Using agent-based modelling to evaluate mitigation measures for moose-vehicle collisions

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Abstract

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Paul Grosman

In northern countries, moose vehicle collisions (MVCs) are often associated with the presence of salt pools near highways. Mitigation measures such as designing compensation salt pools further away from the highway and building fences along highways can be used. Fences are very efficient in reducing MVCs, but wildlife passages are required in order to increase highway permeability. Agent-based modelling (ABM) was used to study the effect on moose movement behaviour near highways of roadside salt pool removal and displacement and to estimate the required density of underpasses in fenced areas. ABM was applied to Highway 175 (Québec) where an extensive telemetry dataset on moose movement was available. The movement rules were based on cover and food quality in GIS forest polygons. Model moose had salt pool spatial memory (SPSM) and, in most cases, road avoidance (RA) behaviour, the opposing effect of which on the number of road crossings was investigated. Completely removing roadside salt pools with no compensation salt pools resulted in the highest highway crossing reductions (by 79%). A conceptual framework was also designed for investigating the movement of moose along fences using ABM. The current spacing of wildlife passages along Highway 175 is markedly larger than the recommended allometric spacing (i.e. based on home range size). The objective was to assess the impact of wildlife crossing distances on highway permeability. Because of the lack of telemetry data near fences, probabilistic and fuzzylogic approaches were proposed to determine movement rules of the model moose. Once the model is implemented, it is anticipated that permeability will increase with decreasing distances between passages, and that a plateau may be observed once the allometric distance is reached.

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Dedication

To the memory of my parents, Samuel and Margaret Grosman (née Boicey).

Contribution of Authors

Chapter 2 was published in *Ecological Modelling* (Grosman *et al.* 2011). There were five co-authors: Paul D. Grosman, Jochen A.G. Jaeger, Pascale M. Biron, Christian Dussault, and Jean-Pierre Ouellet. Paul Grosman designed and programmed the ABM in Java using Repast Simphony, analyzed the results and wrote the first drafts of the article. My supervisors, Jochen Jaeger and Pascale Biron, corrected these drafts and helped develop the research questions and the logical structure of the thesis, Christian Dussault of MRNF and Jean-Pierre Ouellet of UQAR provided the GPS telemetry datasets for the moose and other GIS datasets and valuable comments on the final drafts of the paper.

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List of Acronyms

ABM	Agent-Based Model or Agent-Based Modelling
BNP	Banff National Park
ESRI	Environmental Systems Research Institute, Inc.
GIS	Geographic Information System
GPS	Global Positioning System
LWR	Laurentides Wildlife Reserve
MRNF	Ministère des Ressources naturelles et de la Faune
MVC	Moose-Vehicle Collisions
ODD	Overview, Design, and Details protocol
Repast S	Recursive Porous Agent Simulation Toolkit – Java Simphony version
SIEF	Système d'information éco-forestière
ТСН	Trans-Canada Highway
UQAR	Université du Québec à Rimouski
USD	United States Dollars
WVC	Wildlife-Vehicle Collisions

"Essentially, all models are wrong, but some are useful." - Box and Draper (1987)

1 Chapter 1: Introduction

The environmental effects of roads are numerous and have different reaches into the surrounding landscape. Road effects include chemical damage to vegetation, rivers and wetlands, noise, easier access for invasive species, a barrier effect for migratory species and dispersal of juveniles, wildlife and human traffic injuries and mortality, and property damage (Forman et al., 2003). Some of these effects are limited to the road surface and immediate neighbourhood; others can reach several kilometers into the surrounding landscape (Forman and Alexander, 1998). In this thesis, the focus is on the road mortality of moose (Alces alces) and only driver safety secondarily, in particular, the elimination of roadside salt pools and their displacement and secondly on the use of the allometric method to increase the number of wildlife underpasses in the LWR (Bissonette and Adair 2008). Worldwide, there are several million cervid-wildlife collisions each year resulting in damage to vehicles, human and wildlife deaths and injuries. It is estimated that the damage to vehicles costs around 1 million USD per year (Groot Bruinderink and Hazebroek, 1996). As well, it is estimated that up to half of the wildlife-vehicle accidents with large ungulates go unreported (Seiler, 2005).

Various mitigation measures have been implemented to reduce road mortality. For larger mammals such as ungulates and carnivores, wildlife passages that either cross over or under the roadway are increasingly used (Clevenger *et al.* 2001; Seiler 2004; Dodd *et al.*, 2007c; Dodd *et al.*, 2007a; Olsson and Widen, 2008a, AECOM Tecsult Inc. 2009, 2010). These are often combined with fencing in order to direct the wildlife to these

crossings. Sometimes, existing structures like bridges or culverts can be modified to accommodate wildlife; otherwise, entirely new structures need to be built.

A highway overpass can cost more than one million dollars; an underpass, half a million dollars (Forman *et al.*, 2003). Thus, once these costly wildlife crossings and fencing have been implemented, it is essential that they are monitored for some time to measure their effectiveness in fulfilling their purpose of reducing the barrier effect, reducing wildlife traffic mortality, and reducing biodiversity loss. This is good conservation management practice in order to justify the effort and cost and to review for improvements (Clevenger 2005).

This thesis uses an agent-based modelling (ABM) approach to investigate questions related to the effectiveness of mitigation measures for reducing moose-vehicle collisions near route 175 in the Laurentides Wildlife Reserve (LWR), between Quebec City and Saguenay. Chapter 2 investigated the tradeoffs between road avoidance and salt pool spatial memory with the elimination of roadside salt pools and the creation of compensatory salt pools further from route 175. This chapter was published in 2011 in the journal *Ecological Modelling*, 222 (8) p. 1423-1435, with the title: 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. The third chapter describes the changes that could be done to the ABM to investigate the effect that allometric-scaled spacing of wildlife passages could have on landscape connectivity in the area dissected by highway 175. In this area, about fifty moose-vehicle collisions per year occurred between 1990 and 2002 (Dussault *et al.*, 2006a). The two lane road is currently being expanded into a four lane divided highway at a cost of about a billion CDN dollars. As a

result, an extensive GIS database and detailed reports exist on this project (Consortium Génivar-Tecsult. 2004; BAPE, 2005; Transports Québec *et al.*, 2009). The first part of chapter 1 synthesizes the relevant literature on road ecology, moose behaviour and agent-based modelling. This is followed by the research questions for chapters 2 and 3.

1.1 Literature Review

1.1.1 Road Ecology

Despite the known effects of the automobile on wildlife, limited scientific research had been done until recent years. In a seminal article on the North American moose, Stoner (1925) described a road trip he and his wife did in Iowa and he noted every carcass he found in their 316 mile trip in June and July 1924. He recorded 129 species of reptiles, birds, and mammals for a total of 84 carcasses on the first part of the trip and 141 carcasses on the return. Peterson (1955) in his chapter on accidents has only one sentence on moose-vehicle collisions, showing at that time MVCs were not a real concern at that time. But road ecology has now been recognized as an independent scientific discipline, promoted by the bi-annual International Conference on Ecology and Transportation started in 1996 and the publication of the book (Forman et al., 2003). The fourteen coauthors of the book detailed their knowledge about the ecological effects of roads on landscape and wildlife and the various mitigation measures that could be used to reduce the negative effects. More recently, Safe Passages, Highways, Wildlife, and Habitat Connectivity (Beckmann et al. 2010) was published with seventeen chapters on current practices, ecologically effective transportation projects, effective partnerships (including the Banff National Park Wildlife Crossing Project and the Arizona State Route 260

project), and effective innovations to further reduce WVCs using advanced sensor communications systems, for example..

Forman (2000) has estimated that in the United States, about twenty percent of the contiguous land is ecologically affected by the road network. The effects of these roads are many, and include road injury and mortality to motorists and wildlife, changes in home ranges and population viability, easier access for invasive species, and soil and water changes (Trombulak and Frissell 2000). The various effects of roads extend, on average, 300m each side of the highway but are generally quite asymmetric (Forman and Deblinger, 2000). Moose populations have been increasing in New England and tending to cross highways in the fragmented landscape using railroad crossings and river underpasses (Forman and Deblinger 2000). Because of the well-documented evidence of negative road effects (Roedenbeck *et al.* 2007; Fahrig and Rytwinski 2009), it is crucial to study how best they can be mitigated so that transportation planning in the future could take these research results into consideration.

In 2005, a group of road ecologists met at Rauischholzhausen Castle in Germany to discuss the present state of road ecology and why it was not having a greater impact on transportation planning despite the well-documented evidence of negative road effects (Roedenbeck *et al.*, 2007). They identified five questions that could provide a framework for road ecology. Four of the five questions were concerned with population persistence and one considered how road effects could best be mitigated. As well, they recommended where possible that full before-after-control-impact experimental designs be done. Manipulative experiments have much stronger inferential strength than non-manipulative ones. Where these experiments could not be done, transportation planners should still use

research that had low inferential strength and not demand better results than are possible under the circumstances (Roedenbeck *et al.* 2007).

1.1.2 Moose behaviour

The moose is the largest member of the deer (cervid) family. It can weigh up to 600kg and have a shoulder height of nearly 2m. It has a circumpolar distribution: there are moose in Scandinavia, Russia, Alaska, Canada, and northern US states such as Maine, New Hampshire, Vermont, Michigan and Minnesota (Franzmann and Schwartz 2007). They can live as long as twenty years but their mean life expectancy is 8 years for females and 7 years for males (Franzmann and Schwartz 2007). They are the least gregarious of the cervids; they are essentially solitary except mothers with their young.

Because of their large size combined with the high energy demand on their environment and the generally low nutrient value of their food, moose must consume between 20kg and 30kg per day of forage. Moose eat mainly shrubs, twigs, leaves, shoots and aquatic plants. In winter they depend mainly on willow and they strip bark off trees (Rea and Child 2007).

The rut season starts in September and ends in November. Bull moose will attempt to impregnate more than one cow but there can be competition between males with the older males chasing the younger and immature bulls away from the females. Females actively choose their mates unlike other ungulates (Franzmann and Schwartz 2007). The birthing period runs from late May until early June and typically one or two calves are born per

year depending on habitat quality. The cow has its maximum fertility between 4 and 7 years (Franzmann and Schwartz 2007).

Their main predators are wolves and bears but an adult moose can successfully defend itself from both by standing its ground (Franzmann and Schwartz 2007). Their young, however, often are killed and eaten by these predators.

Moose have the following general annual life cycle: a green (i.e. deciduous leaves present) season: May to September and a dead season (i.e. deciduous leaves absent): October to May (Samson *et al.*, 2002). The green season includes the birthing period, before which any yearlings are chased away and must disperse to a new home range, and the summer feeding period, mainly foraging on deciduous trees, shrubs and aquatic vegetation. Moose have a chronic need for sodium after winter and thus visit roadside salt pools or use wetlands for sodium (Fraser and Thomas, 1982; Miller and Litvaitis, 1992; Dussault *et al.*, 2006a; Leblond *et al.*, 2007b; Laurian *et al.*, 2008a). The dead season consists of the rut, which is also the hunting season, and as winter progresses there is a reduction in moose movement with increased conifer browsing and the seeking of cover protection in the conifer forests.

1.1.3 Moose-vehicle collisions

Moose-vehicle collisions vary spatially and temporally. For example, yearly values in Quebec range between 161 and 310 – with 45 to 50 in the LWR between 1990 and 2002 (Dussault *et al.* 2006a), whereas over 900 MVC have occurred yearly in Newfoundland (Joyce and Mahoney, 2001), and 4,500 in Sweden (Seiler, 2004). The likelihood of a MVC is much higher between dusk and dawn than in the daylight hours (Joyce and

Mahoney, 2001; Dussault *et al.* 2006a). Furthermore, most MVC occur between June 1st and October 31st (Joyce and Mahoney, 2001). There is also a higher risk of MVC at higher traffic volumes (Joyce and Mahoney 2001; Dussault *et al.* 2006a)

In Newfoundland, Joyce and Mahoney (2001) found related predictive factors consisted of time of accident, road conditions and alignment, vehicle speed and occupants and moose sex and age but they did not include any factors that related to the landscape or moose habitat. The authors found that 70% of the MVCs occurred between June 1st and October 31st and that there were more MVCs at high and low moose densities than at medium moose densities. Joyce and Mahoney (2001) attributed this to an interaction with habitat factors, which they did not measure and they considered this finding unreliable.

In the LWR, MVCs are more of a traffic safety issue than a conservation issue since the moose population is not threatened by decline or extirpation.

1.1.4 Mitigation Measures and Their Placement

Mitigation measures to reduce wildlife-vehicle collisions can be directed at the vehicle drivers and the wildlife. Romin and Bissonette (1996) found that even though attempts to mitigate human driver behaviour were more widely used, the mitigation measures taken to modify wildlife behaviour were more successful (Figure 1.1). As Patricia White pointed out in her book Getting Up to *SPEED*: A Conservationist's Guide to Wildlife and Highways, "as it turns out, it's easier to teach animals to change than humans" (White, 2007).

Fencing and wildlife passages over and under the highway were the most successful approaches, whereas mirrors and reflectors, a widely used method, were not very

successful (Forman *et al.* 2003). For drivers, the static warning sign does not appear to be effective; so recently dynamic warning signs, with a flashing light when a large mammal is detected, have been tried (Huijser *et al.*, 2008).

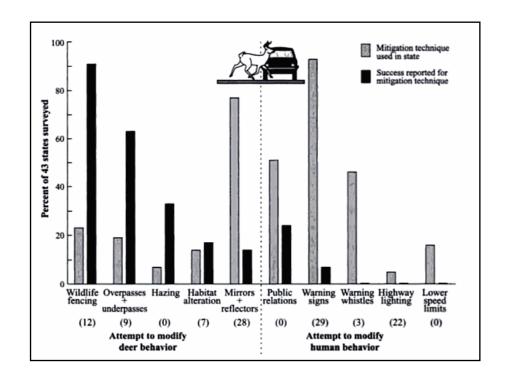


Figure 1.1. Mitigation measures attempted to modify deer or human behaviour. These results are from a 1992 telephone survey of 43 U.S. state natural resource agencies. Source: Forman *et al.* (2003).

et al. A large number of studies evaluated the placement of mitigation measures such as wildlife passages using statistical analyses based on various environmental statistics. These environmental factors were drawn from the immediate area of the WVC, the structural characteristics of the wildlife passages and the behaviour of the focal species (Clevenger and Waltho, 2000a; Joyce and Mahoney, 2001; Clevenger *et al.*, 2002a; Malo *et al.*, 2004; Clevenger and Waltho, 2005; Seiler, 2005; Gunson 2007; Roedenbeck 2007). In Spain, Malo *et al.* (2004) found that high WVC rates were associated with high forest cover, low crop cover, low number of buildings and high habitat diversity. At the local level, WVC were associated with no guardrails, lateral embankments, and large distances from underpasses, crossroads or buildings. In Banff National Park (BNP), highway crossings were shown to increase where the road bisects high quality habitat and lateral cross-valley movements (Clevenger *et al.* 2002b). In Sweden, a convex relationship between traffic volume and MVCs exists: at high traffic volume, the road becomes a complete barrier, at low volume the moose can cross safely more often, but at medium volume, they venture on to the road and get hit more often (Seiler, 2005) thus agreeing with the results of Joyce and Mahoney (2001) mentioned above. Seiler (2005) found that bridges and tunnels did reduce MVCs, and that MVCs increased on roads that went through clear-cuts and young forests.

1.1.5 Effectiveness of Mitigation Measures

The effectiveness of various mitigation measures can be measured on at least three different biological scales: at the level of the organism, population abundance, and genetic flow. Though the first two are easier to quantity, the last, however, needs long-term monitoring programs in order to be assessed, as there is currently a lack of genetic evidence to support whether or not the overpasses are effective (Corlatti *et al.* 2009). One difficulty of this type of study is that even if the animals can cross the road safely their genes may be flowing across but not mating therefore not mixing with those animals on the other side of the road. Riley *et al.* (2006), studying the barrier effect of the Ventura Highway, a 10-12 lane high traffic highway north of Los Angeles, found a home-range

"pile-up" that occurred near the road that even though there were numerous crossings there was a lack of reproductive success by the cougars and bobcats that had crossed.

From the point of view of the vehicle driver, the effectiveness of any mitigation measure should be measured as increased driver safety or as decreased risk of MVC. A number of studies have shown that high exclusion fencing placed along highways can reduce WVCs by 80% to 90% (Clevenger *et al.* 2001; Seiler 2004; Dodd *et al.*, 2007c; AECOM Tecsult Inc. 2009). However, WVCs may still occur at the fence ends, and care should be taken to design fences that curve backwards into the surrounding landscape (Clevenger *et al.* 2001). This design modification has been implemented on the exclusion fencing in the LWR.

