimum Convex Polygon method, were buffered outwards by 625 m so that the model moose found the salt pools at the edges of their home ranges. These 40 home ranges were implemented as a polygon GIS data set in ArcGIS.

The roadside and compensatory salt pool agents had different numbers by scenario as mentioned above. They had two state variables: their location west or east of highway 175, and their x and y location in meters. These salt pools were implemented as a point GIS data set in ArcGIS. The section of the highway 175 north of the junction with highway 169 was represented as a road agent. It had

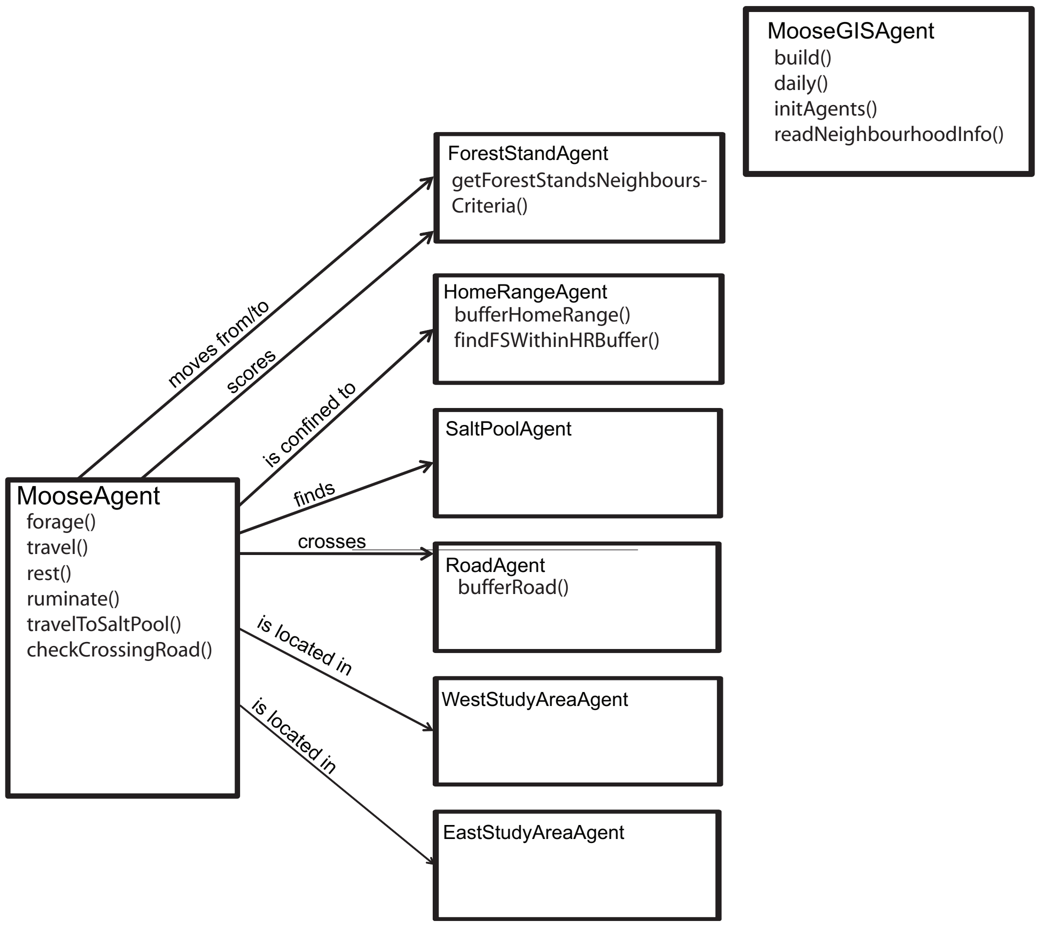

Fig. 2. Unified Modelling Language Diagram of the primary objects in the model.

a width of 45 m presenting a 2-lane undivided highway. The road was implemented as a polygon GIS data set in ArcGIS.

The East study area and west study area agents divided the approximately 26 km wide by 45 km long study area into two polygons so that road crossings were accurately counted. They had no state variables. These 2 agents were implemented as polygon GIS data sets in ArcGIS. The spring and summer time period was chosen for the model as this is when the moose are the most active visitors at salt pools (Leblond et al., 2007b). To match the GPS telemetry storage interval of two hours (Dussault et al., 2007) and the study duration of the empirical research by Laurian et al. (2008a), the model run time was from May 1st to September 30th in 2-h time steps, or Repast Simphony "ticks", resulting in a total of 1836 steps. The run duration in the previous G2009 model was from May 1st to August 31st, or 1476 steps for a total of 7344 time-steps per run. Here, to achieve a total number of model runs of at least 100, we repeated the simulations 34 times for 4 summers, which resulted in 136 runs. The last 3 of the 4 years were used for the analysis of the model moose movement, since in all scenarios, the first year had road avoidance deactivated to let the model moose find the salt pools more easily.

2.3.3. Process overview and scheduling

The 40 model moose used a discrete time step of 2 h. The moose's daily activities were divided into four phases, represented in the internal state of the model moose (Tang and Bennett, 2010): foraging for food, ruminating, resting, and travelling (Renecker and Schwartz, 2007). Following the calibration which was based on habitat use of twelve agent moose compared to twelve real moose, these four activities were assigned equal duration (i.e., 6 h each). These estimates were in the range of reported values for moose activity budget (Renecker and Hudson, 1989). This was slightly different from the G2009 model where resting lasted 8 hours and travelling extended over 4 h. All the moose's daily activities were divided into the same four time durations, each of 6 consecutive hours in the following order: ruminating, travelling, resting, and foraging. All data updated by the submodels were immediately stored in the objects and reported on by the Repast Simphony run-time system (see Section 2.3.4.8 in Section 2.3.4).