From the point of view of the wildlife, the effectiveness of any mitigation measure should be measured as increased highway permeability. Even if a moose population is not at risk, they need to cross the highway to reach high quality habitat, or during the rut season to seek out females, and one-year-old moose need to disperse to find their own home ranges after being forced away by their mothers before the birth of their new siblings. Many studies have monitored wildlife passages after construction to determine their effectiveness (van der Ree *et al.*, 2007). In BNP, the 30 underpasses have been studied for the last 15 years and about 220,000 crossings by eleven different species (but mainly elk) have been detected (Parks Canada Website, 2010), however no individual animal identification was available so it is not possible to know how many individuals used the wildlife passages (Clevenger *et al.* 2009). However, a new study is ongoing in BNP to identify the individual grizzly bears using the wildlife passages by using barb wire to capture their hairs (Clevenger and Sawaya 2010). In Arizona, where Highway

260 was upgraded from a two-lane to a four-lane highway, 8,455 animals were detected in five underpasses between 2002 and 2006 (Dodd *et al.*, 2007a, b, c; Gagnon *et al.*, 2007a, b). In southwestern Sweden, 24 GPS telemetry-collared moose were followed before, during and after an expansion of a two-lane road into a four-lane highway with exclusion fencing and 3 underpasses to study the moose usage of these highway crossings (Olsson and Widen, 2008a; Olsson *et al.* 2008b).

In all three study areas, researchers found that fencing and wildlife passage mitigation measures were effective and significantly reduced ungulate road crossings and mortality, while also reducing landscape connectivity.

Increased traffic noise may affect wildlife passage success (Olsson *et al.* 2008b), although this effect was only detected for heavy tractor-trailers during low volume periods in Arizona (Gagnon *et al.*, 2007b). Underpass openness was deemed important so the elk could see any predators. The use of earthen rather than concrete walls was found to be more acceptable to elk (Gagnon *et al.* 2007b).

Ideally, several mitigation methods such as wildlife crossing fences and escape ramps should be used in combination. Furthermore, an often-neglected aspect of mitigation projects is to ensure that the structures are maintained in the long term; across North America transportation budgets for maintenance are woefully underfunded (Bissonnette and Cramer, 2008). These costs must be factored in cost-benefit analysis of mitigation measures (Huijser *et al.*, 2009).

1.1.6 Landscape Connectivity and Highway Permeability

Wildlife conservation has as one of its main concerns the notion of landscape or habitat connectivity. Connected populations have the following properties in common (Beckmann *et al.* 2010): species have a greater chance of survival, provide greater flexibility to respond to changing environmental conditions such as climate change and habitat fragmentation, species are more resilient to environmental changes and natural disturbances such as droughts and fire, enables breeding between subpopulations, and maintaining continuous habitats can buffer species communities from new diseases, the need for connectivity increases as the effects of habitat fragmentation and climate change increase.

The two concepts of landscape connectivity and highway permeability are two key concepts in road ecology and they are defined below. Landscape connectivity is a concept that refers to how well connected the habitats or resource patches are connected to each other, i.e., how easy or difficult is it for specific species to move between these habitat patches (Taylor *et al.* 1993). Connectivity can be measured in a landscape for the moose by assessing the probability that the moose will move between all points or habitat resource patches (Taylor *et al.* 1993). When a highway is first constructed in a landscape, the landscape becomes less connected because of the highway, and road ecologists must work together with transportation departments to restore some degree of connectivity across the highway using fences, tunnels, culverts, underpasses and overpasses. The landscape will never return to its pristine state, but with mitigation measures, the animals will be able to move over or under the highway without endangering themselves and causing harm to the motorists. Highway permeability as defined by Bissonette and Cramer (2008), "refers specifically to the ability of species of all kinds to move relatively

freely across the roaded landscape ". Thus, permeability is focused on the highway while connectivity refers to the entire landscape. When a highway is first constructed, landscape connectivity is heavily reduced and only when fencing and underpasses are constructed together, does the degree of highway permeability increase again which increases landscape connectivity as well (Dodd *et al.* 2007b).

Fences, by themselves, keep wildlife off the roads up to 80% to 90% of the time (Clevenger *et al.* 2001; Seiler, 2004; AECOM Tecsult, 2010) but with wildlife underpasses installed as well, the fences can funnel wildlife towards underpasses, however, they do hinder movement, increase isolation of sub-populations, and increase travel distances (Beckmann *et al.* 2010). Human use of wildlife passages must be reduced as well since many carnivores and other species will reduce their use of underpasses and overpasses due to human usage. Foster and Humphrey (1995) in a study of the Florida panthers found that human use of underpasses caused the panthers to use the same underpasses less on Highway I-75 through the Florida Everglades. Similar observations were made by Clevenger and Waltho (2000) on the elk and other wildlife in BNP and the TCH, and by AECOM Tecsult (2010) in the LWR. If, however, there is a fence but there are no underpasses in a moose's home range the moose would be expected to expand its home range away from the road (Olsson and Widen, 2008a).

In order to restore some connectivity, a number of steps should be undertaken: firstly, create a joint road ecologist and transportation planning team that will set goals for the project including the identification of focal species using scientific expertise; secondly, create GIS datasets of the landscape that can be evaluated to inform the best project design and identify the present barriers as such developed areas and roads and consider

how changing land use and human activity will affect the focal species in the future; and thirdly, engage the local communities from the beginning; local support often determines a project's success (Beckmann *et al.* 2010).

Identification of safe wildlife crossings is of prime importance since the road-kill data locations may have little to do with where the wildlife can safely cross the highway (Clevenger *et al.*, 2002a). Often a road-kill can occur some distance from a safe wildlife corridor if the animal has been wandering along the highway for some distance.

Landscape connectivity is influenced by the width, number of lanes and other design characteristics of the highway. Traffic volumes of 4,000 to 10,000 vehicles / day create strong barriers to movement across the highway; at 10,000 vehicles / day it becomes a near total barrier to movement across the highway (Iuell *et al.* 2003). Figure 1.2 shows a convex curve for MVCs in Sweden which indicates that most MVCs occur at 4,000 to 6,000 cars per day but at 10,000 cars per day the MVCs drop to near zero since the road becomes a total barrier to movement. The model area had 2,000 MVC sites and the test area had 1,300 MVC sites (Seiler 2005). Large mammals can cross more easily at night when traffic volumes are lowest (Beckmann *et al.* 2010).

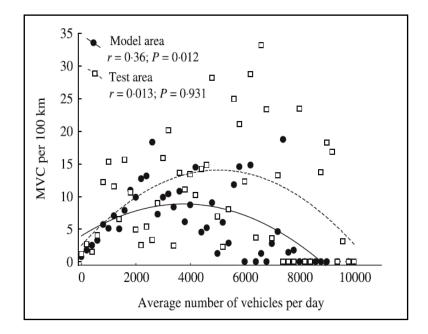
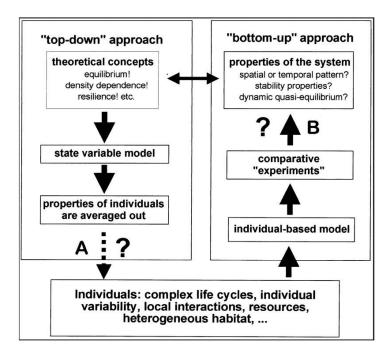


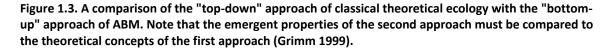
Figure 1.2. The relationship between MVC and traffic volume in Sweden. The model area is in southcentral Sweden and the test area is just north of the model area. Source Seiler (2005).

High landscape connectivity is important for the following reasons: many multihabitat organisms regularly move through the landscape to different habitat types to obtain their daily needs and this allows for movement to repopulate patches that have suffered local population declines or extirpation and can minimize the effects of inbreeding. Barriers such as roads impede these movements resulting in higher road mortality, lower reproduction, and ultimately smaller populations (Forman *et al.* 2003). The species that are most vulnerable to the barrier effect of highways are those that avoid roads but have multiple resource needs and need large amounts of resources that require them to travel over large areas, foraging in a home range, dispersing for young to new home ranges and migration. The barrier effect will affect species differently depending on an animal's movement behaviour, their young's dispersal ability, and their population density. A highway can become the boundary for home ranges for some species such as moose. As well, the cumulative effect of power lines, railways, pipelines and aqueducts on the movement of various species is unknown and requires scientific investigation (Forman *et al.* 2003). The cumulative effect of habitat loss, reduced habitat quality, wildlife mortality and reduced connectivity results in a time lag effect that can take several generations of animals to observe (Forman *et al.* 2003). Thus, the introduction of mitigation measures now may actually be addressing effects that started decades ago. In general, the impact of the virtual ecological footprint of roads must be reduced so that wildlife populations can recover and thrive. As well, mitigation efforts are meant to restore some connectivity but not to return the modified landscape to its original condition (Parks Canada Website, 2010b).

1.1.7 Agent-based modelling

Agent-based modelling is a computer simulation technique which considers individuals in a study area as agents and attempts to implement some of their life history variability, individual resource use and different behaviours into a coherent model to solve or better understand some problems. In contrast with classical theoretical ecology that works top-down and typically stops at the population level and does not consider the individual variability of the species significant, ABMs work bottom-up and consider the variability of individuals crucial to the modelling process and results (Figure 1.3). ABM is now being used in ecology, geography, urban planning sociology, economics and other scientific disciplines (Schelling 1969; Grimm 1999; Railsback and Harvey 2002; Grimm and Railsback 2005a; Anwar *et al.*, 2007; Brown *et al.*, 2008; Tesfatsion 2008; Grosman *et al.*, 2009; 2011).





There is a difference between individual-based and agent-based models, even though many authors use the terms interchangeably. The essential difference is that individuals are more reactive; whereas, agents are more proactive and goal-oriented (Parrott, 2008). In this thesis, the agent moose actively seek out the best forest polygon when travelling, find roadside and compensation salt pool and place them in their spatial memory and actively avoid the road. Thus the virtual moose are more agents and less individuals.

The agent-based modelling approach for the moose was chosen to develop a "bottomup" model that took into account certain individual properties of the virtual moose. If a statistical or system dynamics models like STELLA[™], it would be operating more at the moose population level and not at the individual moose level. An agent-based modelling approach was chosen so that used some of the individual variability of the moose agents. Most existing ABMs work on human individuals; there are few that work on wildlifehuman interactions. The latter include models of Florida panther movements (Cramer and Portier 2001), whale-watching boats and whales in Saguenay-St. Lawrence Marine Park near Tadoussac (Anwar *et al.*, 2007), moose in the Isle Royale National Park in Lake Superior (Booth 1997; Schmitz and Adair 2000) and in the LWR in Québec (Grosman *et al.*, 2009; 2011), Eurasian lynx in the Swiss Alps (Kramer-Schadt *et al.*, 2004) and vultures and artificial feeding stations in France near the Pyrenées mountains (Deygout *et al.*, 2009).

Grimm (1999) and Grimm et al. (2006) remark that, in ecology, too many ABMs are essentially one-off projects that attempt to solve the ecological problem at hand but make no attempt to build a model that could be used again for other problems. They recommend two new ideas, first that ABMs could establish a better conceptual framework by borrowing key concepts from Complex Adaptive Systems (Grimm and Railsback 2005a). These concepts consist of: emergence, adaptation, fitness, prediction, interaction, sensing, stochasticity, collectives, scheduling, and observation. Concepts like adaptation and fitness are already used in classical theoretical ecology, but some of the others such as emergence and collectives are more pertinent to ABM. The second suggestion is to use a concept called "pattern-based modelling" where ABMs attempt not only to produce an emergent pattern that is core to the problem under study but to also produce a pattern not related to the problem under study but still relevant to the individuals under study (Grimm et al., 2005b). If the other patterns also match the real situation well, then the ABM has more "structural realism". A pattern is any behaviour that is more than random variation. Both "weak" and "strong" patterns, that is, patterns

that are not much different from random variation and those that are highly different can be used to construct and validate an ABM. Ideally, a common protocol for describing the purpose and content of an ABM should be used so that it can be better understood by other practitioners and more easily replicated. This protocol is called the Overview, Design, and Details protocol or ODD (Grimm *et al.* 2006; Grimm *et al.* 2010).

1.2 Chapter Themes

The second chapter presents my ABM that assesses the trade-off between road avoidance and attraction by road salt pools by moose. In this ABM, there are five scenarios that have different amounts of the elimination of roadside salt pools along the upper highway 175 and the construction of compensatory salt pools further away from the highway 175. The third chapter describes my revised ABM that explores the allometric method for eighteen scenarios for the placement of wildlife underpasses along highway 175, starting from the current situation of six wildlife underpasses for moose and going up to forty underpasses. In each scenario except the first one that will use the actual fences and underpasses newly constructed for the LWR and highway 175, fences will be constructed along both sides of the Highway 175 so that the moose can be directed towards the underpasses. This ABM has not yet been programmed but the chapter describes the specifications in detail.

1.3 **Objectives and Hypotheses**

The main objective of chapter 2 was to better understand the trade-off between road avoidance behaviour and salt pool spatial memory for moose agents and to implement a better representation of real moose behaviour in the landscape than the previous ABM

(Grosman *et al.* 2009), and thus generate a more reliable predictive modelling tool to examine various mitigation measures for reducing MVCs. We also included in the ABM in chapter 2, a new home range enforcement method, a distance travelled algorithm based on a power-law distribution and a new travelling to salt pools method. The 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 and salt pools. 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 main hypotheses of chapter 2 are that the total elimination of road side salt pools with both road avoidance and salt pool spatial memory activated, should lead to the greatest reduction in moose road crossings and secondarily, the creation of compensation salt pools further from the Highway 175 with both road avoidance and salt pool spatial memory activated should lead to a smaller but still significant reduction in moose road crossings. 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 but it is expected that the road

avoidance factor will be much stronger than the opposing salt pool spatial memory factor. Chapter 2 investigates the relative importance of these two behaviours on moose reactions to roads and management of salt pools as a mitigation measure of MVC.

The main objective of chapter 3 is to use a revised ABM based on the ABM in chapter 2 to assess the impacts and the effectiveness of road exclusion fencing and wildlife underpasses for MVC near the upgraded (from 2 lanes to 4 divided lanes) highway 175 in the LWR. The main research question is: will allometrically-scaled wildlife crossings increase the landscape connectivity compared to the actual fencing and wildlife underpasses newly constructed in the LWR and by how much? There will be eighteen scenarios and the eleventh is the allometrically-scaled one; at that point, there should be a plateauing effect of the number of moose crossings. In this chapter, I develop a conceptual framework to determine the model moose movement rules near fences and underpasses, and I determine the response variables needed to assess the effectiveness of different spacings of wildlife passages.

The hypotheses of chapter 3 are that the allometrically-scaled placement of wildlife underpasses, which has never been tested before, should lead to a far greater number of moose road crossings that the current situation with just six wildlife underpasses and that the number of moose road crossings should reach a plateau at the allometrically-scaled number of wildlife underpasses. Accordingly, the allometrically-scaled placement of wildlife crossings (Bissonette and Cramer, 2008) would be the recommended principle for the placement distance of crossing structures for moose.

2 Chapter 2: 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

2.1 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 moose's spatial memory of salt pools 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 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 maximizing their energy (or mineral) intake at all costs, but they try to consume a reasonable amount of resources while minimizing other risks like mortality on the road (Dussault et al., 2005; Laurian et al., 2008b). This tradeoff 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.

2.2 Methods

2.2.1 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 (Figure 2.1). The LWR is a 7861km² 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 550cm 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).

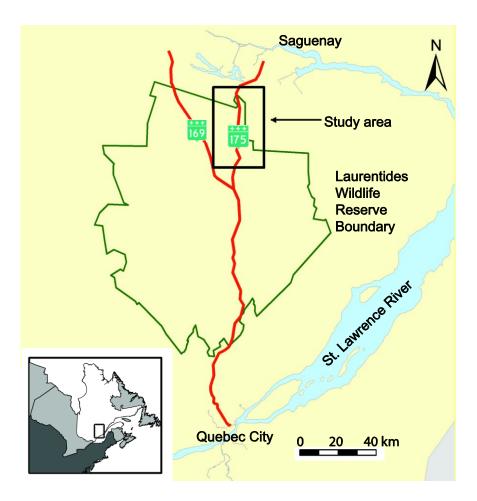


Figure 2.1. The study area is indicated by the black rectangle centered on the upper portion of HW175 above the junction with HW169. The boundary of the Laurentides Wildlife Reserve (LWR) is outlined in green. The LWR is situated between Québec City and Saguenay in the Province of Québec, Canada.

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), eco-forest 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 2.1). 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).

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

Table 1.1. 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. Source: Dussault *et al.* (2006b).

2.2.2 Salt pool management scenarios

Five scenarios were studied with the model in order to cover a range of salt pool management options (Table 2.2):

- 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 500m 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 500m 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 vectorbased. 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).

Scenario		# Roadside Salt Pools	# Compensation Salt Pools	
1.	Current Situation	36	0	
2.	100% Salt Pool Removal, No Comp. Salt Pools	0	0	
3.	100% Salt Pool Removal, 100% Comp. Salt Pools	0	18	
4.	2/3 Salt Pool Removal, No Comp. Salt Pools	12	0	
5.	2/3 Salt Pool Removal, 2/3 Comp. Salt Pools	12	12	

Table 2.2. The five salt-pool management scenarios with the number of roadside and compensation salt pools in each case.

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. (Figure 2.2). 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.

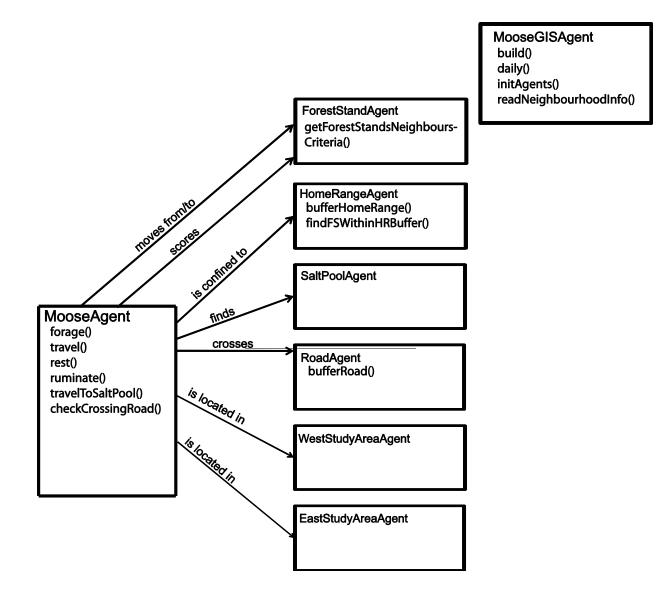


Figure 2.2. Unified Modelling Language Diagram of the primary objects in the model.

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 2.2), 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 500m 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 75m 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 625m. The 40 home ranges that corresponded to 40 real annual moose home ranges, constructed using the Minimum Convex Polygon method, were buffered outwards by 625m 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 a width of 45m 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 26km wide by 45km 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 sub-models 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.

2.3.3 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 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.

2.3.5 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).

2.3.6 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.

2.3.7 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 500mof 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.

2.3.8 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.

2.3.9 Observation

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

- 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 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.

2.3.10 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 625m 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 45m(22.5m on either side) and buffered outwards 477.5m on each side that created a road buffer of 500m. As well, the East Study Area and west study area agents were created.

2.3.11 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 500m of the forest polygon and whether or not the highway 175 was within 75m 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 45m 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.

2.3.12 Detailed processes and sub-models

2.3.12.1 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.

2.3.12.2 Road avoidance behaviour

Laurian *et al.* (2008b) found that moose in general avoid a buffer strip up to 500m wide around paved roads except when obtaining sodium from roadside salt pools in June and July. Thus, a 477.5m buffer around the 45m 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. Since the highway is 45m wide, we subtracted 22.5m from 500m on both sides to get 477.5m. 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 500m 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 50m buffer of the paved road. Laurian *et al.* (2008b) found that 4 of the 47 moose (8.5%) highly preferred the 0–50m 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 500m buffer of the paved road for these non-road avoiders.

2.3.12.3 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 25m (from 0m to 1000 m), was represented by a power law probability distribution:

$$y = 8999.2 x^{-1.592}, R^2 = 0.89$$
 (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 160m (in both horizontal and vertical directions), whereas the average distance when travelling to an adjacent forest polygon was about 1034m.

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 125m after calibration against the real moose, using a total travel distance in one summer of 2,537km, 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:

horizontal direction = distance
$$* \cos (angle);$$
 (2)

vertical direction = distance
$$* \sin (angle);$$
 (3)

For travelling, a distance was chosen from the power law probability distribution (Eq. (1)) using the maximum forage distance, initially set to 125m, as a lower limit, and the maximum travel distance, initially set to 550m, 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 275m in the model to reflect this.

2.3.12.4 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 2.1). 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 200m 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 100m of a salt pool; 3 if a forest polygon was within 250m of a salt pool; 2 if a forest polygon was

within 500m of a salt pool; 1 if a forest polygon was within 1000m of a salt pool; and 0 if a forest polygon was more than 1000m 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 73km² (range: 28–208km²). 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 (Figure 2.3a). The 40 model moose corresponded to 21 real moose (since some real home ranges were for the same moose but for different years) (Figure 2.3b). 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.

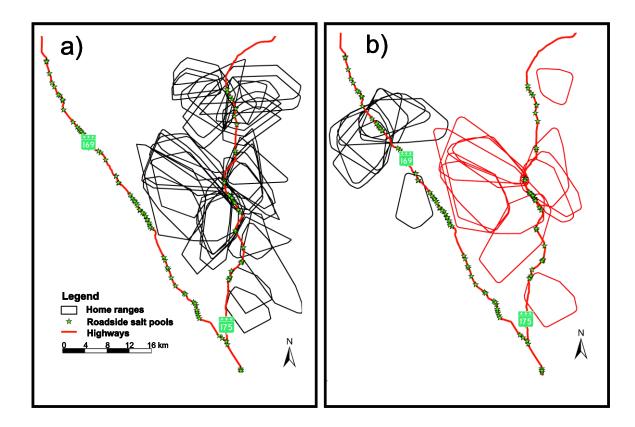


Figure 2.3. (a) Home ranges for the 40 model moose used in the model which were based on the home ranges of 21 real moose (b). The home ranges of the 12 real moose near highway 175 that were used for validation are highlighted in red.

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 3.7m 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.

2.3.12.5 Foraging and ruminating sub-models.

When foraging or ruminating, a travel distance between 0m and 125m 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 sub-models 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.

2.3.12.6 Resting sub-model

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

2.3.12.7 Travelling sub-model

When travelling, a travel distance between 125m and 550m 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 75m 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.

2.3.12.8 Travelling to a salt pool sub-model

When travelling to a salt pool, if salt pool spatial memory was activated, and the timestep equaled one of the pre-selected time-steps, then the moose chose the salt pool closest to its current location. A travel distance between 275m and 550m 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 roadavoider, 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 2way 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).

2.4 Results

2.4.1 Model validation

The validation was done using 12 real moose and the corresponding 12 model moose that both had their home ranges near Highway 175 (highlighted in red on Figure 2.3b). 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 2.3). 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.

Moose type : Real vs. current situation (4 cases)	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

Table 2.3. Comparison of the number of road crossings and the proportion of locations within 500m. 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.

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 217km for the road avoidance off and salt pool spatial memory on to 227km 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 behaviour 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 247km per moose. However, the variability in the distances travelled by the model moose was low (with a minimum of 250km and a maximum of 260 km). This contrasted with the marked variability in the real moose, ranging from 155km to 402 km. The highest distance belonged to a yearling female 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) (Figure 2.4). 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 2.1, Figure 2.4). 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 Mi30 and 7 of the real 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 2.3). 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.

2.4.2 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 interaction (Table 2.4). 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 2.4). 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 2way 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 2.4). 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 2.4), 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.

Factors	Coefficients (summary)	Coefficients (individual)	P value (summary)	P value (individual)	Partitioning of Variance (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%

Table 2.4. 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.

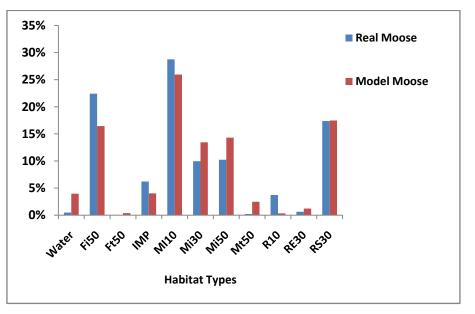


Figure 2.4. A comparison of the habitat use of the 12 real moose with home ranges near Highway 175 with the 12 model moose. The proportion of time corresponds to the number of time steps spent in each habitat divided by the total number of steps for the model and real moose, respectively.

2.4.3 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 (Figure 2.5a, Table 2.5). 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 (Figure 2.5a). 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 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 analyzed 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, Figure 2.5b), 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.

scenario	RAB	SPSM	Crossings	Reduction%	t-tests p-	t-tests p-
					values	values 999 perms
1	Yes	Yes	4.24			
(current situation)						
	Yes	No	2.93			
	No	Yes	17.78			
	No	No	11.50			
2	Yes	Yes	0.88	79.28%	< 0.001	0.001
	Yes	No	1.01	65.49%	0.007	0.001
	No	Yes	9.20	48.26%	0.007	0.004
	No	No	9.34	18.75%	0.500	0.514
3	Yes	Yes	2.13	49.88%	0.031	0.029
	Yes	No	1.30	55.54%	0.018	0.021
	No	Yes	14.87	16.35%	0.420	0.454
	No	No	10.56	8.15%	0.755	0.745
4	Yes	Yes	3.30	22.13%	0.339	0.327
•	Yes	No	1.84	37.30%	0.134	0.127
	No	Yes	15.33	13.77%	0.473	0.465
	No	No	11.27	1.92%	0.940	0.942
5	Yes	Yes	2.65	37.50%	0.097	0.101
	Yes	No	1.99	32.01%	0.198	0.188
	No	Yes	15.67	11.83%	0.552	0.563
	No	No	10.72	6.76%	0.789	0.788

Table 2.5. This table lists the 5 scenarios with each of the four combination of the two factors: road avoidance and salt pool spatial memory, the average number of moose road crossings averaged over 3 years, road crossing reductions percentages, the t-test p-values and the t-test p-values with 999 permutation tests. The t-tests were performed in R using the t-test program with 999 permutation tests. (Legendre, 2010).

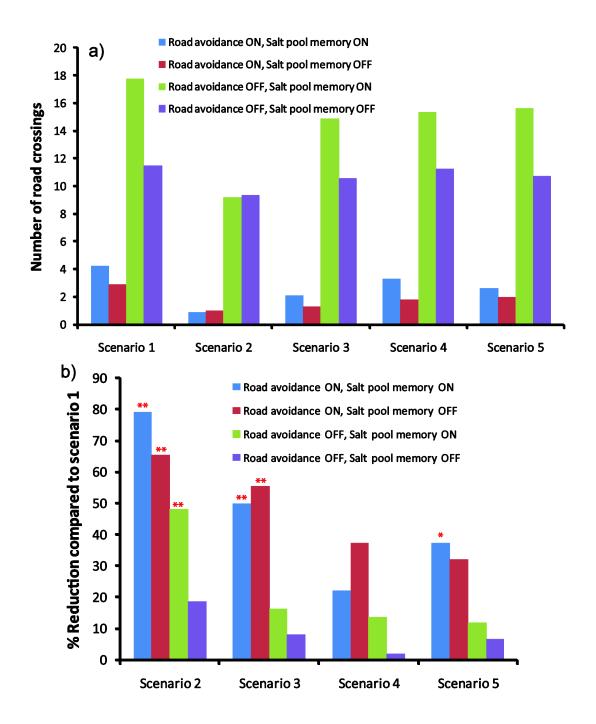


Figure 2.5. (a) Number of moose road crossings per moose per summer in the five scenarios and (b) model moose road crossing reductions compared to the current situation (Scenario #1). The double stars indicate a statistically significant p-value (<0.05) and the single star represents a significant p-value 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.

2.5 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 scenarios with road avoidance active exhibited far fewer road crossings in each scenario than in the scenarios where the moose did not avoid the road (Figure 2.5a). 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 (Figure 2.5a). 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 500m 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.

2.6 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 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 (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 2.5) as an indication of inter-individual variability.

This model could be extended to be then used for other ungulates such as elk and 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 4lane highway 175 in the Laurentides Wildlife Reserve. These measures include fencing with double emergency escape gates, and wildlife underpasses.

3 Chapter 3: An evaluation of the allometric method that places more wildlife passages and increases highway permeability, using an agent-based model

3.1 Introduction

Although various mitigation measures can be implemented to reduce road mortality, for larger mammals such as ungulates and carnivores, wildlife passages that either cross over or under the roadway are increasingly used (Clevenger *et al.* 2001; Seiler 2004; Dodd *et al.*, 2007c; AECOM Tecsult Inc. 2009, 2010). These are combined with fencing in order to direct wildlife to these crossings. Sometimes, existing structures like bridges or culverts can be modified to better accommodate wildlife; otherwise, entirely new structures need to be built. The placement of wildlife underpasses has not had much of an ecological basis up until now but has been based mainly on hot-spot analysis of the environmental factors in the immediate proximity of wildlife vehicle collisions (Bissonette and Adair 2008; Bissonette and Cramer 2008). Fences keep wildlife off the highways (Clevenger *et al.* 2001; Seiler 2004; Dodd *et al.*, 2007c; AECOM Tecsult Inc. 2009, 2010), but one of the most relevant questions is how much do wildlife crossings increase highway permeability after the highway and fences installation have reduced the landscape connectivity to near zero in some areas?

Bowman *et al.* (2002) discovered that variance in maximum and median dispersal distance among terrestrial mammals was more directly correlated to their home range size (74%) than their body size (50%). Thus, the placement of wildlife passages should be

based on home range size of the focal species (i.e. the moose), rather than were their body size. For example, Bissonette and Adair (2008) and Bissonette and Cramer (2008) determined that the square root of the species home range size corresponded to the optimal placement of wildlife passages to increase highway permeability. In fact, most terrestrial fauna tend to move many short distances and only occasionally move long distances (Benhamou, 2007). This movement equates to a power-law distribution (Atkinson *et al.* 2002; Schick *et al.* 2008). Carsignol *et al.* (2005), for example, suggested placing crossings structures for small- and medium-sized fauna at a distance of about 300m as a rule of thumb. In the LWR, based on the annual home range areas of the 47 moose that were followed through GPS telemetry, the allometric scaling would result in an average of 7km of daily movement distance. This average is quite a bit higher than the daily movement distance of 3.52km reported by Bissonette and Adair (2008) that was extracted from a paper by Courtois *et al.* (1998) that studied moose in eastern Québec, Canada.

In Banff National Park (BNP), there are 30 passages over 75km, for an average spacing of 2.5km, along the Trans-Canada Highway; along the Arizona State Route 260, there are 11 underpasses and 6 bridges over 27km, i.e. 1.6km spacing on average, and along the Highway 93 in Montana there are 42 passages over 91km or 2.2km average distance between passages (Beckmann *et al.* 2010). All of the average distances between passages in these projects are lower than the daily movement distance of elk of 3.52km recommended by Bissonette and Adair (2008), thus these three projects are within the allometrically-scaled placement of wildlife passages for elk. In the south-west of Sweden, there is a segment of 15km with 6 over-passages and under-passages whose average

distance is 2.5km and the allometric distance is 2.2km for the focal species, the moose (Olsson *et al.*, 2008b). In Spain, the focal species focal is the wild boar, there is 183km with 43 passages whose average distance is 4.26km and the allometric distance is 13.28km (Subdued and Al 2008). In England, there is a segment of 59km of the road with 47 passages thus an average distance of 1.26km for the focal species, the deer. The allometric distance is 1.24km (Langbein. 2010). In the LWR, however, there are only 6 moose passages over 174km corresponding to an average spacing of 29km between wildlife passages. If we only consider the more problematic northern and southern slopes of the LWR where most of the MVC occurred between 1990 and 2002, the average spacing still remains quite high, i.e. 17km for the northern slope and 26km for the southern slope (Figure 3.2).

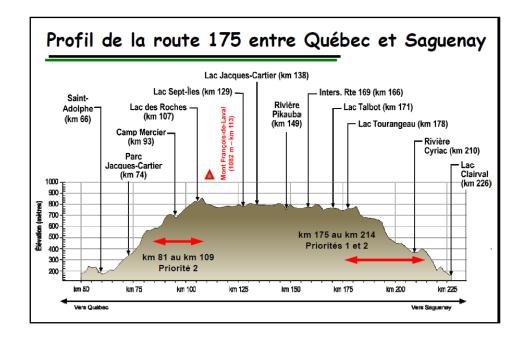


Figure 3.1. Elevation profile of the LWR displaying the top priority areas for mitigation measures on Highway 175 in the LWR. The moose density is much higher on the southern (left) and northern (right) sections than in the middle plateau due to the higher food quality due to the mixed deciduous forest compared to the coniferous forest on the plateau. Source: Donald Martel, MTQ. BAPE Presentation (2005). Thus, the spacing of the 6 moose wildlife passages is considerably larger than the daily movement distance of the moose estimated from their home ranges as 7km. It is also considerably larger than the spacing used in other projects in North America. Although local environmental factors such as funding, topography, and engineering may, in practice, outweigh the allometry principle (Beckmann *et al.*, 2010), the very large distances between passages in the LWR need to be further investigated for their impact on highway permeability.

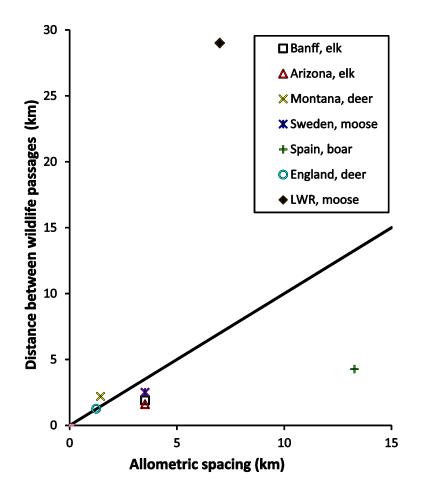


Figure 3.2. This figures shows the allometric distances for 7 focal species in North America and Europe on the x-axis and the actual distances between passages on the y axis. One can see the LWR is an outlier.

When there are no wildlife underpasses for the moose within their home ranges, and the portion of the home range intersected by the fence and covering the road is inaccessible, we would expect the moose to compensate for this home range loss by expanding its home range outward in the other direction. Olsson and Widen (2008a) stated in their results that "most of the moose that had home ranges that were bisected by the highway prior to the fencing changed their movement behaviour and moved their home ranges to the west of the highway after fencing." Olsson and Widen (2008a) found, as well, that after fencing was implemented, the number of home ranges intersecting the highway decreased from 26% (10 of 38) to 13% (5 of 38). However, in order to get accurate information on the moose's behaviour near fences and underpasses, it is essential to use GPS telemetry collars on moose after fencing and underpasses have been constructed. This would help answer key questions for moose movement rules such as: "When they first encountered a fence along the highway, what percentage of the moose follow the fence and what percentage return to their home ranges?", "How long do the moose follow the fences?" or "How many different moose are actually using the underpasses?" In a study on Arizona State Route 260 that focused on pre- and postconstruction of fencing and underpasses, Dodd et al. (2007b) used GPS telemetry collars on elk to determine the highway permeability. They found that the passage rates (# crossings / # approaches) was 0.43 ± 0.15 after reconstruction compared to 0.86 ± 0.09 for the sections during the reconstruction of the highway, the fences, and underpasses and the control sections.