2.3.4. Design concepts

2.3.4.1. Basic principles. The ABM imposed moose movement behaviour using the input values contained in the forest polygon GIS datasets. The food value was assigned the largest weight given the size of the moose and the large amount of browse they eat daily. Proximity to salt pools was given the next highest weight given that moose were sodium deficient at the end of winter and had either to eat aquatic vegetation or make quick trips to the roadside or compensatory salt pools. Since aquatic vegetation is not fully mature in this area until mid-July, the moose are likely to visit salt pools. As well, if salt pool spatial memory was activated (see Sections 2.3.4.5 and 2.3.7.1) and the model moose had found and thus remembered the location of one or more salt pools, then in the second, third and fourth years the model moose made a number of trips (according to a Poisson distribution based on a mean of 2.1 (Laurian et al., 2008a)) to the closest salt pool in June and July. Given that 90% of moose were road-avoiders but they must get salt for their diet, these two factors worked against each other. Moose visiting roadside salt pools have a high probability of getting hit by automobiles. This ABM looked at these 2 factors with 5 different scenarios of salt pool locations to investigate their interplay. We hoped to produce a prototype ABM that could be developed into a useful tool for road ecologists and highway transportation planners in regions where road salt is an important element of winter road safety.

2.3.4.2. Emergence, adaptation, interaction, and collectives. There was no emergent behaviour from the model since most of the model moose movement behaviour was imposed. There was no adaptation in this ABM as the rules remained constant throughout the ABM. There were also no interactions between the moose agents and no collectives in the model. These 40 model moose were solitary creatures with no herding instincts.

2.3.4.3. Objectives. The objectives of the model moose were twofold: obtain enough food every day to survive and seek out salt pools to overcome their sodium deficiency from their winter months.

2.3.4.4. Learning. Moose with activated salt pool spatial memory remembered the salt pool locations when they found salt pools within their home ranges. When the time was scheduled to go to a salt pool, they chose the closest one to their current location. Moose without salt pool spatial memory had to continually look for salt pools and had no memory of them after they had found them. Thus, they did not learn. The first option is the more realistic one according to previous studies (Leblond et al., 2007b; Laurian et al., 2008a,b).

2.3.4.5. Prediction. Moose with activated salt pool spatial memory remembered salt pool locations and when the scheduled time came to go to a salt pool, they moved directly to it with purpose.

2.3.4.6. Sensing. The model moose used the forest polygon's values of food quality, cover quality, proximity to salt pools, proximity to water bodies and slope to determine the score of each forest polygon that they wanted to travel to. As well, if road avoidance was activated, and the forest polygon was within 500 m of the highway 175, then the food quality, cover quality, and proximity to water bodies values were degraded to enforce road avoidance as a habitat quality attribute.

2.3.4.7. Stochasticity. After the scores of the next potential forest polygons to travel to were obtained, a limited amount of randomness was applied to the scores (see Grosman et al. (2009) for details) so that the highest scoring forest polygon was not always the one chosen. As well, when salt pool spatial memory was activated, a Poisson distribution was used to choose the time steps at which a moose went to a salt pool.

2.3.4.8. Observation. All data created by the ABM were used for analysis. The following reports were issued by the Repast Simphony ABM:

1. The Moose Crossing report listed the total number of moose road crossings by year, and the total number of moose road approaches by year for each moose and each run.
2. The four Habitat Use reports, for each run, listed by year the total number of visits to each of the 11 habitat types by each model moose.
3. The Distance Travelled report listed the estimate of distance travelled in each of the 4 years by scenario and run and by model moose.
4. The Salt Pool Discovery report listed which model moose have discovered salt pools, and at what time steps in years 2–4 they should proceed directly to one of its discovered salt pool, for each run.
5. The Road Avoider report listed by scenario each model moose and whether it was a road-avoider or not.
6. The Foraging Same Habitat report counted by model moose the number of times while foraging it moved outside its forest polygon to a neighbour with the same habitat type, for each and scenario.
7. The Detailed Data log listed by time step for each run and scenario, the current location, animal identification, year, month, day and hour, the current and previous forest polygon, habitat type selected, activity type, distance travelled that day and total distance travelled so far.
8. The Habitat Use, Distance Travelled, Moose Crossings and Salt Pool Discovery reports for the last 3 years were combined for the 102 runs per scenario and summarized to determine the number of moose-road crossings while travelling, the total distance travelled by the model moose, and their habitat use.

2.3.5. Initialization

There were 40 model moose with their home ranges that started from the same May 1st, 2005 noon locations in each year. These locations were taken from the corresponding real moose's May 1st, 2005 noon locations.

There were 10,575 forest polygons initially in each of the five scenarios. There were five sets of forest polygon and salt pool GIS datasets for the five different scenarios. The forest polygon GIS datasets differed only in their proximity to salt pool values since each scenario had a different number of salt pools. The roadside salt pools were based on real data, however, for the compensatory salt pools, only 4 existed on highway 175; the rest were created by the modeller. The home-range agents, at initialization, first buffered themselves outward 625 m and then determined which forest polygons were within their buffered home ranges. The model moose were not allowed to travel outside their (buffered) home ranges.

Between 0 and 36 salt pools agents were created, depending on which scenario was being run. The road agent was created with an initial width of 45 m (22.5 m on either side) and buffered outwards 477.5 m on each side that created a road buffer of 500 m. As well, the East Study Area and west study area agents were created.

2.3.6. Input data

The model used the forest maps from the MRNF for the 10,575 forest polygons with their food quality, cover quality, and slope values. The values for proximity to salt pools, proximity to water bodies, number of salt pools within the forest polygon, whether or not the highway 175 was within 500 m of the forest polygon and whether or not the highway 175 was within 75 m of the forest polygon were determined by the modeller and inserted into the forest polygon GIS datasets; however, only the proximity to salt pool values were different by scenario.

As well, the model used the following other GIS datasets: 40 model moose with initial locations, 40 model moose home ranges, highway 175 with a 45 m width (between kilometer markers 169 and 221), salt pool locations: both roadside and compensatory, East and West polygons that divided the study area into two sections based on the highway 175.

2.3.7. Detailed processes and submodels

2.3.7.1. Salt pool spatial memory. In the G2009 model, the model moose had to hunt for the salt pools continuously and had no spatial memory of any salt pools that they found. In the new model, the moose agents had a memory of the locations of one or more salt pools that they had found within their buffered home ranges. As a moose travelled on the landscape in the model and found a forest polygon containing a salt pool, it remembered this salt pool location and could then visit it again in subsequent simulation years. The model moose had a spatial memory of more than one salt pool and it could have discovered salt pools in any year even if it had already found one before. The distance decay function of movement step lengths (described below, Eq. (1)) was still kept when the salt pool spatial memory was turned off.