3.2 Fences and underpasses in the LWR

Various studies have shown that exclusion fencing beside roads can lead to a reduction in WVC by 80% to 90% (Clevenger et al. 2001; Seiler 2004; Dodd et al. 2007c; AECOM Tecsult Inc. 2009, 2010). Olsson and Widen (2008a) found that exclusion fencing with three underpasses for moose in south-western Sweden reduced the number of MVC by 67-89%, thus, creating increased motorist safety but may have had a negative effect on moose access to resources as well as gene flow and re-colonization rates on more sparsely populated areas. In a second study, Olsson *et al.* (2008b) found that overpass use by moose declined as traffic volume increased but that the 5-7 moose that did use the overpass annually was enough to maintain gene flow between previously isolated subpopulations. In the LWR, there were 50 MVCs per year between 1990 and 2002. Now with the fences and underpasses, there were 31 MVCs in 2009, all in the unfenced areas, many of them just beyond the end of the fences. Fences are 2.4 m high, and were installed on 23km in the northern section and on 37km in the southern section (Figure 3.3). There is also a 2-km fence near the Jacques-Cartier passage, and a 4.5km fence at Lac Tourangeau, which was a former test site for an electric fence installation by ElectroBraidTM (Leblond *et al*, 2007a). In the fenced areas in the northern and southern parts of the LWR there were hardly any moose road crossings of Highway 175, with only moose and hunters, kayakists, and fishermen using the wildlife crossings (AECOM Tecsult 2010).

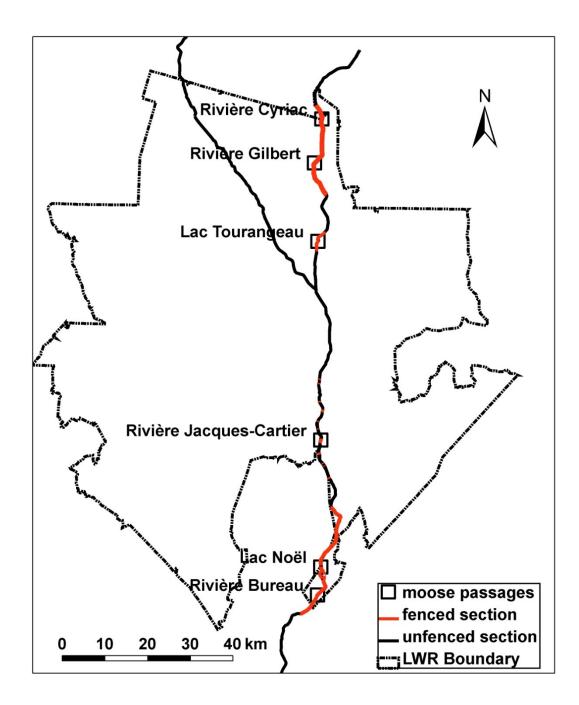


Figure 3.3. LWR fenced areas and wildlife underpasses for moose.

There are six moose wildlife crossings in the LWR, two in the southern section, two in the northern section, one at the discharge from Lac Tourangeau and one at the Jacques-

Cartier River (Figure 3.2). Salt blocks were installed to attract moose at the entrances of each wildlife crossing on both sides of the road. After the BAPE approval of the Highway 175 expansion from a 2-lane highway to a 4-lane highway, the Québec government mandated AECOM Tecsult to monitor the moose road crossings on Highway 175 for 5 years, from 2006 to 2011. AECOM Tecsult sent out biologists and technicians by bicycle every 3 weeks in the summer from May to September to monitor both fenced and unfenced sections of Highway 175 and report the crossings and approaches. As well, motion-detection cameras were placed in each underpass to monitor large and small fauna crossings. There is a marked increase (38%) in the number of crossings between 2009 and 2010, which seems to indicate that moose are quickly learning how to find these passages (Table 3.1). However, the 6 passages are not used evenly. The Bureau River underpass was designed for small fauna but it is nevertheless highly used by moose (Table 3.1). On the contrary, the Jacques-Cartier river underpass is not used very much, perhaps because the moose are not able to see through the underpass to the other side and thus turn around instead, or because there is only 4km of fencing surrounding the underpass which may not be enough to funnel them towards it (AECOM Tecsult 2010; Beckmann et al. 2010).

Underpasses	km marker	2009	2010
Bureau	87	33	108
Noel	95	117	91
Jacques-Cartier	128	3	7
Tourangeau	178	6	18
Gilbert	199	13	32
Cyriac	210	17	4
Totals		189	260

Table 3.1 Underpass crossings of moose for 2009 and 2010 in the LWR. Source: Y. Leblanc, (AECOMTecsult, pers. comm).

3.3 **Objectives and Research Questions**

Underpasses are designed to increase landscape connectivity by allowing the moose to travel under the highway to reach suitable habitat for foraging, mating, etc. However, very little is known on the behavior of moose near fences and wildlife passages. In this chapter, we develop an ABM approach to compare the impact on road permeability of different spacing distances between wildlife passages in the LWR, including the allometrically-scaled wildlife crossing approach of Bissonette and Adair (2008). The ABM model used in the previous chapter will be modified to investigate the use of the fences and underpasses by the model moose. The basic rules for the modelled moose behaviour in the LWR. Thus this study plans to build a ten year model of moose behaviour showing that different placements and numbers of wildlife underpasses and fencing will lead to different numbers of moose road crossings. The allometrically-scaled placement of wildlife crossing should result in a higher level of highway permeability than the actual

installed wildlife crossings. The highway permeability will be measured by number of moose underpass crossings. These patterns can be used to develop insights into the long-term effectiveness of mitigation measures for reducing MVC.

The general objective of this part of the research is to use an agent-based model to assess the effectiveness and the impacts of mitigation measures of road exclusion fencing and wildlife underpasses for MVCs along the upgraded (2 lanes to 4 divided lanes) highway 175 in the LWR. Thus the main research question is: will allometrically-scaled wildlife crossings increase the highway permeability compared to the actual fencing and wildlife underpasses newly constructed in the LWR and by how much? The specific objective of this chapter is to develop a conceptual framework to determine the model moose movement rules near fences and underpasses, and to determine the response variables needed to assess the effectiveness of different spacing of wildlife passages.

3.4 Modelling approach

As in the previous chapter, the study area is in the LWR situated between Québec City and Ville de Saguenay, Québec, Canada (Figure 3.1). However, here the entire Highway 175 within the LWR is examined. The GIS files described previously (e.g. forest polygons) are used. The highway was buffered with the forest polygons for 10km on either side of Highway 175.

The weights and five travelling parameters based on the scientific literature on moose in the LWR (Dussault *et al.* 2004, 2005, 2006a, 2007) used to score potential forest polygon destinations will be used directly from the previous model. These five

parameters were food and cover qualities, proximity to compensation salt pools and water and slope. The five weights, after calibration were 0.45 for food quality, 0.10 for cover quality, 0.10 for proximity to water, 0.30 for proximity to compensation salt pools, and 0.05 for slope. These weights would have to be adjusted seasonally for the fall rut when males stop eating for a time and the winter season when females seek more cover in conifers.

The ABM model used to examine highway permeability will be based on the same movement rules and corresponding weights as the ABM model used to investigate the impact of salt pool management (Chapter 2). However, several new modules will need to be added in order to simulate the movement of moose near fences and wildlife passages. The conceptual framework to determine the model moose movement rules near fences and underpasses is described in the sections below. This will be followed by some results on calibration and validation, by anticipated results and by a discussion on the issues that need to be examined in order to implement this conceptual framework as a simulation model.

3.4.1 Moose Home Range Creation

The first major change compared to the model described in chapter 2 is to let the model moose determine their own home ranges instead of imposing a home range as in chapter 2. In the previous ABM (Grosman *et al.* 2011) home ranges were imposed on the model moose, but we thought it was better that the model moose create their own home ranges, since, in this chapter, it focuses on road crossings and highway permeability, the produced moose home ranges need to be in the vicinity of the Highway 175. Therefore,

the ABM was run with no home range enforcement and road avoidance activated for nine moose except for the following real moose: L06 2003, L06 2004, and L25 2003 which are their GPS telemetry collar ids (Breton et al, 2006). The model was run 10 times for 12 months to determine after how much time the model moose would cover an area comparable to the real moose's home range, using their locations to determine the corresponding home range. For the non-road avoiders food, cover and proximity to water bodies values were degraded by 1 instead of 3 for the road-avoiders in order to reduce their highway proximity by a small degree. The averages of home range areas based on point locations were extracted from the 10 runs for the 2-month, 4-month, 6-month, and 12-month periods. These were compared with the 12 home ranges for the real moose (Table 3.2). The averages for the 2 months are lower than the average of the real moose and those for 4 months are higher. Thus, a run of 3 months was deemed best to obtain average home range areas for the model moose that are comparable to the real moose's averages. The next step in the calibration process will be to compare these home ranges to the real ones mentioned above to see if they match reasonably well in habitat composition and road interaction.

Animal	Real Moose	2 months	4 months	6 months	12 months	RoadAvoiders
L06_2003	57.1	58.0	138.2	168.8	276.2	N
L06_2004	54.8	38.7	126.2	139.2	244.3	N
L14	25.2	23.4	59.2	78.3	129.3	Y
L17	24.1	20.3	53.0	68.9	106.7	Y
L19	46.8	21.5	62.2	99.2	155.1	Y
L25	82.4	36.0	91.0	111.0	172.5	N
L36_2004	75.6	33.4	101.4	123.9	202.4	Y
L36_2005	55.9	36.8	72.9	99.3	115.1	Y
L43_2004	60.3	24.8	60.9	79.1	116.3	Y
L45_2004	48.2	28.6	67.1	86.8	161.2	Y
L46	35.7	32.6	64.0	93.0	141.8	Y
L54	86.1	30.9	83.9	102.4	146.0	Y
km ²	54.3	32.2	81.9	104.4	162.3	

Table 3.2. The real moose home range areas (km²) with the model moose average home ranges areas after the model is run for 2, 4, 6, and 12 months. Thus a run of 3 months would produce home range areas that are most similar to the 12 real moose's home range areas.

Home range sizes were determined using the minimum convex polygon estimator (Mohr, 1947). Girard *et al.* (2002) found that 100 to 300 GPS telemetry locations annually or 20 to 100 GPS telemetry locations seasonally were necessary to reach a plateau in MCP home range estimation. They also found that high bias occurred below these values. This minimum convex polygon estimation is one of the most commonly used techniques of habitat use. A more accurate analysis of habitat use using the GPS telemetry of the 47 real moose and the underlying SIEF forest maps supplied by MRNF was performed as well of the actual habitat use by the 47 real moose over the three years of the MRNF-UQAR study (Figure 3.4). This analysis with the MCP home ranges sizes gives a better representation of the actual habitat use by the 47 real moose since the MCP alone included areas within their home ranges that the 47 real moose did not visit and use. An analysis of the eleven habitat types with food and cover quality based on the Habitat Quality Indicators developed by Dussault *et al.* (2006b) was also performed on these 71 home ranges (Table 3.3). The mixed intolerant 10 year old habitat type was the

most popular for the real moose and they spent over thirty percent of their time there (Figure 3.4).

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

Table 3.3. The 11 habitat types in the SIEF maps for the LWR with the Habitat Quality Indicators for food and cover qualities.

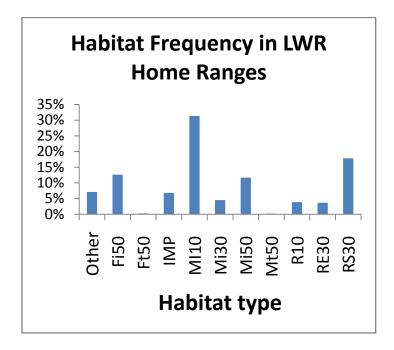


Figure 3.4. The eleven habitat types and their total forest polygon usage percentage for the 71 annual home ranges of the 47 real moose.

As in Chapter 2, home range enforcement will still be implemented, now using the dynamically-created home ranges from the three-month runs instead of imposing a home range from the annual real moose home ranges. These home ranges will not be buffered outwards 625m since there are no roadside salt pools in the new model and compensation salt pools will already be within their home ranges.

3.4.2 Model Moose Following Fences

The major new process in this ABM will be the movement rules for model moose moving along fences. There are no telemetry data available to document moose movement along fences in the LWR and, to the best of my knowledge, there are no telemetry data for any species near fences and wildlife passages elsewhere. Thus, the conceptual framework described here for model moose is quite speculative and would need to be tested against real moose behaviour. The first new movement rule concerns the situation where a moose starts at the back of its home range and proceeds towards Route 175. When a model moose encounters a forest polygon with a fence within it for the very first time, it must decide if it will follow the fence and, if so, in which direction. Since we do not have any empirical data on this decision, a stochastic approach will be used based on three cases: 1) most moose would tend to turn their back to the fence, and only 25% of the moose decide to follow the fence; 2) half the moose (50%) follow the fence and half the moose return to their home range further away from the road; 3) most moose (75%) tend to follow the fence. There is no way to know which of these three cases is closest to reality, but it is very likely that between 25% and 75% of real moose encountering a fence would tend to follow it (C. Dussault, pers. comm.).

The second decision for the model moose following the fence is which way to move: left or right? Since there is no a priori reason for a moose to go one way rather than another way, a 50% probability of turning left or right will be used. After the model moose decides to follow the fence, the moose will proceed along the fence in the chosen direction, moving to the next forest polygon it its home range that has a fence in it.

The third decision for movement rules comes into play once a model moose following a fence reaches the end of its home range. Based on our knowledge of moose behaviour, it is estimated that the moose could follow the fence at least for 1km and at most for 10km past its home range limit (C. Dussault, pers. comm.). In order to implement this variability in model moose's behaviour, fuzzy logic will be used to progressively degrade food, cover and water quality in forest polygons beyond the home range limit. Three decreasing fuzzy logic sigmoidal functions will be applied to the moose travelling along the fences at the limit of their home range (Figure 3.5).

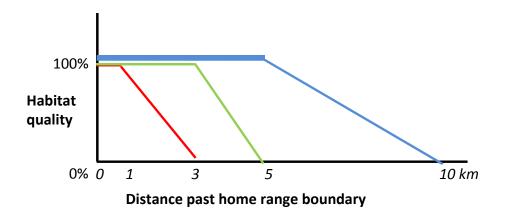


Figure 3.5. Fuzzy functions for the degradation of habitat using 3 maximum distances (3 5 and 10km) once the moose reaches the limit of its home range.

The presence of salt blocks at the entrance of wildlife passages must also be taken into account in the movement rules. This can have two effects. First, it is expected that the presence of a salt block will encourage moose to follow the underpass to the other side of route 175, where it will continue foraging on the other side of the road. Secondly, the moose will place the location of the salt blocks and wildlife underpass in its spatial memory, so that the next time, it can proceed to the underpass with purpose. As well, if the female moose has brought its one or two yearlings with her through the crossing, the yearlings will have spatial memory of the salt block and underpass, as well, and can use it independently when they are forced out by their mothers after one year and need to find their own new home ranges. Thus, once a model moose has a spatial memory of the ence with

purposeful direction and then use the underpass instead of using the fuzzy logic algorithm to determine its movement distance along the fence.

Road avoidance, compensation salt pools, the travel distance algorithm and the weights and travelling parameters from the previous model described in chapter 2 will all be used in this model as well. Road avoidance will still be a factor in the new model since the highway is wider, thus the noise from the highway and the traffic volumes will be greater as well. As in the previous model, we will choose the road-avoiders and the non road-avoiders randomly. New forest polygons 500m from the new rights-of-way and the exclusion fences will be identified and provided with a reduced food, cover and distance to water bodies values for the road-avoiding model moose but not for the non road-avoiding ones. These values will be used in the fuzzy logic function to determine the probability that the model moose will continue to follow the fence when it is outside its home range boundary. Road avoidance will always be active for 90% of the model moose since we have determined in the previous model that this has the best affinity to the real moose behaviour.

All roadside salt pools are drained away immediately due to the new engineering work on Highway 175 so the salt will go directly into the aquatic environment. Compensation salt pools will be continued to be built off forestry secondary roads of Highway 175. As their actual locations are not known, a number of compensation salt pools will be built in the model from 500m to 1,500m from the fences or the rights-of-way. Once a model moose has found a compensation salt pool, it will add it to its spatial memory and then visit it according to a Poisson distribution with a mean of 2.1 to plan its trips (Laurian *et al.* 2008a). It will seek out the closest compensation salt pool to its current location in the

months of June and July as done in the previous model. In the new model, spatial memory of salt pools will always be activated, since we found in the previous model that this produced results that had the best fidelity to the real moose's results.

The travel distance algorithm that was based on the power-law distribution y = 8999.2 $x^{-1.592}$, with a $R^2 = 0.89$, derived from the 2 hour time steps of the 12 real moose will still be used in the new model for foraging (0m to 125m), ruminating (0m to 125m), travelling (125m to 550m) and travelling to salt pools (275m to 550m). When, however, the moose encounters a fence for the first time and decides to follow it, a different algorithm will be used where the model moose will follow the fence using neighbouring forest polygons that each contains a fence.

3.5 Scenarios

To assess the impact of distance between underpasses on road permeability in the LWR, we suggest using 100 model moose with a time-step of 2 hours for 10 years starting with the current situation of six underpasses. The results from this scenario #1 (current situation) will be compared to the number of real moose crossings through the underpasses. Once the model is validated, seventeen new scenarios will be run to assess the impact of progressively reducing the average distance down to and less than the allometric distance, which corresponds to scenario #11 (Table 3.4):

Scenarios	Underpasses	Average distance (km)
		between underpasses
1 (current situation)	6	29.0
2	8	21.8
3	10	17.4
4	12	14.5
5	14	12.4
6	16	10.9
7	18	9.7
8	20	8.7
9	22	7.9
10	24	7.3
11 allometric distance	26	6.7
12	28	6.2
13	30	5.8
14	32	5.4
15	34	5.1
16	36	4.8
17	38	4.6
18	40	4.4

Table 3.4. The eighteen scenarios starting with the current situation with six underpasses and proceeding to scenario 18 with 40 underpasses. Even though the scenario #11 is the correct allometrically-scaled one, we want to see that the permeability effects will be with the wildlife underpasses even closer together than scenario #11.

Each scenario will be run for the 3 cases (25%, 50% or 75% of moose following fences) and for the three different fuzzy functions to degrade the habitat values of food, cover and proximity to water bodies beyond the home range limit thus the home range limits will not be enforced.

3.6 Response and explanatory variables

The following response and explanatory variables will be used in the statistical methods of redundancy analysis and forward selection described in the appendix.

There will be seven response variables for each model moose for each scenario:

- The number of wildlife underpasses selected by the model moose,
- The number of moose crossings at wildlife underpasses,
- Food quality selected by forest polygon per year,
- Cover quality selected by forest polygon per year,
- Distance travelled per year,
- The total time spent in 2 hour time steps on each side of the road by forest polygon per year, and
- The habitat use by the model moose on each side of the road by forest polygon per year.

There will be five explanatory variables for each scenario:

- The total number of wildlife underpasses available per scenario,
- food available per forest polygon,
- cover available per forest polygon,
- proximity to water bodies per forest polygon, and

• slope per forest polygon.

Each forest polygon near the road will have new Boolean codes for the following properties:

- a fence cuts completely through it (yes/no),
- an underpass entrance exists in it (yes/no),
- the presence of an escape gate (yes/no), and
- a distance decay function for the presence of a salt block.

As well, the female moose will have a new field indicating how many yearlings they have accompanying them.

3.7 Statistical Methods

Redundancy analysis, using the extension of multiple regression to model multivariate response data (Legendre and Legendre, 1998; Gotelli and Ellison, 2004), will be performed in the **R** statistical language on the seven response variables and the five explanatory variables to determine which of the response variables and the explanatory variables have the most impact on the 100 model moose. This will be done for all eighteen scenarios. As well, forward selection will be also performed in the **R** statistical language on the variables to see which variables contributed most to the R^2 values, which are part of the redundancy analysis output. Graphs displaying the number of moose road crossings versus density of wildlife crossings structures will be displayed for all eighteen scenarios. It is expected that the allometrically-scaled placement of wildlife crossings of

scenario #11 will have greater highway permeability compared to the current situation of the fences and crossings in the LWR and we may see a levelling off of the highway permeability at scenario #11.

3.8 Home Ranges Characteristics: validation data

In order to assess the validity of the model, the current situation (scenario #1) will be validated using a comparison with the real moose's home range characteristics. Using the GPS telemetry data from the 47 GPS collared moose in the LWR, we created 71 annual home ranges (Table 3.5) using the minimum convex polygon method from Beyer (2004). Most of the 47 moose had GPS data for more than one year, so 71 annual home ranges were created using each year of the 47 moose resulting in 71 annual home ranges. The average area was 53km² and the areas ranged from 15km² to 172km². The square root of each home range i.e. the daily movement distance is also displayed in Table 3.5. The daily movement distance of the 71 annual home ranges was 7km.

		Daily Distance			Daily Distance
Animal_An	Area (Km²)	(km)	Animal_An	Area (Km²)	(km)
L01_2003	42	6.5	L28_2004	49	7.0
L03_2003	33	5.7	L28_2005	51	7.1
L03_2004	32	5.7	L29_2003	34	5.8
L04_2003	29	5.4	L29_2005	27	5.2
L04_2004	42	6.5	L30_2003	36	6.0
L05_2003	64	8.0	L30_2004	27	5.2
L06_2003	47	6.9	L30_2005	15	3.9
L06_2004	37	6.1	L31_2004	133	11.5
L06_2005	29	5.4	L32_2004	40	6.3
L07_2003	75	8.7	L33_2004	41	6.4
L11_2003	186	13.6	L34_2004	49	7.0
L12_2003	46	6.8	L34_2005	74	8.6
L12_2004	45	6.7	L35_2004	148	12.2
L13_2003	80	8.9	L35_2005	73	8.5
L14_2003	40	6.3	L36_2004	60	7.7
L14_2004	27	5.2	L36_2005	68	8.2
L14_2005	17	4.1	L37_2004	14	3.7
L17_2003	37	6.1	L38_2004	41	6.4
L18_2003	75	8.7	L39_2004	23	4.8
L18_2004	43	6.6	L40_2004	78	8.8
L18_2005	21	4.6	L40_2005	60	7.7
L19_2003	36	6.0	L41_2004	28	5.3
L19_2004	17	4.1	L42_2004	27	5.2
L19_2005	41	6.4	L42_2005	41	6.4
L20_2003	108	10.4	L43_2005	52	7.2
L21_2003	43	6.6	L44_2005	41	6.4
L21_2005	14	3.7	L45_2005	47	6.9
L22_2003	48	6.9	L46_2005	78	8.8
L23_2003	45	6.7	L47_2005	53	7.3
L25_2003	76	8.7	L48_2005	101	10.0
L26_2003	149	12.2	L49_2005	26	5.1
L27_2003	40	6.3	L50_2005	45	6.7
L27_2004	34	5.8	L51_2005	67	8.2
L27_2005	29	5.4	L53_2005	47	6.9
L28_2003	32	5.7	L54_2005	172	13.1
			L55_2005	50	7.1

Table 3.5. The 71 annual home ranges of the real 47 GPS collared moose.

An analysis was also performed about how many of the 71 annual home ranges of the real moose were intersected by either Highways 169 or 175 in the LWR (Figure 3.6). Most home ranges had either 0% intersection with the highways (28) or 10% intersection (26).

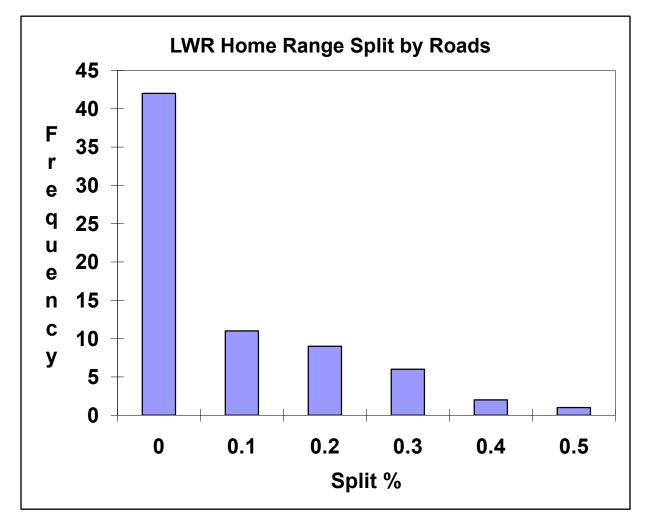


Figure 3.6. The 71 annual home ranges and their percentage intersection with highways 169 and 175 for the real 47 GPS-telemetry collared moose.

Finally, the slopes were calculated for each forest polygon within the 71 annual home ranges (Figure 3.7). In general, real moose tend to follow ridges or river valleys and not go up and down hills (Dussault *et al.* 2005).

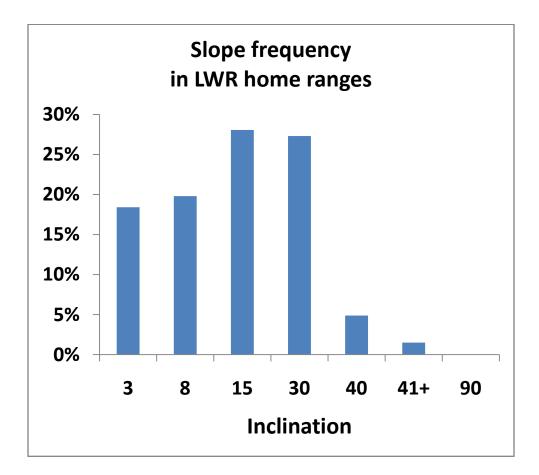


Figure 3.7. The slope percentages for the 71 real moose annual home ranges for the 47 real moose.

3.9 Anticipated Results

Thus, an overall increase in highway permeability is expected as the number of wildlife crossings increases. It is also expected that highway permeability would increase

with an increase in the fuzzy buffer width which allows moose to travel beyond their home range limit when following a fence. These two expectations are summarized in Figure 3.8. On the one hand, it is possible that permeability would increase in a linear way as the number of wildlife passages increases (Figure 3.8a). However, it is also possible that highway permeability would level off at some point, likely when the distance between wildlife passages is close to the allometric distance (Figure 3.8b). Until the ABM is created, run and analyzed for all scenarios, it is not possible to know what impact the number of wildlife passages has on permeability and what the slope of the curve is. Figure 3.8b is similar to figure 6 in Pfister *et al.* (2002) where they graph the number of mammal wildlife crossings versus the width of the wildlife crossings.

Redundancy analysis and forward selection will be applied to the seven response variables for each model moose for each scenario and the five explanatory variables for each scenario. Tri-plot graphs that show the response and explanatory variables as arrows and the locations of the 100 model moose will be displayed as well. Whichever variables are closest to each of the 100 model moose in the eighteen scenarios determines the relative importance of each variable to that particular model moose. We should be able to summarize the most important response and explanatory variables by scenario.

Forward selection will also be applied to each of the eighteen scenarios, as a secondary method to determine which of the response or explanatory variables contribute most to the R^2 value of the each of the scenarios' redundancy analysis. Forward selection starts with no variables and adds one at a time until the R^2 value is exceeded. Forward selection can only give some indication of the important variables in the model; but since

the statistical computation is not independent, the outputs should not be tried as final but only as guidance (Legendre and Legendre, 1998).

I expect that the redundancy analysis and the forward selection for the scenarios below the allometrically-scaled scenario #11 will show that Food Selected, and Food Available will be the most important response and explanatory variables, but as the scenarios reach #11 and beyond, I expect that the number of wildlife underpasses selected by the model moose and the number of wildlife underpasses available will become the most important response and explanatory variables.

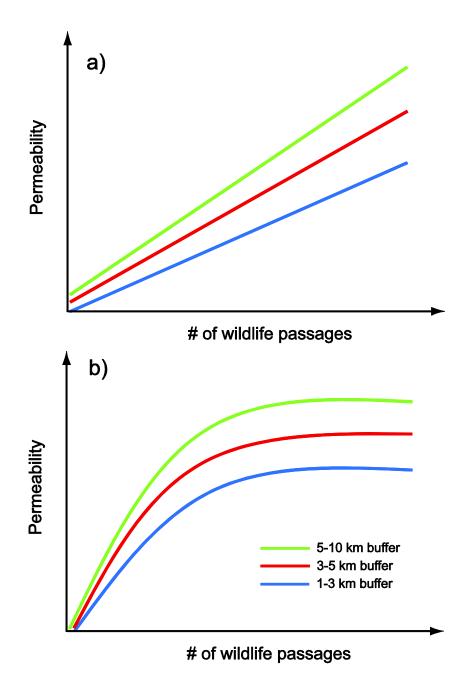


Figure 3.8. Possible changes in permeability with increasing number of wildlife underpasses for a) the case where permeability continually increases as more underpasses are available, and b) the case where a plateau is reached where increasing the number of underpasses no longer affects permeability.

3.10 Discussion

The modelling approach for the model moose following fences and then discovering the salt blocks at the entrances of the underpasses and the underpasses themselves is quite theoretical since there is no empirical GPS data available to use to validate the modelling approach. We know, however, that the real moose have been using the underpasses in the LWR as shown in Table 3.1 and their wildlife passages have increased by 38% from 2009 to 2010. The increase in wildlife passages suggests that the real moose are learning to use the underpasses quite quickly. Thus, the modelling approach should result in increased levels of highway permeability as the numbers of wildlife passages increase scenario by scenario. So the allometric method used in the revised ABM should produce much higher highway permeability than the real six underpasses in the LWR for the moose and the allometric method itself is an important first step in increasing highway permeability for moose. It may not be possible to place wildlife passages on a strictly allometric basis given that the road project's fiscal constraints, local topography and other local factors thus the spacing of the wildlife passages will be probably further apart (Beckmann et al. 2010).

As the number of scenarios increase, the number of model moose wildlife passages will increase as well. This will result in increased highway permeability that will lead to more landscape connectivity. Landscape connectivity, as defined by Taylor *et al.* (1993), can be measured for model moose by the movement probability between resource patches. In figure 3.3, one can see that the most popular habitat type selection for the real moose is MI10 (mixed intolerant hardwoods, 10 years old), RS30 (conifers 30 years old), and MI50 (mixed intolerant hardwoods, 50 years old). Similar results should appear for

the later scenarios for the model moose as the highway permeability and landscape connectivity increases.

This revised ABM is using the weights on the five parameters of food, cover, proximity to compensation salt pools, proximity to water bodies and slope as the ABM in chapter 2. These parameters and weights, however, are imposed on the behaviour of the model moose and no variability is expressed except by the different habitat types in each model moose's home range and the final bit of randomness applied to the choice of the best forest polygon to travel to next.

The home range enforcement process is the same as in the ABM in chapter 2 except when moose are following fences or they have spatial memory of underpasses and can go directly to them. The power-law distribution for moose movement is also the same as the ABM in chapter 2 except when moose are following fences or they have spatial memory of underpasses and can go directly to them. Since all the roadside salt pools are drained immediately by the new Highway 175 configuration, we have created compensation salt pools in all of the 100 model moose home ranges. Since the salt pool algorithm will be implemented in the revised ABM as well, they will use the compensation salt pools only since the roadside salt pools are all drained away automatically into the aquatic sustems.

The creation of the model moose home ranges must be validated by the data from the 71 real moose home ranges. If the model moose home range areas are greater than one standard deviation of the real moose home range areas or the number of model moose home ranges are split by the highway is greater than one standard deviation from the real moose home ranges road splits, or the slopes of the forest polygons in the model moose home ranges are greater than one standard deviation from the real moose home ranges are greater than one standard deviation from the model moose home ranges are greater than one standard deviation from the model moose home ranges are greater than one standard deviation from the model moose home ranges are greater than one standard deviation from the model moose home ranges are greater than one standard deviation from the model moose home ranges are greater than one standard deviation from the model moose home ranges are greater than one standard deviation from the model moose home ranges are greater than one standard deviation from the model moose home ranges are greater than one standard deviation from the model moose home ranges are greater than one standard deviation from the model moose home ranges

or the habitat use frequencies of the model moose home ranges are greater than one standard deviation from the real moose home ranges habitat use frequencies, then the model home range creation process will have to be rerun until each of these four model moose categories are within one standard deviation of the real moose categories.

Since the process of the moose following fences has neither GPS calibration nor validation data, it was decided that, for each of the eighteen scenarios, we will have three separate versions in each scenario: when the moose follow the fence for the first time, they will follow it 25% 50% or 75% of the time; otherwise, they return to their home range. As well, when they first encounter the fence and do decide to follow it, a normal distribution is used to decide if they will proceed left or right. When they reach the boundary of their home range, they must decide to continue or not. At this point the food, cover and proximity to water bodies are degraded and these values are fed into a sigmoidal fuzzy logic function to determine if they continue. Obviously, this process is quite speculative and not based on any GPS data on the moose following fences. Since there is no GPS data available, the process, though, is highly theoretica.l is If GPS data will become available in the future, the process could be reworked.

There are eighteen scenarios and the eleventh is the correct allometrically-scaled one for the Highway 175 in the LWR. It was decided to extend the scenarios beyond the eleventh in order to determine if the number of wildlife passages reach a plateau after the eleventh or continue to increase. Obviously, the spacing of the wildlife passages using the entire 174km length of Highway 175 is not very practical, since the majority of the MVCs occurred in the northern and southern slopes and not on the central plateau which has an abundance of conifers which is not the moose's favourite tree type. It was thought

better, however, to space the underpasses using the entire length of the Highway 175 and not consider the habitat differences as important.

The seven response and five explanatory variables as well as the locations of the 100 model moose for each scenario will be used in redundancy analysis to produce tri-plot graphs. These tri-plot graphs that will determine which of the seven response and five explanatory variables are most important to each of the locations of the 100 model moose; for each scenario, the results will then be summarized to determine which of the response or explanatory variables have the overall most important impact of the 100 model model moose in each scenario. As the number of wildlife passages increase, as mentioned in the anticipated results, it is expected that the number of wildlife passages available and selected should become the most important explanatory and response variables, respectively. If this does not occur, however, and other variables are more important then we will have to reconsider the impact that wildlife passages have on the model moose.