In order to implement this module, it was essential to know how frequently real moose visit salt pools. Observations by Laurian et al. (2008a) in the LWR showed that the total number of moose salt pool visits varied from 1 to 5 per summer, with a mean of 2.1 visits per summer. The model moose chose the salt pool that was closest to their current location at the time step that triggered a salt pool visit, regardless of whether or not it was located on the same side of the road as the model moose's location. If the model moose was a road-avoider (see below) then it left the salt pool area quickly; if it was one of the few non-road-avoiders, then it did not.

When salt pool memory was turned on, once a model moose had chosen a salt pool from the ones it remembered, in the scoring method of the travel process the Proximity to Salt Pools weight (initially set to 0.30) of this moose was set to zero, and the other weights were increased proportionally so that the sum of the weights remained equal to one. For those moose that did not find a salt pool in the first year, the proximity to salt pools weight was still used for determining the next forest polygons to move to in subsequent years. When salt pool spatial memory was turned off, the moose could find up to 3 salt pools, after which the above scoring method of the travel process was applied to reflect that moose would not be attracted to salt pools any more.

2.3.7.2. Road avoidance behaviour. Laurian et al. (2008b) found that moose in general avoid a buffer strip up to 500 m wide around paved roads except when obtaining sodium from roadside salt pools in June and July. Thus, a 477.5 m buffer around the 45 m buffered paved road (representing both the two-lane road and the distance from the road shoulder to the forest) was created and used for modelling road avoidance behaviour. All polygons that intersected with this buffer were split up into separate polygons. If the interior point of the longest bisector of a forest polygon was within the buffered area that included the road then its food quality, forest cover quality and proximity to water body values were decreased to reflect the lower attractiveness of these polygons for road avoiders. In the second and subsequent years, the food quality value, the forest cover quality value and the proximity to water body values of the forest polygons within the 500 m buffer were all reduced by 3 (with a minimum value of 0). These three parameters initially could have values from 5 to 1, 4 to 1, and 5 to 1, respectively. The reduction by 3 was determined by calibrating the resulting moose road crossings against the 12 real moose crossing values.

There were, however, a few moose that spent a considerable amount of time within a 50 m buffer of the paved road. Laurian et al. (2008b) found that 4 of the 47 moose (8.5%) highly preferred the 0–50 m strip next to the road. Thus, in the model scenarios, four model moose out of 40 (10%) were selected randomly by Hawth's Tools (Beyer, 2004) and configured to not be road avoiders; thus, the food, cover, and proximity to water bodies values were not degraded within the 500 m buffer of the paved road for these non-road avoiders.

2.3.7.3. Distance travelled. The movement distances of the 12 real moose in the database used in the G2009 model from May 1st to Aug 31st, using bins of 25 m (from 0 m to 1000 m), was represented by a power law probability distribution:

$$y = 8999.2\,x^{-1.592}, \quad R^2 = 0.89 \tag{1}$$

where x represents the bin number (from 1 to 40) and y represents the corresponding frequency. The moose generally moved short distances in 2 h when foraging or ruminating, and longer distances when travelling, but longer distances were chosen less frequently. Equation (1) was used to generate movement distances for the model moose. This approach differs from the one used in G2009 model where the distribution of movement distances was uniform with a maximum movement distance while foraging of 160 m (in both horizontal and vertical directions), whereas the average distance when travelling to an adjacent forest polygon was about 1034 m.

For foraging and ruminating activities, the model moose were restricted to their current forest polygon with the exception of moving to an adjacent forest polygon of the same habitat type. This happened about 20% of the time in a simulation run. The maximum forage distance was determined to be 125 m after calibration against the real moose, using a total travel distance in one summer of 2,537 km, and taking into account that three of the real moose's GPS telemetry records ended before September 30th, which resulted in a smaller total distance travelled than by the model moose.

A random movement angle between 0° and 359° using a uniform distribution function was then chosen (angle between the previous and the new movement direction). Applying the following trigonometric functions, a new target foraging or ruminating location was determined:

$$\text{horizontal direction} = \text{distance} * \cos(\text{angle}); \tag{2}$$

$$\text{vertical direction} = \text{distance} * \sin(\text{angle}); \tag{3}$$

For travelling, a distance was chosen from the power law probability distribution (Eq. (1)) using the maximum forage distance, initially set to 125 m, as a lower limit, and the maximum travel distance, initially set to 550 m, as an upper limit. All forest polygons that intersected a circle with a radius of the chosen travel distance within the model moose's home range were selected. These were scored using the weighted parameters to determine which forest polygon would be selected.

When salt pool spatial memory was active and it was time for a moose to visit a salt pool, the moose moved with intentional direction and speed that was higher than regular travel speed (Laurian et al., 2008a). The minimum travel distance was increased to 275 m in the model to reflect this.

2.3.7.4. Parameters and weights. External environmental factors were incorporated in the ABM through habitat use rules that determined which forest polygon to move to in the next time step. The rules were based on the five most significant parameters extracted from the current scientific literature on moose in the LWR (Dussault et al., 2004, 2005, 2006a, 2007). These were food quality, cover quality (protection from predators and thermal stress), slope, proximity to water bodies and streams, and proximity to roadside salt pools. Food quality was assigned a value from 1 to 5 and cover quality was assigned a value from 1 to 4 based on the habitat suitability index developed by Dussault et al. (2006b) (Table 1). Moose prefer to move along ridges and valleys rather than climbing or descending hills (Leblond et al., 2010). Accordingly, four slope categories were created, where 5 corresponds to shallow slopes (<8%), 4 to slopes between 9% and 30%, 1 to slopes between 31% and 40% and 0 to slopes >41%. Water bodies are important for sodium intake and staying cool to avoid thermal stress. Three classes of proximity to water bodies were created based on distance: 5 for bordering a water body, 3 for polygons less than 200 m from a water body and 0 for distances greater than 200 m. Finally, proximity to salt pools was coded as an attribute of the forest polygons as a distance decay function with 5 if a forest polygon contained a salt pool; 4 if a forest polygon was within 100 m of a salt pool; 3 if a forest polygon was within 250 m of a salt pool; 2 if a forest polygon was within 500 m