The strengths of the first and revised ABMs are, firstly, that agent-based modelling in wildlife ecology is a bottom-up modelling simulation tool of great potential in wildlife ecology. The movement parameters and activity durations are based on the scientific literature by UQAR and MRNF researchers and Franzmann and Schwartz (2007) for both regular travel and travel to salt pools, resting, ruminating, and foraging. The power-law distribution for travel was based on an analysis of 12 real moose for the five months of summer in the LWR. Road avoidance for 90% of the model moose came from Laurian (2008a) and salt pool spatial memory came from a paper by Leblond *et al.* (2007b), which are both papers on the behaviours of real moose. Home range enforcement was

applied to the ABM in chapter 2 and will be used in the revised ABM as well, except when moose are travelling near fences.

There are three main weaknesses in my first and revised model. Firstly, in my first ABM there is no real bottom-up variability applied to the model moose except, as mentioned above, their road avoidance, their different habitat types in their home ranges and the randomness applied the final choice of the next forest polygon to travel to. Secondly, since the actual movement data for real moose by fences is not known, the parameters used for the algorithm is quite speculative in nature. If GPS data on moose and elk movement by fences could be obtained then we could establish movement criteria that are based on real calibration and validation information instead of using these speculative parameters. A third weakness in the revised ABM is that the linear distance of the 71 real home ranges was 7km, but when we look at the 21 real moose for the five summer months between May 1st and Sept. 30th, the linear distance is just 1.6km, a difference of 5.4km. Thus, if we take the real daily movement distance of the 71 real home ranges for the year we will find a lower number than 7km and that number could be used for a recalibration of the scenarios and thus choosing a lower number scenario than scenario #11.

Since, currently, my ABM is the only one about mitigation measures on MVCs in the world, no direct comparison can be made to another ABM on MVCs. I have used, however, the scientific literature of John Bissonette, Anthony Clevenger, Norris Dodd, Christian Dussault, Catherine Laurian, Mathieu Leblond, Mattias Olsson and Andreas Seiler, among others. Their work on large ungulates and other wildlife in Utah, BNP, Arizona, the LWR, and Sweden inspired my work on my ABM. I hope that my

anticipated results for the application of the allometric method near Highway 175 in the LWR will show that the method will work as a necessary first step in planning wildlife overpasses and underpass before local factors are applied to a project. In particular, I used the results of Dussault, Laurian and Leblond to plan my first ABM (in particular, road avoidance from Laurian and salt pool spatial memory from Leblond) which will still be the core of my revised ABM. For my revised ABM, I used the allometric method of Bissonette and Adair (2008) and then added various speculative processes for moose following fences.

Subsequent monitoring is needed using track pads, motion-detection cameras and GPS telemetry collars to understand how moose behave near wildlife passages. In particular, a program of GPS telemetry collars with a time-step of 30 minutes would be crucial in identifying the moose that decide to follow the fences and those that do not, and for how long they follow the fences before giving up. GPS telemetry collars would also be useful for identifying the moose that use the underpasses instead just having the motiondetection cameras that photograph the moose but cannot identify them. Without GPS data on the moose following fences, it is impossible to decide objectively how long to program into the ABM the distance the model moose will follow the fence or if it returns immediately to its home range. A few studies have used GPS telemetry collars on moose to study highway crossing rates at newly-constructed wildlife passages over and under highways (Dodd et al., 2007a; Olsson and Widen, 2008a) but none used the GPS data to study the moose's movement along fences. Their GPS data, however, probably does contain information about the moose's and elk's behaviour near fences, how many moose and elk followed the fences, and for how long. As well, the GPS data probably has the

information on how many moose and elk decided not to follow the fence and return to its home range. I have communicated with both researchers about their GIS datasets but I have not received any GIS datasets from them yet.

With appropriate calibration and validation data, however, and after local conditions such as topography, hot-spot analysis of moose road kill data, the density of the moose populations on the northern and southern slopes, and the plateau of the LWR, and the fiscal and engineering constraints placed on a highway upgrade project are taken into account, the placement of the moose underpasses can then be customized in the ABM based on these local conditions and constraints, and the individual variability of the moose following the fences and using the underpasses. As well, if we have the GPS telemetry data, we can determine how long the real moose follow fences and how many return to their home ranges and do not follow the fences at all. Then highway designers can use this revised ABM as a tool to optimize the number and location of wildlife passages for different species of wildlife.

3.11 Conclusion

In order to restore some highway permeability after roads have been placed on the landscape and most connectivity between moose sub-populations has been lost, it is essential to not only erect fences to exclude large fauna from the highway, which reduces wildlife highway permeability (but increases motorist safety). It is also important to place wildlife underpasses and overpasses using the allometric method that uses the linear daily distance determined by the square root of the moose's home range area. These measures together are expected to reduce human and moose injury and mortality and lead to both

fewer moose road passages at grade and more highway permeability using the underpasses.

Given fiscal constraints, local topography, and other local factors, it may not be possible to place wildlife passages on a strictly allometric basis, thus the spacing of the wildlife passages will probably be further apart (Beckmann *et al.* 2010). These constraints could only partially reduce the barrier effect of Route 175 and not increase the highway permeability to the extent that the allometrically-scaled wildlife passages would. If the wildlife underpasses are placed in known hotspots, however, it will reduce the MVCs thus improving motorist safety and moose survival. After the wildlife passages to ensure that this placement was effective. This monitoring can be accomplished using sand track pads in the wildlife underpasses, motion-detection ReConyx[™] cameras at the entrances and exits of the wildlife underpasses and most importantly, the installation of GPS telemetry collars on the moose to determine their behaviour near fences and underpasses and also to identify the moose that used the underpasses.

As stated in Beckmann *et al.* (2010), "General public knows little about the conflict between wildlife and transportation but conservation advocates are in a prime position to educate the public". It is important for both road ecology scientists and conservationists to reach out to the public and the transportation authorities and to educate them about the loss of connectivity that highways cause to wildlife populations such as moose. In Newfoundland, there are about 700 moose-vehicle collisions per year and there are no fences on the TCH. A class-action lawsuit against the government of Newfoundland by members of the public whose family members have been killed or paralysed in these

collisions has just been introduced in the Supreme Court of Newfoundland and Labrador. This lawsuit has been recently certified (CBC, 2011). Anthony Clevenger went to Newfoundland on March 31st, 2011, and told the government that neighbouring provinces were using exclusion fencing and underpasses on their highway and they should do the same (St.-John's Telegram. 2011). With the introduction of exclusion fencing and wildlife overpasses and underpasses for large fauna some degree of increased permeability can be achieved. It is the purpose of this revised ABM to use the allometric method and then quantity the expected/predicted increase in permeability that it can achieve.

This revised ABM could be applied to any other location where fences and underpasses are being constructed on highways to prevent MVCs, such as Sweden, Alaska, Ontario and Northeastern United States. Since the moose is essentially a solitary creature except for a female moose and its yearling, the revised ABM would have to be modified for the herd property of other members of the cervidae family of species. This could be done, and then, the new ABM would also be available to study the movement behaviour near roads of such members of the cervidae family as white-tailed deer, woodland caribou, and elk. The next steps for this work are to actually program the revised ABM, execute the eighteen scenarios and analyze the results.

4 CHAPTER 4: THESIS CONCLUSION

My ABM work, particularly in chapter 2 but perhaps eventually, chapter 3 as well, has contributed to the science of road ecology. The salt pool elimination and displacement ABM was the first in the world and, in general, its results agreed the results of other MRNF and UQAR researchers studying moose in the LWR. When the revised ABM in chapter 3 is programmed, executed and analyzed then the results may contribute to the science of road ecology as well. Proper data and information is essential and then road ecology scientists can join with developing highway construction projects to produce better results for humanity and wildlife. Projects such as the Banff National Park Project with its overpasses and underpasses have inspired new efforts in North America and around the world (Beckmann *et al.* 2010). Clear goals in planning new projects in transportation must be done with both motorist safety, and wildlife connectivity in mind. As well, road ecologists must reach out and give seminars, briefings and presentations to the general public so that they can support these new types of projects (Beckmann *et al.* 2010).

Moose-vehicle collisions are a problem throughout the circumpolar regions of the world. The focus of this thesis has been changing moose behaviour, in particular, using agent-based modelling to evaluate the effects of eliminating and relocating roadside salt pools with the competing factors of road avoidance and salt pool spatial memory (Chapter 2), and to evaluate the effects of the allometric method for placing wildlife underpasses and fences on Route 175 in the LWR (Chapter 3). The total elimination of roadside salt pools with road avoidance and salt pool spatial memory activated produced the moose road crossing reductions that were most similar to the real moose. Roadside

salt pools attract moose to the roads, thus their elimination will reduce MVCs. This elimination would cause the moose to return to the lakes and resume eating aquatic vegetation. In the new configuration of Highway 175, however, with the expansion from 2 to 4 lanes, the roadside salt pools will be drained in all cases. Transports Québec is creating compensation salt pools further from the Highway 175. The moose will have access to compensation salt pools within their home ranges. This ABM could be used with some modifications such as more individual variability based on gender and age for transportation planning for salt pool elimination and displacement in any circumpolar region that uses a lot of road-salt. As mentioned in chapter 2, the management implications following from the results of the first ABM are that a total elimination of roadside salt pools is the best alternative for both the moose and the drivers, but since Transports Québec is creating compensation salt pools they should be at least 500m from the right-of-way of the Highway 175 to eliminate the road avoidance factor.

In the second model, the allometric method was described and eighteen scenarios were created with increasing numbers of wildlife underpasses. The current situation in the LWR has six moose underpasses. This revised ABM has not been yet been programmed but the most probable hypothesis is that the results will show that the number of moose wildife passages will reach a plateau at the allometric-scaled scenario #11. This would be due, in part, to the overall density of moose populations in the LWR. There are only so many moose close to the highway 175 in the LWR so it is likely that the numbers of wildlife passages will reach a plateau at some density of underpasses. But until the ABM is executed and analyzed, we will not know if the model wildlife passages reach a plateau at some point or just keep increasing. A GPS telemetry program for the moose following

the fences and using the underpasses would be essential for reducing the speculative aspects of the revised ABM and instead using real GPS data to calibrate and validate the model moose movement behaviour near fences and underpasses. Thus, if the allometric method works and produces a plateauing effect after scenario #11, it will lead to good results.

The management implications for the two different anticipated results are as follows: in case of plateauing highway permeability, if the allometrically-scaled scenario #11 is before the plateau or is after the plateau, we can say that the allometric method is flawed because the curve plateaus after or before scenario #11. If, however, the allometricallyscaled scenario #11 coincides with the start of the plateau, then we can state that the allometric method works. In the case of the ever-increasing highway permeability, however, if the allometrically-scaled scenario #11 has no real effect, and we can state that the allometric method does not work in this case. Thus, if the allometrically-scaled scenario #11 coincides with the start of the plateau in figure 3.7b then we can state that the allometric method works, otherwise, we can only state that it is flawed or, in the case of figure 3.7a, it does not work at all.

Two of the weaknesses in my first and revised model are that in the first ABM there is no real bottom-up variability applied to the model moose except their different habitat types in their home ranges and the randomness applied the final choice of the next forest polygon to travel to. Secondly, in the revised ABM, since the actual movement data is for real moose by fences is not known, the parameters used for the algorithm is quite speculative in nature.

Finally, agent-based modelling in wildlife ecology has a strong potential and is a relatively recent method that can be used along with other classical ecological methods as statistical, GIS, and systems analysis using Stella[™], for example, at the population level. ABM can inform scientists, decision-makers, and the general public on issues with roads and wildlife (McLane *et al.* 2011). It is an approach that can be used to model the movement behaviour of any number of large terrestrial species to better determine outcomes for wildlife that must cross the highway to visit habitats on the other side of the highway for foraging, mating, dispersal, or birthing purposes. Though this is the only ABM on MVCs, there are other wildlife ecologists creating ABMs on other wildlife species such as woodland caribou, wolves, and whales, for example (Metsaranta, 2008; Musiania *et al.* 2010; Chion *et al.* 2011). As ABM usage increases in the fields of road ecology, wildlife ecology and geography, we should see many new and important results in these fields.

4.1 Future Research

In my future research, since my current ABM has no individual variability besides road avoidance and different habitat types in their home ranges, I will apply some more individual variability to the model moose mainly based on sex and age to complete the life cycle of the model moose using the following properties: good cover stands are less desired by males than females during spring, summer and early winter, moose trade off food availability with avoidance of deep snow and predators, females with calves differ from solitary female moose in that they seek protection from predation by choosing better cover, yearlings are kicked out just 2 weeks before birth of new moose to find their own home ranges, females search for isolated sites for birthing with good cover to reduce

stress and avoid predation, and in the rut season most male moose gradually stops eating, and they fight with other males to see which will dominate and have most of the access to the females (Franzmann and Schwartz. 2007). Further details can be found in the Appendix under the heading: Future Research.

Other processes that will be added to all scenarios are: yearling dispersal, birth, hunting by humans and predators such as wolves and bears, reduced highway maintenance budgets, gates left open and increased human traffic in large wildlife underpasses. The first three processes will produce a more complete lifecycle for the moose but the last three are more important in developing a more complete ABM with more emphasis on other causes for MVCs.

5 Bibliography

- AECOM Tecsult Inc. 2010. Suivi environnemental du projet d'amélioration de la route 175à quatre voies divisées – Grande faune 2009 : Efficacité des aménagements pourla grande faune. Rapport final présenté au ministère des Transports du Québec, à l'Université du Québec à Rimouski et au ministère des Ressources naturelles et de la Faune, Service de la faune terrestre et de l'avifaune. 35 p. et annexes. (en français.)
- AECOM Tecsult Inc. 2009. Suivi environnemental du projet d'amélioration de la route 175 à quatre voies divisées – grande faune 2008 : Efficacité des aménagements pour la grande faune. Rapport final présenté au Ministère des Transports du Québec, à l'Université Du Québec à Rimouski et au Ministère des Ressources Naturelles et de la Faune, Service de la faune terrestre et de l'avifaune. 33 pages et annexes. (en français.)
- Anselin, L., 2004. GeoDa an introduction to spatial data analysis. Spatial Analysis Lab, University of Illinois.
- Anwar S.M., Jeanneret C.A, Parrott L, and Marceau D.J. 2007. Conceptualization and implementation of a multi-agent model to simulate whale-watching tours in the St. Lawrence estuary in Quebec, Canada. *Environmental Modelling & Software*, 22(12):1775-87.
- Atkinson, R. P. D., Rhodes, C. J., Macdonald, D. W. and Anderson, R. M. 2002. Scalefree dynamics in the movement patterns of jackals. *Oikos*, 98: 134–140.
- BAPE. 2005. Rapport d'enquête et d'audience publique. Bureau d'audiences publiques sur l'environnement. Report nbr 214. (en français.)
- Benhamou S. 2007. How Many Animals Really Do The Lévy Walk? *Ecology*, 88(8), 1962–1969.
- Bennett, D.A., and Tang, W., 2006. Modeling adaptive, spatially aware, and mobile agents: Elk migration in Yellowstone. *International Journal of Geographical Information Science*. 20, 1039–1066.
- Beyer, H.L., 2004. Hawth's Analysis Tools for ArcGIS. http://www.spatialecology.com/htools Accessed June 19, 2009.
- Beckmann, J.P, Clevenger, A.P, Huijser, M, and Hilty J. 2010. *Safe Passages: Highways, Wildlife, and Habitat Connectivity.* Island Press. Washington, D.C.

- Bissonette J.A. and Adair W. 2008. Restoring habitat permeability to roaded landscapes with isometrically-scaled wildlife crossings. *Biological Conservation* 141(2):482-8.
- Bissonette J.A. and Cramer P.C. 2008. *Evaluation of the use and effectiveness of wildlife crossings*. Washington, D.C.: Transportation Research Board. Report # 615.
- Benhamou, S. 2007. How many animals really do the Levy walk? *Ecology*. 88(8) 1962-1969.
- Booth G. 1997. Gecko: A continuous 2-D world for ecological modeling. *Artificial Life Journal* 3(3):147-63.
- Bowman J, Jaeger J.A.G, and Fahrig L. 2002. Dispersal distance of mammals is proportional to home range size. *Ecology* 83(7):2049-55.
- Box, G. E. P. and Draper, N.R. 1987. *Empirical model-building and response surfaces*. Wiley. New York.
- Breton, L., Courtois, R., Dussault, C. *et al.* 2006. Étude du comportement de l'orignal par rapport aux axes routiers et aux clôtures électriques dans la réserve faunique des Laurentides. Québec : Ressources naturelles et faune Québec, Transports Québec; Rimouski : Université du Québec à Rimouski, 75p. (en français.)
- Brown D.G., Robinson D.T., An L., Nassauer J.I., Zellner M., Rand W., and Riolo R., Page S.E., Low B. 2008. Exurbia from the bottom-up: Confronting empirical challenges to characterizing complex systems. *GeoForum* 39(2):805-18.
- Carsignol, J. 2005. Aménagements et mesures pour la petite faune : guide technique, [Bagneux], SETRA. (en français.)
- CBC. 2011. Moose collision felt like hammer to head: Manning. June 10, 2011. http://www.cbc.ca/news/canada/newfoundland-labrador/story/2011/06/10/nl-fabianmoose-610.html. Accessed June 30, 2011.
- Chion C., Lamontagne P., Turgeon S., Parrott L., Landry J.-A., Marceau D.J., Martins C.C.A., Michaud R., Ménard N., Cantin G., and Dionne S. 2011. Eliciting cognitive processes underlying patterns of human-wildlife interactions for agent-based modelling. *Ecological Modelling*. 222 (14), 2213-2226.
- Clevenger A.P. and Waltho N. 2000a. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. *Conservation Biology* 14(1):47-56.

- Clevenger A.P., Wierzchowski J., Chruszcz B., and Gunson K. 2002b. GIS-generated, expert-based models for identifying wildlife habitat linkages and planning mitigation passages. *Conservation Biology* 16(2):503-14.
- Clevenger, A.P., Chruszcz, B., and Gunson, K.E., 2001. Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin*. 29, 646–653.
- Clevenger, A.P., Chruszcz, B., Gunson, K., and Wierzchowski, J. 2002a. *Roads and wildlife in the Canadian Rocky Mountain Parks - Movements, mortality and mitigation*. Final report to Parks Canada. Banff, Alberta, Canada.
- Clevenger AP. 2005. Conservation value of wildlife crossings: Measures of performance and research directions. *Gaia-Ecological Perspectives for Science and Society* 14(2):124-9.
- Clevenger A.P. and Waltho N. 2005. Performance indices to identify attributes of highway crossing structures facilitating movement of large mammals. *Biological Conservation* 121(3):453-64.
- Clevenger A.P., Chruszcz B., and Gunson K.E. 2001. Highway mitigation fencing reduces wildlife-vehicle collisions. *Wildlife Society Bulletin* 29(2):646-53.
- Clevenger A.P., Ford A.T., and Sawaya M.A. 2009. Banff wildlife crossings project: Integrating science and education in restoring population connectivity across transportation corridors. Final report to Parks Canada agency. Radium Hot Springs, British Columbia, Canada. 165 p.
- Clevenger, A.P., and Sawaya, M.A. 2010. Piloting a non-invasive genetic sampling method for evaluating population-level benefits of wildlife crossing structures. *Ecology and Society* **15**(1): 7. <u>http://www.ecologyandsociety.org/vol15/iss1/art7/</u>.
- Consortium Génivar-Tecsult. 2004. *Analyse globale de la problématique de la grande faune et la route 175*. étude d'impact du projet d'amélioration de la route 175 à 4 voies divisées du km 84 au km 227 (143 km) dans la Réserve Faunique des Laurentides et dans la ville de Saguenay. rapport final présenté au Ministère des Transports du Québec. (en français.)
- Corlatti L, Hacklaender K, and Frey-Roos F. 2009. Ability of wildlife overpasses to provide connectivity and prevent genetic isolation. *Conservation Biology* 23(3):548-56.
- Courtois, R., Labonte, J. and Ouellet, J.-P. 1998. Déplacements et Superficie du Domaine Vital de l'Orignal, Alces alces, dans l'Est du Quebec. Canadian-Field Naturalist,

Vol. 112 602–610. (en français.)

- Cramer P.C. and Portier K.M. 2001. Modeling Florida panther movements in response to human attributes of the landscape and ecological settings. *Ecological Modelling* 140:51-80.
- Deygout C, Gault A, Sarrazin F, and Bessa-Gomes C. 2009. Modeling the impact of feeding stations on vulture scavenging service efficiency. *Ecological Modelling* 220(15):1826-35.
- Dodd N.L., Gagnon J.W., Manzo A.L., and Schweinsburg R.E. 2007a. Video surveillance to assess highway underpass use by elk in Arizona. *Journal of Wildlife Management* 71(2):637-45.
- Dodd N.L., Gagnon J.W., Boe S., and Schweinsburg R.E. 2007b. Assessment of elk highway permeability by using global positioning system telemetry. *Journal of Wildlife Management* 71(4):1107-17.
- Dodd N.L., Gagnon J.W., Boe S., Manzo A.L., and Schweinsburg R.E. 2007c. Evaluation of measures to minimize wildlife-vehicle collisions and maintain permeability across highways: Arizona route 260. Final report 540. FHWA-AZ-07-540. Phoenix, Arizona, USA: Arizona Dept. of Transportation.
- Dray, S., Legendre P., and Peres-Neto P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbours matrices. (PCNM). _ Ecological Modelling. 196: 483-493.
- Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L., and Larochelle, J., 2004. Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience*. 11, 321–328.
- Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L., and Jolicoeur, H., 2005. Linking moose habitat use to limiting factors. *Ecography*. 28, 619–628.
- Dussault C., Poulin M., Courtois R., and Ouellet J.-P. 2006a. Temporal and spatial distribution of moose-vehicle accidents in the Laurentides Wildlife Reserve, Quebec, Canada. *Wildlife Biology* 12(4):415-25.
- Dussault, C., Courtois, R., and Ouellet, J.-P., 2006b. A habitat suitability index model to assess moose habitat selection at multiple spatial scales. *Canadian Journal of Forest Research*. 36, 1097–1107.

- Dussault C., Ouellet J.-P., Laurian C., Courtois R., Poulin M., and Breton L. 2007. Moose movement rates along highways and crossing probability models. *Journal of Wildlife Management*. 71(7):2338-45.
- Dyer, S.J., O'Neill, J.P., Wasel, and S.M., Boutin, S., 2002. Quantifying barrier effects of roads and seismic lines on movements of female woodland caribou in north-eastern Alberta. *Canadian Journal of Zoology* 80, 839–845.
- Environment Canada and Health Canada. (2001). *Priority substances list assessment report for road salts*. Retrieved March 26, 2008 from <u>http://www.hc-sc.gc.ca/ewh-semt/pubs/contaminants/psl2-lsp2/road salt sels voirie/index e.html</u>.
- ESRI, 2009. ArcView 9.3. Environmental Systems Research Institute Inc. Redlands, California.
- Fahrig, L., and Rytwinski T. 2009. Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and Society* 14(1): 21. http://www.ecologyandsociety.org/vol14/iss1/art21/.
- Forman R.T.T. and Alexander L.E. 1998. Roads and their major ecological effects. Annual Review of Ecology and Systematics 29:207-31.
- Forman R.T.T. 2000. Estimate of the area affected ecologically by the road system in the United States. *Conservation Biology* 14(1):31-5.
- Forman R.T.T. and Deblinger R.D.. 2000. The ecological road-effect zone of a Massachusetts (USA) suburban highway. *Conservation Biology* 14(1):36-46.
- Forman, R.T.T., Sperling, D., Bissonette, J.A., Clevenger, A.P., Cutshall, C.D., Dale, V.H., et al., 2003. Road Ecology: Science and Solutions. Island Press, Washington, DC.
- Foster M.L. and Humphrey S.R. 1995. Use of Highway Underpasses by Florida Panthers and Other Wildlife. *Wildlife Society Bulletin*, Vol. 23 (1). 95-100.
- Franzmann A.W. and Schwartz C.C.. 2007. *Ecology and Management of the North American Moose*. 2nd Edition ed. Denver. University Press of Colorado.
- Fraser D. and Thomas E.R. 1982. Moose-vehicle accidents in Ontario: Relation to road salt. *Wildlife Society Bulletin.* 10(3) :261-5.

- Gagnon J.W., Theimer T.C., Dodd N.L., Boe S., and Schweinsburg R.E. 2007a. Traffic volume alters elk distribution and highway crossings in Arizona. *Journal of Wildlife Management* 71(7):2318-23.
- Gagnon J.W., Theimer T.C., Dodd N.L., Manzo A.L., and Schweinsburg R.E. 2007b. Effects of traffic on elk use of wildlife underpasses in Arizona. *Journal of Wildlife Management* 71(7):2324-8.
- Girard I., Ouellet, J.-P., Courtois R., Dussault C., and Breton L. 2002. Effects of Sampling Effort Based on GPS Telemetry on Home-Range Size Estimations. *Journal of Wildlife Management*, 66(4), 1290-1300.
- Gilbert, N., 2008. Agent-Based Models. Sage Publications, Los Angeles, California.
- Gotelli, N.J., and Ellison, A.M., 2004. *A Primer of Ecological Statistics*. Sinauer Associates Inc., Sunderland, MA.
- Grimm V. 1999. Ten years of individual-based modelling in ecology: What have we learned and what could we learn in the future? *Ecological Modelling* 115(2-3):129-48.
- Grimm V. and Railsback S.F. 2005a. *Individual-based modeling and ecology*. Princeton: Princeton University Press.
- Grimm V., Revilla E., Berger U., Jeltsch F., Mooij W.M., Railsback S.F., Thulke H.H., Weiner J., Wiegand T., and DeAngelis D.L.. 2005b. Pattern-oriented modeling of agent-based complex systems: Lessons from ecology. *Science* 310(5750):987-91.
- Grimm V., Berger U., Bastiansen F., Eliassen S., Ginot V., Giske J., Goss-Custard J., Grand T., Heinz S.K., Huse G. *et al.* 2006. A standard protocol for describing individual-based and agent-based models. *Ecological Modelling* 198(1-2):115-26.
- Grimm V., Berger U., DeAngelis, D.L., Polhill, J.G., Giske, J., and Railsback S.F. 2010. ODD Protocol For Describing Individual-Based And Agent-Based Models: A First Update. *Ecological Modelling*. 221(23). 2760-2768.
- Groot Bruinderink, G.W.T.A., and Hazebroek, E., 1996. Ungulate traffic collisions in Europe. *Conservation Biology*. 10, 1059–1067.
- Grosman P.D., Jaeger J.A.G., Biron P.M., Dussault C., and Ouellet J.-P.. 2009. Reducing Moose–Vehicle collisions through salt pool removal and displacement: An agent-

based modeling approach. *Ecology and Society* 14(2). http://www.ecologyandsociety.org/vol14/iss2/art17/.

- Grosman P.D., Jaeger J.A.G., Biron P.M., Dussault C., and Ouellet J.-P.. 2011. Trade-off between road avoidance and attraction by roadside salt pools in moose: An agentbased model to assess measures for reducing moose-vehicle collisions. *Ecological Modelling*. 222(8) 1423-1435.
- Gunson K. 2007. Multi-scale spatiotemporal statistical analyses of moose-vehicle collisions in Vermont. United States New York: State University of New York College of Environmental Science and Forestry.
- Huijser M.P., McGowen P., Fuller J., Hardy A., Kociolek A., Clevenger A.P., Smith D., and Ament R.J.. 2008. Wildlife-vehicle collision reduction study: Report to Congress.
- Huijser M.P., Duffield J.W., Clevenger A.P., Ament R.J., and McGowen P.T.. 2009. Cost–Benefit analyses of mitigation measures aimed at reducing collisions with large ungulates in the United States and Canada: A decision support tool. *Ecology* and Society 14(2). 15 p.<u>http://www.ecologyandsociety.org/vol14/iss2/art15/</u>.
- Iuell, B., Bekker, G. J., Cuperus, R., Dufek, J., Fry, G., Hicks, C., Hlavác, V., Keller, V. B., Rosell, C., Sangwine, T., Torslov, N. and Wandall, B. le Maire (eds) (2003): Wildlife and traffic: A European handbook for identifying conflicts and designing solutions. KNNV Publishers.
- Jaeger J.A.G., Bowman J., Brennan J., Fahrig L., Bert D., Bouchard J., Charbonneau N., Frank K., Gruber B., and von Toschanowitz K.T.. 2005. Predicting when animal populations are at risk from roads: An interactive model of road avoidance behavior. *Ecological Modelling* 185(2-4):329-48.
- Jolicoeur, H., and Crête, M., 1994. Failure to reduce moose-vehicle accidents after a partial drainage of roadside salt pools in Québec. *Alces* 30, 81–89.
- Joyce T.L. and Mahoney S.P.. 2001. Spatial and temporal distributions of moose-vehicle collisions in Newfoundland. *Wildlife Society Bulletin* 29(1):281-91.
- Kramer-Schadt S., Revilla E., Wiegand T., and Breirenmoser U. 2004. Fragmented landscapes, road mortality and patch connectivity: Modeling influences on the dispersal of eurasian lynx. *Journal of Applied Ecology* 41:711-23.

- Langbein J. 2010. Pilot study to assess the potential of selected existing structures on the A30 and A38 trunk roads to provide safer crossing places for deer. The Deer Initiative. Deer Initiative Research Report 10/1. Langbein Wildlife Associates.
- Laurian, C., Dussault, C., Ouellet, J.-P., Courtois, R., Poulin, M., and Breton, L., 2008a. Behavioural adaptations of moose to roadside salt pools. *Journal of Wildlife Management* 72, 1094–1100.
- Laurian, C., Dussault, C., Ouellet, J.-P., Courtois, R., Poulin, M., and Breton, L., 2008b. Behavior of moose relative to a road network. *Journal of Wildlife Management* 72, 1550–1557.
- Leblond M., Dussault C., Ouellet J.-P., Poulin M., Courtois R., and Fortin J. 2007a. Electric fencing as a measure to reduce moose-vehicle collisions. *Journal of Wildlife Management* 71(5):1695-703.
- Leblond M., Dussault C., Ouellet J.-P., Poulin M., Courtois R., and Fortin J. 2007b. Management of roadside salt pools to reduce moose-vehicle collisions. *Journal of Wildlife Management* 71(7):2304-10.
- Leblond, M., Dussault, C., and Ouellet, J.-P., 2010. What drives fine-scale movements of large herbivores? A case study using moose. *Ecography* 33 (6), 1102–1112.
- Legendre, P. and Legendre, L. 1998. *Numerical Ecology*. 2nd English Edition. Elsevier Science BV. Amsterdam.
- Legendre, P., 2010. 2-way ANOVA and t-tests with permutations. http://www.bio.umontreal.ca/legendre/. Accessed October 10, 2010.
- Malo J.E., Suarez F., and Diez A.. 2004. Can we mitigate animal-vehicle accidents using predictive models? *Journal of Applied Ecology* 41(4):701-10.
- Mata C, Hervas I., Herranz, J., Suarez F., and Malo J.E. 2008. Are motorway wildlife passages worth building? Vertebrate use ofroad-crossing structures on a Spanish motorway *Journal of Environmental Management*. 88: 407–415
- Metsaranta, J.M. 2008. Assessing factors influencing the space use of a woodland caribou Rangifer tarandus caribou population using an individual-based model. *Wildlife Biology* 14: 478-488.
- McLane A.J., Semeniuk C., McDermid G.J., and Marceau D.J. 2011. The role of agentbased models in wildlife ecology and management. *Ecological Modelling*, 222, (8) 1544-1556.

- Miller, B.K., and Litvaitis, J.A., 1992. Use of roadside salt licks by moose, *Alces alces*, in northern New Hampshire. *Canadian Field-Naturalist*. 106, 112–117.
- Mohr, C.O., "Table of Equivalent Populations of North American Mammals." *American Midland Naturalist*, Vol. 37 (1947) 223–249.
- MRNF, 2010. Inventaires aériens d'orignaux dans les réserves fauniques des Laurentides et de Portneuf. <u>http://www.mrn.gouv.qc.ca/capitale-nationale/orignaux.jsp</u>. Accessed November 9, 2010.
- MTQ. 2009. Grands Projets: Axe routier 73 / 175. <u>http://www.mtq.gouv.qc.ca/portal/page/portal/grands_projets/trouver_grand_projet/axe_routier_73_175</u>. (en français.)
- Musiania M., Anwar S.M., McDermid G.J., Hebblewhite, M., and Marceau, D.J.. 2010. How humans shape wolf behavior in Banff and Kootenay National Parks, Canada. *Ecological Modelling* 221(19). 2374–2387.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. *PNAS* 105, 19052–19059.
- Olsson M.P.O. and Widen P. 2008a. Effects of highway fencing and wildlife crossings on moose alces alces movements and space use in southwestern Sweden. *Wildlife Biology* 14(1):111-7.
- Olsson M.P.O., Widen P., and Larkin J.L. 2008b. Effectiveness of a highway overpass to promote landscape connectivity and movement of moose and roe deer in Sweden. *Landscape Urban Planning* 85(2):133-9.
- Parks Canada Website, Banff National Park of Canada, Highway Fencing and Wildlife Crossings. 2010a. <u>http://www.pc.gc.ca/eng/pn-np/ab/banff/docs/routes/sec3.aspx</u>. Accessed June 28, 2011.
- Parks Canada Website, Banff National Park of Canada, Highway Fencing and Wildlife Crossings, Emerging Principles of Road Ecology. 2010b. <u>http://www.pc.gc.ca/eng/pn-np/ab/banff/docs/routes/sec3.aspx</u>. Accessed June 29, 2011.
- Parrott, L. 2008. Ecological Informatics: Adaptive Agents. In: Jørgensen, S.E. and Fath, B. (Eds.), Encyclopedia of Ecology, vol. 1 of 5, pp. 47-51. Oxford: Elsevier.

Peterson, RL. 1955. North American Moose. Toronto: University of Toronto Press.