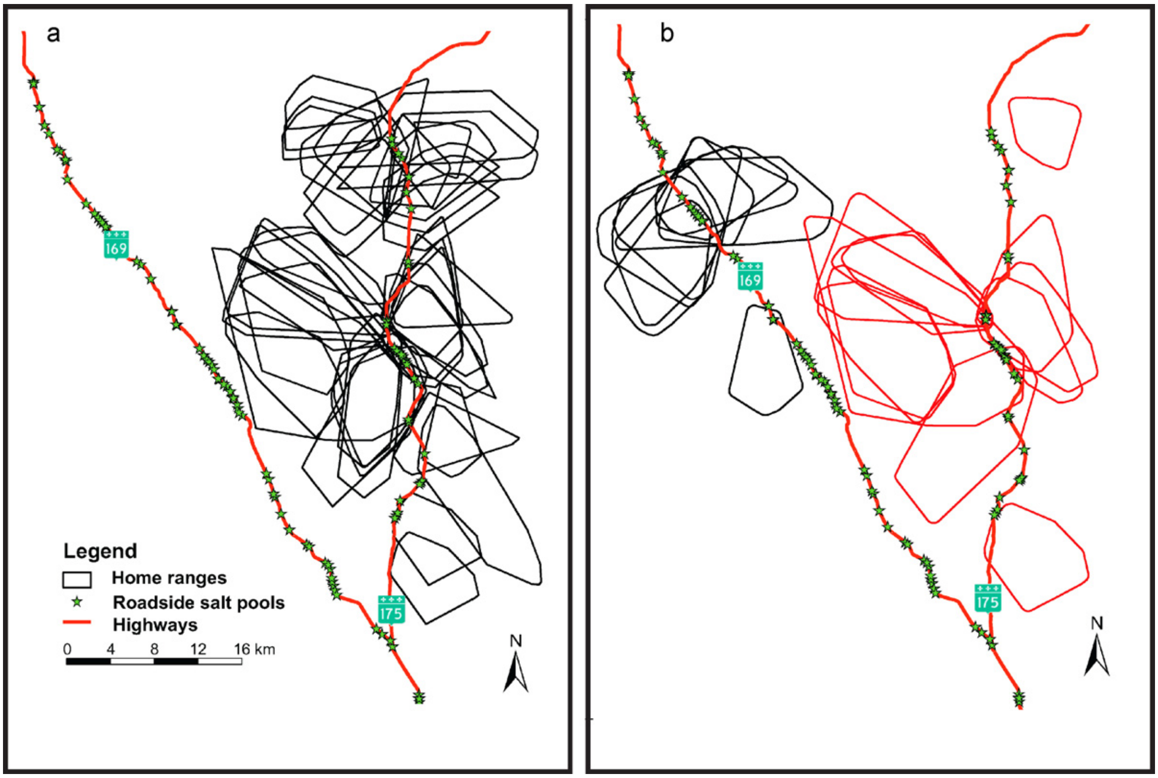

Fig. 3. (a) Home ranges for the 40 model moose used in the model which were based on the home ranges of 21 real moose (b). The home ranges of the 12 real moose near highway 175 that were used for validation are highlighted in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

of a salt pool; 1 if a forest polygon was within 1000 m of a salt pool; and 0 if a forest polygon was more than 1000 m away from a salt pool.

Weights were applied to each of the five parameters, resulting in an overall "attractiveness" score for each polygon. These scores were turned into preferences that were normalized to 100%. After a re-calibration using 12 real moose, the weight of proximity to salt pools was decreased by 0.05 and the food quality parameter was increased by 0.05 compared to the G2009 model.

The yearly home ranges of 68 real moose along highways 169 and 175 were created using the minimum convex polygon method of Hawth's Tools (Beyer, 2004). The home ranges were drawn around the GPS telemetry locations for the May 1st to September 30th time period and buffered outward by a value of 625 m. This buffer width was calibrated so that the model moose living in these home ranges could find the roadside salt pools that were often located at the edge of their home ranges. Without the buffer, some moose would not have enough room to find the roadside salt pools. These buffered model moose home ranges had an average area of 73 km^2 (range: 28–208 km^2). Because the ABM domain is around highway 175, real moose home ranges that encompassed highway 169 were moved by translation and rotation near highway 175. From this dataset, the home ranges of 40 model moose were randomly selected (Fig. 3a). The 40 model moose corresponded to 21 real moose (since some real home ranges were for the same moose but for different years) (Fig. 3b). Each real moose home range was determined on an annual basis: from January 1st to December 31st. Each of the 40 model moose had home ranges based on the 21 real moose, and some of the model moose home ranges were duplicated by shifting them approximately 500–3000 m. To validate the model, 12 of the 21 pairs of real and agent moose were used. The starting forest polygon locations for each model moose were determined by using the May 1st noon-time location of each corresponding real moose. The number of moose agents in this study was considerably higher than the 12 model moose that were used in the G2009 model.

What the real moose were doing and where they were moving between the recorded locations was not known. The model moose, however, do not move around between their 2-h time steps. Thus, a road crossing was only counted if the 2-h movement line segment crossed or intersected the pavement portion of highway 175. This pavement portion is defined as a 3.7 m buffer on each side of the road center line that represents highway 175. Each moose road crossing was logged in the moose crossing report by animal identification, date and time. The initial constant weights for the five variables (food quality (0.45), cover quality (0.10), slope (0.05), proximity to water bodies (0.10) and proximity to salt pools (0.30)) contained in each forest polygon were calibrated against a subset of the real moose.

For scenario #2, since there were no salt pools in the GIS landscape and it was assumed in the model that the moose knew that there were no salt pools, the weight of the Proximity to Water Bodies parameter was correspondingly increased to 0.40.

2.3.7.5. Foraging and ruminating submodels. When foraging or ruminating, a travel distance between 0 m and 125 m was randomly selected from the power law distribution, and a direction was randomly selected between 0° and 359°. If this travel distance was within the model moose's current forest polygon or an adjacent one that has the same habitat type, it moved there. Then the following state variables were recorded for these submodels and all the subsequent ones: date and time, activity type, distance travelled for that day and for the year, habitat type, totals for the eleven habitat types, the new and 2 previous forest polygons visited.

2.3.7.6. Resting submodel. When resting, the model moose remained in its current forest polygon and did not move.

2.3.7.7. Travelling submodel. When travelling, a travel distance between 125 m and 550 m was randomly selected from the power law distribution. This travel distance corresponded to the radius of a circle used to choose the forest polygons that intersected this circle (except, of course, the current forest polygon). Since the moose could not travel outside its own home range, only forest polygons within the buffered home range were chosen. Then using the five state variables from each forest polygon: and multiplying each of the five variables by the calibrated weights, a total score was determined for each possible destination forest polygon. If the target polygon was within 75 m of the 45 m-buffered paved road then the food and cover weights were reversed, i.e., the food weight was multiplied by the forest cover quality value and the cover weight was multiplied by the forest food quality value. This reflected the moose's behaviour in the vicinity of the highway where it valued forest cover more than food instead of the normal situation where food was valued over cover (Dussault et al., 2007).

As well, if salt pool spatial memory was activated, the proximity to salt pools weight was reduced to 0 and the values were redistributed proportionally to the other 4 weights. Then some randomness was applied to the scores, so that the best scoring forest polygon was not always selected, and the moose travelled to the midpoint of the longest bisector of the chosen forest polygon. If salt pool spatial memory was activated, and the chosen forest polygon contained a salt pool, it was recorded in the moose‘s memory. If salt pool spatial memory was not activated, then just the number of salt pools in the moose‘s home range was increased by 1. Finally, the moose road crossing process was invoked, to count any road crossing by the moose.

2.3.7.8. Travelling to a salt pool submodel. When travelling to a salt pool, if salt pool spatial memory was activated, and the time-step equalled one of the pre-selected time-steps, then the moose chose the salt pool closest to its current location. A travel distance between 275 m and 550 m was randomly selected from the power law distribution for each time-step and the moose proceeded in a straight line towards the salt pool until it reached the salt pool. Finally, the moose road crossing process was invoked, to count any road crossing by the moose. If the moose was a road-avoider, then it left the area quickly; otherwise, it did not. If salt pool spatial memory was not activated, the moose found a maximum of 3 salt pools per year.

2.4. Statistics

Statistical tests used a significance level of 0.05 and 0.1. A 2-way ANOVA was performed on the road crossing results, both for summary scenario data ($n = 20$) and for the individual moose level ($n = 800$). The two fixed factors were road avoidance and salt pool spatial memory. In addition, permutation tests that shuffled both the rows of the summary scenario and individual moose road crossing data 999 times were performed. The resulting p-values of these 2-way ANOVAs were compared to the p-values of the 2-way ANOVA permutation tests. To investigate if the reductions in moose crossings and in total distance travelled due to roadside salt pool removal and displacement were statistically significant, we performed Student's t-tests on the 102 runs (i.e. 34 runs for each of the years 2–4) comparing each of the four salt pool removal or displacement scenarios with its first scenario (where all original salt pools were present). All statistical tests were performed in the R statistical language (R Development Core Team, 2009).

Table 3
Comparison of the number of road crossings and the proportion of locations within 500 m from the road between the 12 real moose and the corresponding 12 model moose with road avoidance and salt pool spatial memory turned on or off for the current situation (scenario #1). The real moose are averaged over one summer whereas the model moose values are averaged over 3 summers.

Real moose vs. model moose's current situation (4 combinations)	Average number of road crossings/moose/summer	Proportion of moose locations <500 m from roads (%)
Real (telemetry data)	4.4	7.8
Model with road avoidance ON and salt pool memory ON	2.0	2.6
Model with road avoidance ON and salt pool memory OFF	1.3	1.7
Model with road avoidance OFF and salt pool memory ON	12.4	12.4
Model with road avoidance OFF and salt pool memory OFF	9.0	8.7

3. Results

3.1. Model validation

The validation was done using 12 real moose and the corresponding 12 model moose that both had their home ranges near HW 175 (highlighted in red on Fig. 3b). The 12 model moose data were extracted from the current situation scenario (#1, where all salt pools are present), as this corresponded to the situation experienced by real moose during the telemetry follow-up. The validation was based on distance travelled, habitat use, number of road crossings, and proportion of locations within a 500-m buffer zone around highways. The latter two variables were expected to be affected by road avoidance behaviour and salt pool spatial memory since they were related to movement patterns near the roads, whereas overall habitat use and distance travelled should be primarily affected by food and cover quality habitat.

The number of road crossings and the proportion of locations within a 500-m buffer varied markedly in the model moose dependent on whether road avoidance and salt pool spatial memory were activated or not (Table 3). As expected, there were more moose close to the road (and thus more crossings) when road avoidance behaviour was turned off, resulting in a number of road crossings much greater than observed in the telemetry database. The model moose with both road avoidance and salt pool spatial memory activated produced the best results when comparing to the real moose data.

The average foraging and ruminating distances for the four combinations of road avoidance and salt pool spatial memory for the current situation salt pool scenario were all the same (30 km). The travel distances did not differ much between the four combinations of moose behaviour (i.e. from 217 km for the road avoidance off and salt pool spatial memory on to 227 km for the case of road avoidance on and salt pool spatial memory off). Thus, no conclusion can be drawn from foraging, ruminating and travelling distances about the question of which behavior is more realistic when modelling moose movement.

When examining the 40 model moose with road avoidance and salt pool memory, the average travelled distance per moose was 255 km. This is very close to the average distance travelled by the 21 real moose, which was 247 km per moose. However, the variability in the distances travelled by the model moose was low (with a minimum of 250 km and a maximum of 260 km). This contrasted with the marked variability in the real moose, ranging from 155 km to 402 km. The highest distance belonged to a yearling female

Table 4
Results of two 2-way ANOVAs on the summary absolute number of moose road crossings by scenario ($n = 20$) and on the individual absolute number of moose road crossings by scenario ($n = 800$), with the partitioning of variance for the individual cases and the coefficients of the two factors and of the interaction (Legendre, 2010).

Factors	Coefficients (summary)	Coefficients (individual)	*p*-Value (summary)	*p*-Value (individual)	Partitioning of variance explained (individual)
Road avoidance	−5.798	−5.801	<0.001	<0.001	83.5%
Salt pool spatial memory	6.958	6.955	0.01	0.001	3.9%
Road avoidance: salt pool spatial memory	−3.066	−3.0642	0.06	0.04	12.6%

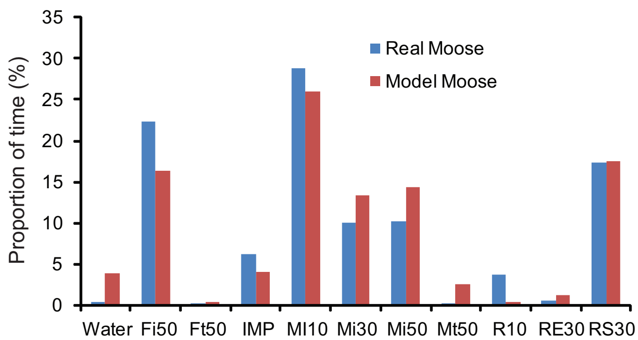

Fig. 4. A comparison of the habitat use of the 12 real moose with home ranges near HW 175 with the 12 model moose. The proportion of time corresponds to the number of time steps spent in each habitat divided by the total number of steps for the model and real moose, respectively.

seeking out a new home range after being pushed away by her mother in anticipation of new offspring.

We summarized habitat use for each of the 11 habitat types for the 12 real moose and the corresponding 12 model moose (with both road avoidance behaviour and salt pool spatial memory activated) (Fig. 4). For most habitat types, the counts corresponded reasonably well. The greatest differences between the real moose and the model moose were observed for the three habitat types Mi30 (mixed and intolerant hardwoods 30 years old), Mi50 (mixed and intolerant hardwoods 50 years old), and Fi50 (deciduous intolerant hardwoods up to 50 year old) (Table 1, Fig. 4). When the details of the home ranges of the 12 real moose were examined, it appeared that 9 of the 12 real moose did not use much of habitat type Mi30 and 7 of the 12 real moose did not use much of habitat type Mi50. As for Fi50, almost all of this habitat type is in the northern half of the study area. We interpret the differences between the real and the model moose as a consequence of the inter-individual variation in the real moose – which may partly be a response to differences in habitat availability among the various home ranges. This was not reflected in the model moose. The numbers were much closer for habitat type Mi10 reflecting the fact that real moose preferred to forage in forests that are regenerating after a forest cut, which was well reproduced in the model moose.

These results confirmed that the inclusion of road avoidance behaviour and of salt pool spatial memory for moose agents provided a better representation of real moose behaviour in the vicinity of roads (Table 3). In addition, the results confirmed that the habitat selection rules that were based on the weighted average of the five parameters of food, cover, slope, proximity to salt pools and proximity to water bodies with some stochastic variability were reasonable. Considering that the ABM moose agents were coded with a realistic but simplified set of behavioural features, these validation results were encouraging. The model adequately simulated moose movement, although with a somewhat reduced variability compared to real moose.

3.2. Salt pool memory and road avoidance

Two 2-way ANOVAs were performed on the summary ($n = 20$) and individual moose absolute road crossing totals ($n = 800$) to assess the influence of road avoidance behaviour and salt pool spatial memory both separately and in their interaction (Table 4). When examining results on the summary data, road avoidance behaviour had a statistically significant effect on number of road crossings (p-value < 0.001), salt pool spatial memory was also significant (p-value = 0.01), but the interaction between the two factors was only statistically significant at the 10% level (p-value = 0.06) (Table 4).

When the 2-way ANOVA with crossed fixed factors was performed on the individual moose by scenario, the p-value for the effect of salt pool spatial memory decreased from 0.01 to 0.001, probably due to the increased sample size. The p-value of the interaction between the two factors changed from 0.06 in the summary scenarios to 0.04 in the individual scenarios, making it statistically significant at the 5% level. The 2-way ANOVA permutation tests gave similar p-values to the 2-way ANOVA.

When the partitioning of variance (Gotelli and Ellison, 2004) was performed on the 2-way ANOVA for the individual moose road crossings, it was found that 83% of the explained variance was due to the road avoidance factor, 4% was due to the salt pool spatial memory factor and 13% was due to the interaction of the two factors (Table 4). Road avoidance was thus clearly the most important, which was expected since there were few visits to salt pools each year. The coefficients for the road avoidance and the salt pool spatial memory factors had opposite signs (Table 4), meaning that their effects on the moose movement were in opposite directions: road avoidance repelling the model moose from the road and salt pool spatial memory attracting them to the road.

3.3. Number of road crossings in the five scenarios

In order to assess the potential influence of inter-individual variability, independent and combined influences of road avoidance and salt pool memory in different scenarios of salt pool removal and displacement were examined. This also allowed us to assess the sensitivity of the model to road avoidance and salt pool memory behaviour. The number of road crossings varied markedly depending on whether or not road avoidance and salt pool memory were activated, and depending on the salt pool mitigation scenario (Fig. 5a, Table 5). Simulations in which road avoidance was activated clearly resulted in fewer crossings, whereas salt pool memory tended to increase the number of crossings compared to runs where this option was deactivated as evident in scenarios 1, 3, 4, and 5 (this would not be apparent in scenario 2 since there were no salt pools). These two behavioural features therefore played against each other, as expected, but road avoidance dominated, although the impacts of these two factors varied with salt pool mitigation scenarios. With both road avoidance and salt pool spatial memory on and all 36 roadside salt pools present (current situation, scenario #1), there was an average of 4.24 road crossings per moose per summer (Fig. 5a). When salt pool spatial memory was turned off, the road crossings dropped by 31% (to 2.93). With both road avoidance and salt pool spatial memory on and all the roadside salt pools removed and the 18 compensation roadside salt pools present (scenario #3), there was an average of 2.13 moose road

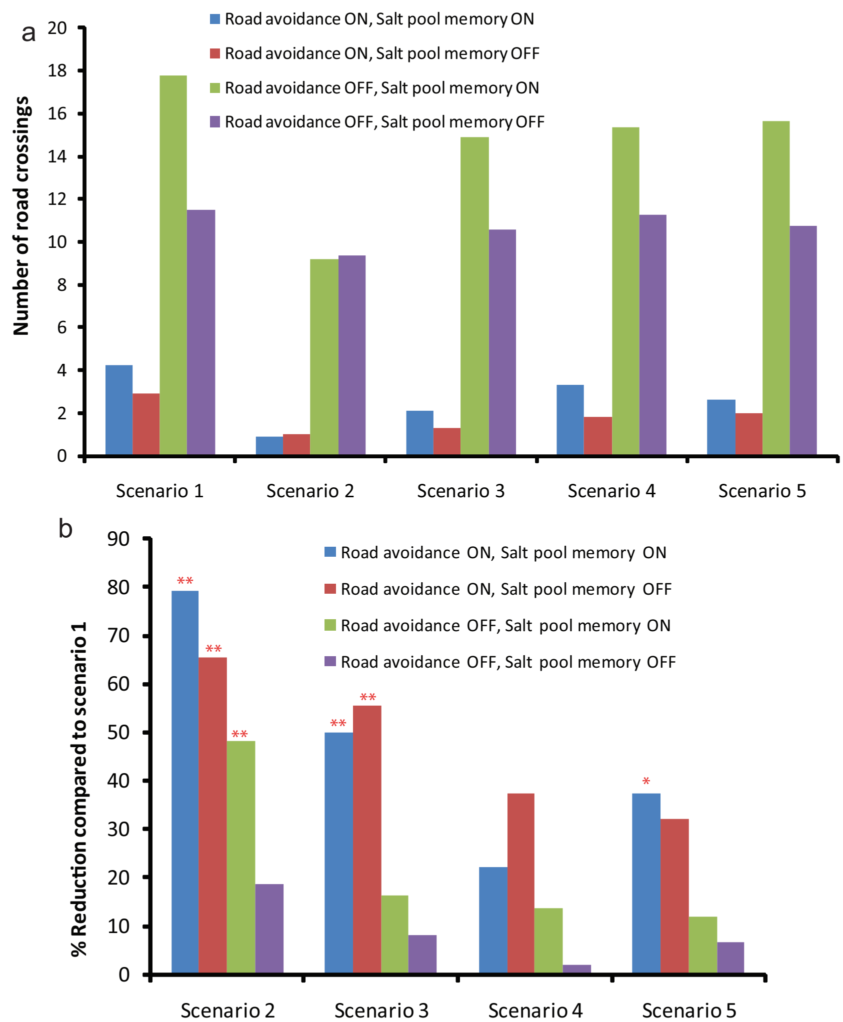

Fig. 5. (a) Number of moose road crossings per moose per summer in the five scenarios and (b) model moose road crossing reductions compared to the current situation (Scenario #1). The double stars indicate a statistically significant p-value (<0.05) and the single star represents a significant p-value at $p < 0.10$. Scenario 2 has no salt pools at all. Scenario 3 has no roadside salt pools and 18 compensation salt pools. Scenario 4 has 12 roadside salt pools with no compensation salt pools and Scenario 5 has 12 roadside salt pools with 12 compensation salt pools. The figure is based on the three year averages of the road crossings for the 40 model moose.

crossings per summer. When salt pool spatial memory was turned off, road crossings dropped by 39% (to 1.30). The biggest impact of salt pool memory was for scenario #4, where 2/3 of salt pools were removed with no compensation pools, and the road crossings dropped by 44% (from 3.30 to 1.84 road crossings per moose per summer) when salt pool spatial memory was turned off, although this difference was not statistically significant. Thus, when salt pool spatial memory was on, it tended to increase moose road crossings in all the scenarios where there were roadside or compensation salt pools present regardless of whether road avoidance was on or off.

The results can also be analysed in terms of reductions in moose road crossings compared to the current situation (current situation, scenario #1). In the first set of simulations with both road avoidance and salt pool spatial memory active, scenarios #2 (all salt pools removed) and #3 (all salt pools removed with equivalent compensation pools) showed significantly fewer crossings than in the current situation (scenario #1, Fig. 5b), with reductions of 79% ($p < 0.001$) and 50% ($p = 0.031$), respectively. When only road avoidance was activated (no salt pool memory), moose were continually searching for salt pools. This resulted in higher reductions in road crossings than in those scenarios where moose remembered the location of salt pools. When salt pool memory was active, the moose travelled to the road and then from time to time crossed it. Since the compensatory salt pools were further from the road in scenarios 3 and 5, the moose hunted and discovered these salt pools without necessarily crossing the road. With road avoidance on and salt pool spatial memory off, scenarios #2 and #3 were significantly different from the current situation with road reductions of 65% ($p = 0.007$) and 56% ($p = 0.020$), respectively. Without road avoidance, the moose road crossings were much higher and the reductions in scenarios 3, 4 and 5 were smaller. In the fourth set of scenarios with both road avoidance and salt pool spatial memory off, salt pool management scenarios did not influence the number of road crossings. As well, Student's t-tests between simulations with salt pool memory on or off (with no road avoidance) showed no significant differences for all scenarios.

4. Discussion

This study has demonstrated that agent-based modelling (ABM) is a worthwhile approach for the study of moose-road interactions. Our results show that both road avoidance behaviour and salt pool spatial memory of the moose agents affect the predicted numbers of road crossings by moose as a consequence of the removal and displacement of roadside salt pools. However, road avoidance behaviour was shown to be the more influential factor. The scenar-

Table 5
Statistical tests for the 5 scenarios with each of the four combinations of the two factors: road avoidance behaviour (RAB) and salt pool spatial memory (SPSM) for the average number of moose road crossings per moose averaged over 3 years and road crossing reduction percentages. The Student's *t*-tests were performed in R using the Student's *t*-test program with 999 permutation tests (Legendre, 2010).

Scenario	RAB	SPSM	# Crossings	Reduction (%)	Student's *t*-tests *p*-values	Student's *t*-tests *p*-values 999 perms
1 (Current situation)	Yes	Yes	4.2			
	Yes	No	2.9			
	No	Yes	17.8			
	No	No	11.5			
2 (No salt pools)	Yes	Yes	0.89	79	<0.001	0.001
	Yes	No	1.0	66	0.007	0.004
	No	Yes	9.2	48	0.017	0.016
	No	No	9.3	19	0.500	0.514
3 (No salt pools with compensation salt pools)	Yes	Yes	2.1	50	0.031	0.029
	Yes	No	1.3	56	0.018	0.021
	No	Yes	14.9	16	0.420	0.454
	No	No	10.6	8	0.755	0.745
4 (Two-thirds of salt pools removed)	Yes	Yes	3.3	22	0.339	0.327
	Yes	No	1.8	37	0.134	0.127
	No	Yes	15.3	14	0.473	0.465
	No	No	11.3	2	0.940	0.942
5 (Two-thirds of salt pools removed with compensation salt pools)	Yes	Yes	2.7	38	0.097	0.101
	Yes	No	2.0	32	0.198	0.188
	No	Yes	15.7	12	0.552	0.563
	No	No	10.7	7	0.789	0.788

ios with road avoidance active exhibited far fewer road crossings in each scenario than in the scenarios where the moose did not avoid the road (Fig. 5a). When salt pool spatial memory was turned on, it resulted in slightly higher numbers of road crossings than when it was turned off. This is probably due to the planned salt pool visits. When road avoidance behaviour was turned off, the model moose did not leave the road quickly after visiting the salt pool. When salt pool spatial memory was turned off and only the distance decay function was used to find salt pools, it resulted in fewer road crossings due to the fact that the model moose do not always find salt pools near the road in the second and subsequent years, particularly when the moose avoided the road.

A detailed analysis of the movement of all model moose for the current situation, (scenario #1) revealed the presence of 4 outliers in the database, which corresponded to two different situations. First, when a lake was present near the road, the model moose tended to be attracted to the lake and stayed in its vicinity since even though the Proximity to Water Bodies score had been reduced from 5 to 2 near roads, this was still enough to attract the model moose. This was particularly the case when salt pool spatial memory was activated since, when the moose had found a salt pool, the weight for the proximity to water bodies factor was increased proportionally as the proximity to salt pools weight was reduced to zero. The second type of unusual behaviour was related to the road avoidance algorithm which reduced by 3 the score of food and cover quality near roads. This did not entirely prevent agent moose from getting close to the road area when habitat near the road was of very high quality. When removing these 4 outliers from our analysis, fewer road crossings per moose occurred in the first scenario.

It is interesting to note that the road avoidance effect was the dominant factor in scenario #2 when the roadside salt pools were completely removed with no compensatory salt pools but in scenario #3, the placement of the compensatory salt pools generated a substantial increase in the number of crossings (Fig. 5a). It is also important to note that many MVCs in the LWR involve young moose who are dispersing from their mother's home range to find their own home ranges and wander onto the highway (Y. Leblanc, AECOM Tecsult Inc., pers. comm.). In this study, the age of moose was not used and dispersal was not considered.

The results suggest that the most effective management strategy is to remove all salt pools without creating any compensatory ones, and to let the moose return to foraging for aquatic plants to satisfy their sodium dietary requirement. These observations were also noted in the G2009 simulations where the reductions were between 49% and 16% (with the same order of the scenarios as in the current model), but the reductions are significantly higher in this improved model which better takes into account the real moose's road avoidance behaviour that has been noted in several empirical studies (Dyer et al., 2002; Forman et al., 2003; Dussault et al., 2007; Leblond et al., 2007a,b; Laurian et al., 2008a,b). If compensation salt pools are still considered necessary, then moving the compensation salt pools beyond 500 m from the road (as far as possible) should lead to better results. Compensation salt pools were indeed used in the LWR, in combination with the drainage of roadside salt pools (which were filled with stones). These are relatively simple and inexpensive means of reducing MVCs. Other solutions to MVCs such as fencing may be more efficient, but their cost is high. For example, in the LWR, fencing is estimated at CDN$40,000 to $60,000 per kilometer (Y. Leblanc, AECOM Tecsult Inc., pers. comm.). These high cost, however, must be compared to the average cost of MVC (including vehicle repair costs, human injuries and fatalities, towing, etc.), estimated at US$31,000 (Huijser et al., 2009). Thus, the fencing of the road should be cost-effective in many situations.

The inclusion of salt pool spatial memory proved to be a useful addition to the model. Moose agents are not omniscient but neither are they just reactive to their immediate environment. They can have a certain level of perception, memory, and understanding of their surroundings – in this case, of their home range (Miller and Litvaitis, 1992; Gilbert, 2008). For this reason, Bennett and Tang (2006) applied spatial memory at the level of the herd in an agent-based model of elk movement in Yellowstone National Park (U.S.A.). They modelled the elk herd's winter migration north out of the park, when snow cover reached a certain threshold to reach land that had less snow cover. They did not, however, compare scenarios with and without spatial memory at the herd level.

The previous G2009 model used fixed distance steps, whereas the intra-patch and inter-patch sampling of movement distances in the new model was obtained from the power law probability distribution based on the actual distance travelled by the real moose. This led to more consistent and accurate distance results compared to the G2009 model. Sampling from a power law distribution produced an animal movement pattern called the Lévy flight or walk which is considered to be a more accurate representation of foraging herbivores like moose than Brownian or purely random motion (Viswanathan et al., 1999; Reynolds and Rhodes, 2009). In future models, however, more variability in the distance travelled by model moose could be introduced based, perhaps, on the age and sex of the moose. Higher numbers of model moose and higher numbers of model runs are likely to make several more of the observed differences in road crossings and reductions statistically significant (due to higher sample size). Therefore, the lack of statistical significance in some reductions of the current results should be interpreted with caution.

5. Conclusion

Our agent-based model with improved road avoidance and memory of previous visits to salt pools has produced results that are more consistent with field studies of moose behaviour involving roads and salt pools in the LWR (Laurian et al., 2008a,b; Leblond et al., 2007a,b). When both road avoidance and salt pool memory were active, i.e. the most realistic simulations compared to real moose behaviour, the two largest reductions of road crossings (79% and 50%) occurred when all road-side salt pools were removed, without and with compensation salt pools, respectively. There is, however, a trade-off in the two behaviours as salt pool memory tends to increase the likelihood that a moose will get near a road (and potentially cross it), but road avoidance greatly reduces the potential road crossings. Of the two factors, road avoidance clearly is the more important one. However, for those moose that do not avoid roads (around 10% according to the study by Laurian et al. (2008b)), lower road crossing reductions were predicted. The largest reductions in the number of road crossing (79%) were much higher than the estimated reduction of 44% based on empirical data reported by Dussault et al. (2006a). However, since moose exhibit some variability in their behaviour including high or low levels of road avoidance (Laurian et al., 2008b), managers should also consider the reductions in road crossings predicted for individuals with lower (or no) road avoidance and no salt pool memory (Table 5) as an indication of inter-individual variability.

This model could be extended to be then used for other ungulates such as elk or deer, but herd behaviour would have to be added since the current model reflects moose which is mainly a solitary species. The model will be expanded in future research to also evaluate the effectiveness of newly-implemented mitigation measures on the upgraded 4-lane highway 175 in the Laurentides Wildlife Reserve. These measures include fencing with double emergency escape gates, and wildlife underpasses.

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