- Pfister H. P., Keller V., Heynen D., And Holzgang O. 2002. Wildtierökologische Grundlagen im Strassenbau = Bases écologiques pour la faune dans la construction routièreEcological basis for fauna in the road building. Strasse und Verkehr. 88(3), 101-108 (in German)
- R Development Core Team, 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <u>http://www.R-project.org</u>.
- Railsback S.F. and Harvey B.C. 2002. Analysis of habitat-selection rules using an individual-based model. *Ecology* 83(7):1817-30.
- Railsback, S.F., Lytinen, S.L., and Jackson, S.K., 2006. Agent-based simulation platforms: review and development recommendations. *Simulation* 82, 609–623.
- Rea R.V. and Child K.N. 2007. Wildlife Data Centre Featured Species Moose. *Wildlife Afield* 4(2). 285-317.
- van der Ree, R, van der Grift, E., Mata, C., and Suarez, F. 2007. Overcoming the barrier effect of roads – how effective are mitigation strategies? An international review of the use and effectiveness of underpasses and overpasses designed to increase the permeability of roads for wildlife. Proceedings of the 2007 International Conference on Ecology and Transportation; 2007; Raleigh, NC: Irwin Center for Transportation and the Environment, North Carolina State University.
- Renecker, L.A., and Hudson, R.J., 1989. Seasonal activity budgets of moose in aspen dominated boreal forests. *Journal of Wildlife Management* 53, 296–302.
- Renecker, L.A., and Schwartz, C.C., 2007. Food habits and feeding behaviour. In: Franzmann, A.W., Schwartz, C.C. (Eds.). Ecology and Management of the North American Moose. University Press of Colorado, Boulder, Colorado, USA. 403–439.
- Repast Simphony, 2008. Repast Organization for Architecture and Design. <u>http://repast.sourceforge.net</u>. Accessed June 19, 2009.
- Reynolds, A.M., and Rhodes, C.J., 2009. The Levy flight paradigm: random search patterns and mechanisms. *Ecology* 90, 877–887.
- Riley S.P.D., Pollinger J.P., Sauvajot R.M., York E.C., Bromley C., Fuller T.K., and Wayne R.K.. 2006. A southern California freeway is a physical and social barrier to gene flow in carnivores. *Molecular Ecology* 15(7):1733-41.

- Roedenbeck I.A., Fahrig L., Findlay C.S., Houlahan J.E., Jaeger J.A.G., Klar N., Kramer-Schadt S., and van der Grift E.A. 2007. The Rauischholzhausen Agenda for Road Ecology. *Ecology and Society* 12(1):11. http://www.ecologyandsociety.org/vol12/iss1/art11/.
- Roedenbeck, I.A. 2007. Landscape-scale Effects of Roads on Wildlife. P.h. D. Thesis, Giessen
- Romin, L.A., and Bissonette, J.A., 1996. Deer-vehicle collisions: status of state monitoring activities and mitigation efforts. *Wildlife Society Bulletin*. 24, 276–283.
- Samson, C., C. Dussault, C., Courtois, R. and Ouellet, J.-P.. 2002. Guide d'aménagement de l'habitat de l'orignal. Société de la faune et des parcs du Québec, Fondation de la faune du Québec et ministère des Ressources naturelles du Québec, Sainte-Foy. 48 p. (en français.)
- Schelling T.C. 1969. Models of segregation. *The American Economic Review*. Papers and Proceedings of the Eighty-First Annual Meeting of the American Economic Association. 59(2):488-93.
- Schick, R. S., Loarie, S. R., Colchero, F., Best, B. D., Boustany, A., Conde, D. A., Halpin, P. N., Joppa, L. N., McClellan, C. M. and Clark, J. S. 2008. Understanding movement data and movement processes: current and emerging directions. *Ecology Letters*. 11: 1338–1350. doi: 10.1111/j.1461-0248.2008.01249.x.
- Schmitz O.J. and Adair W. 2000. Combining field experiments and individual-based modelling to identify the dynamically relevant organizational scale in a field system. *Oikos* 89:471-84.
- Seiler A. 2004. Trends and spatial patterns in ungulate-vehicle collisions in Sweden. *Wildlife Biology* 10(4):301-13.
- Seiler A. 2005. Predicting locations of moose-vehicle collisions in Sweden. *Journal of Applied Ecology* 42(2):371-82.

Stoner D. 1925. The toll of the automobile. Science 41(1568):56-7.

St.-John's Telegram. 2011. Province condemned for inaction on moose dangers. April 1, 2011. <u>http://www.thetelegram.com/News/Local/2011-04-01/article-2388483/Province-condemned-for-inaction-on-moose-dangers/1</u>. Accessed June 30, 2011.

- Tang, W., and Bennett, D.A., 2010. Agent-based modeling of animal movement: a review. *Geographic Compass* 4, 682–700.
- Taylor, P. D., Fahrig, L., Henein, K. and Merriam, G. 1993. Connectivity is a vital element of landscape structure. *Oikos* 68:571–573.
- Tesfatsion, L. (2008). General Software and Toolkits, Agent-Based Computational Economics (ACE) and Complex Adaptive Systems (CAS). [cited 2008 January 15]. Available from: <u>http://www.econ.iastate.edu/tesfatsi/acecode.htm</u>.
- Transports Québec, Tecsult-AECOM, and Ministry of Ressources naturelles et de la faune, 2009. GIS datasets for the LWR and Route 175. Quebéc.
- Trombulak S.C. and Frissell C.A. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* 14(1):18-30.
- Viswanathan, G.M., Buldyrev, S.V., Havlin, S., da Luz, M.G.E., Raposo, E.P., and Stanley, H.E., 1999. Optimising the success of random searches. *Nature* 401, 911– 914.
- White, P. 2007. GETTING UP TO *SPEED*: A Conservationist's Guide To Wildlife and Highways. Washington, D.C. Defenders of Wildlife.

6 Appendix

6.1 Redundancy Analysis and Forward Selection not Presented in Chapter 2

The following redundancy analysis, forward selection and the Comparison of R^2 and adjusted R^2 for scenarios 1, 6, 11, and 16 and the real moose were in my term paper for my course on **Analyse quantitative des données biologiques**, given by Prof. Legendre at the Université de Montréal, last year (Grosman 2010, unpublished) but not used for our article in *Ecological Modelling* in Chapter 2.

6.2 Methods

6.2.1 Redundancy Analysis

Redundancy analysis (RDA) is a form of canonical analysis that is a "direct extension of multiple regression to the modelling of multivariate data" (Legendre and Legendre, 1998). One first forms a Y matrix of response variables and a X matrix of explanatory variables. RDA assumes that there is a causal relationship from the explanatory variables to response variables. **rdaTest**, the R function from the rdaTest library:

<u>http://www.bio.umontreal.ca/Casgrain/prog/labo/fonctions_r/rdaTest_1.7.zip</u>, used in this study has the following inputs:

- 1. Y: a matrix which represents the response table,
- 2. X, a matrix which represents the explanatory variables,
- 3. W: a matrix which represents an optional table of co-variables,
- scale.Y: =TRUE or FALSE. TRUE means Y should be standardized, i.e. the variables are of different physical dimensions or FALSE which means the values should only be centred on their means,

- test.F: NULL is the default and then the user is asked if he wants to test the F statistic. If TRUE or FALSE is indicated then the program follows that instruction,
- nperm: gives the number of permutations for the F-statistic. If NULL, then the program asks the user; if nperm = 0, then the permutation tests are not executed; if a positive value is entered then that number of permutation tests are executed,
- 7. silent: if FALSE, then the output is displayed on the R console.

Since in this analysis, both the X and Y matrices were centred and standardized before being submitted to the **rdaTest** R function, the **scale** parameter was left at its default. The **scale**(X.mat, center=T, scale=T) R function was used instead of the **apply**(X.mat, 2, scale, center=TRUE, scale=TRUE) because the **apply** R function stripped off the moose identifications and replaced them with site numbers but the **scale** R function preserved them. All other defaults were used, so the program asked for the F-statistic to be performed, the answer was **Yes** and the number of permutation tests was set to **999**. The **rdaTest** R function used for the 5 RDA was of the following format:

rdaMM.out = rdaTest(Y, X).

After execution, the **rdaTest** R function produces a number of immediate outputs and the result of printing the **rdaMM.out** object:

 the eight (real moose) or nine (model moose) explanatory variables X matrix's variance inflation factors. If a value is equal to 0 then that variable is completely collinear. for; the value is 0 for entirely collinear variables. The co-variables are not included in this calculation,

- 2. the R^2 and adjusted R^2 values,
- 3. the F statistic and the p-value of the 999 permutation tests,
- 4. a list of:
 - i. number of objects,
 - ii. number of response variables,
 - iii. number of explanatory variables,
 - iv. number of canonical eigenvalues, and
 - v. total variance.
- 5. The five canonical eigenvalues,
- The relative eigenvalues calculated as a percentage of the total variance (5 values),
- 7. the cumulative percentage variance of the species data (5 values),
- 8. a U matrix of canonical eigenvectors normalized to 1 with scaling #1 preserving Euclidean distances for the five response variables,
- a U matrix of canonical eigenvectors normalized to square root of the eigenvalue with scaling #2 preserving relationships between variables for the five response variables.
- a F matrix of the moose scores with scaling #1, preserving Euclidean distances for the 5 axes. It is computed by multiplying the eigenvalues by the centered and scaled Y matrix,
- a Z matrix of fitted object scores with scaling #1, preserving Euclidean distances for the 5 axes. It is computed by multiplying the eigenvalues by the fitted values of the centered and scaled Y matrix ,

- 12. a second F matrix of object scores but with scaling #2 preserving relationships between variables for the 5 axes,
- a second Z matrix of fitted object scores with scaling #2 preserving relationships between variables for the 5 axes,.
- 14. a bi-plot scores of eight or nine explanatory variables with scaling #1,preserving Euclidean distances for the 5 axes,
- 15. a bi-plot scores of eight or nine explanatory variables with scaling #2 preserving relationships between variables for the 5 axes,
- a table of cumulative fit (in percent) per moose as fraction of variance of moose for the 5 response variables,
- a vector of that explains the amount of variance for a total percent fit per moose for the 5 response variables,
- 18. the F test probability,
- 19. the number of permutation tests performed, 999,
- 20. the probability (p-value) associated with the F test,
- 21. the original X matrix but after it has been centered and scaled for use by the plotting function,
- 22. R^2 (unadjusted).

Using the **plot.rdaTest** R function, a tri-plot graph is produced with both the response variables, explanatory variables and the moose identifications. I can then examine this triplot to determine which moose are most affected by which response variables and which explanatory variables.

Since both the Y and X matrices of all the RDAs have been centered and standardized, the arrow length does not show the effect size, however, the arrows do indicate the direction and loadings on the x and y canonical axes.

The **rdaTest** R function was executed five times and five tri-plots were produced using the following command : **plot.rdaTest(rda.out, scaling=2, mul.env=1.75, mul.spe=1.75)**, scaling = 1 means that the Euclidean distances between the site locations are preserved and scaling = 2 is called a correlation bi-plot and means that the relationship between the response variables are preserved, the environmental and species (response variables) arrows were multiplied by 1.75 to make them easier to read. These tri-plots are included in the **Results** section:

- 1. the 21 real moose,
- 2. the 40 model moose: scenario #1,
- 3. the 40 model moose: scenario #6,
- 4. the 40 model moose: scenario #11, and
- 5. the 40 model moose: scenario #16.

6.2.2 Construction of the X and Y Matrices for the RDA analysis of the Real and Model Moose

Real Moose:

There were 5 response variables with the animal collar id: road crossings, food, cover, distance travelled in 5 months, salt pools in buffered home range. There were 8 environmental variables with the animal collar id: food quality, cover quality, Proximity to Salt Pools, Proximity to Water Bodies, Slope, number of Salt pools in home range,

intersection with road: Yes or no, percentage of forest polygons within 500m of the roads.

Model Moose:

There were 5 response variables with the animal collar id: road crossings, food, cover, distance travelled in 5 months, average number of salt pools found in buffered home range. There were 9 environmental variables with the animal collar id: food, cover, proximity to salt pools, proximity to water bodies, slope, number of salt pools in home range, intersection with road: Yes or no, percentage of forest polygons within 500m of the roads, percentage of forest polygons within 75m of the roads.

Real Moose : X Matrix

- 1. In ArcGIS, the 21 real moose home ranges were buffered outwards by 625m.,
- 2. The forest polygons within the 625m-buffered home ranges were selected,
- 3. The averages of Slope, Proximity to Salt Pools, and Proximity to Water Bodies were calculated using the statistics function in ArcGIS,
- the percentage of forest polygons within 500m of Highway 175 and number of Salt pools within its home range were determined using the Select by Location function in ArcGIS,
- 5. whether or not the home range intersected Highway 175 was determined visually,
- 6. the following eight attributes were used for each of the 21 real moose for these selected forest polygons:
 - a. Food quality average,

- b. Cover quality average,
- c. Proximity to Salt Pools average,
- d. Proximity to Water Bodies average,
- e. Slope average,
- f. Number of Salt pools within its home range,
- g. whether or not the home range intersected Highway 175, and
- h. the percentage of forest polygons within 500m of Highway 175.
- 7. On the tri-plot, these eight parameters are identified as follows:
 - Food Available, Cover Available, ProxSP, ProxWB, Slope, Salt Pools
 Available, Intersection, and Road500m.

Real Moose : Y Matrix

- 1. In ArcGIS, 21 real moose home ranges were buffered outwards by 625m,
- The real moose locations were joined to the selected forest polygons for the home range to produce a shapefile that included both the moose locations with its forest polygon information,
 - 3. the following five attributes were calculated for each of the 21 real moose:
 - a. Number of crossings,
 - b. The average of the food quality at each forest polygon that the real moose visited,

- c. The average of the cover quality at each forest polygon that the real moose visited,
- d. the distance in meters that the real moose travelled from May 1^{st} to Sept 30^{th} , and
- e. The number of salt pools that were visited.
- 4. On the tri-plot, these five parameters are identified as follows:
 - Crossings, Food Selected, Cover Selected, Distance, and Salt Pools Selected.

Model Moose : X Matrix

- 1. In ArcGIS, 40 model moose home ranges were buffered outwards by 625m.
- 2. The forest polygons within the 625m-buffered home ranges were selected.
- the following nine attributes were calculated for each of the 40 model moose for scenario #1 for these selected forest polygons:
 - a. Food quality average,
 - b. Cover quality average,
 - c. Proximity to Salt Pools average,
 - d. Proximity to Water Bodies average,
 - e. Slope average,
 - f. Number of Salt pools within its home range,

- g. whether or not the home range intersected Highway 175,
- h. the percentage of forest polygons within 500m of Highway 175, and
- i. the percentage of forest polygons within 75m of Highway 175.
- 4. On the tri-plot, these nine parameters are identified as follows:
 - a. Food Available, Cover Available, ProxSP, ProxWB, Slope, Salt Pools
 Available, Intersection, Road500m and RoadCover75m.

Model Moose : Y Matrix

- 1. In ArcGIS, the 40 model moose home ranges were buffered outwards by 625m.
- Using the reports produced by the model, four Java utility programs were created to join the Distance Travelled, Habitat Use, Salt Pool Discovery and Road Crossing text files into four files per scenario.
- the following five attributes were calculated for each of the 40 model moose for scenario #1:
 - a. Average number of crossings,
 - The average food quality at each forest polygon that the model moose visited,
 - c. The average cover quality at each forest polygon that the model moose visited,

- d. the average distance in meters that the model moose travelled from May 1^{st} to Sept 30^{th} , and
- e. The average number of salt pools that were visited.
- 4. On the tri-plot, these five parameters are identified as follows:
 - Crossings, Food Selected, Cover Selected, Distance, and Salt Pools Selected.

6.3 Forward Selection of Parameters

I used forward.sel of the packfor library <u>http://r-forge.r-</u> project.org/R/?group_id=195"http://r-forge.r-project.org/R/?group_id=195 (Dray *et al.* 2006), to perform the forward selection of variables in the real moose RDA and the model moose`s scenario #1 RDA.

Forward selection starts with no explanatory variables in the model and adds one variable at a time until the R2, adjusted R2 value, alpha value, the R2more parameter, a large drop in F-statistic or the number of selected variables is reached. In particular, the adjusted R2 value is a good criterion for stopping the forward selection procedure. the addition of the adjusted R2 value to the alpha value does result in better model selection (Blanchet *et al.* 2008). If the R2of the variable is below the R2more parameter the method stops. The variables are added based on their size of their R2 value, as long as their p-value is below the α level set in the input parameters of **forward.sel** (the default α for **forward.sel** is 0.05). I am generally trying to satisfy the principle of parsimony (Ockham's razor) where unnecessary assumptions or variables should not be proposed in

a hypothesis or , in other words, keep it as simple as possible while still, adequately, explaining the solution to the problem.

This **forward.sel** method of the **packfor** library has two improvements over the forward selection method in Canoco (ter Braak and Šmilauer, 2002) which had a highly inflated Type I error (in other words, falsely rejecting a correct null hypothesis and an overestimation of the amount of explained variance (Blanchet *et al.* 2008). Forward selection and stepwise selection, in general, can only give some indication of the important variables in the model; but since the statistical computation is not independent, the outputs should not be tried as final but only as guidance (Legendre and Legendre, 1998). Also, all previous selected variables are kept in the results even though they may have contributed only a small amount of the R^2 compared to some of the other variables selected later in the method.

Forward Selection is similar to the procedure in CANOCO but is based on permutation procedure using residuals from the reduced model. Y is multivariate, with five response variables. As well, there is a parametric version of forward selection, **forward.sel.par,** that does not use the permutation tests. I also use this R function for the real moose and the model moose of scenario #1.

I used the following parameters for the **forward.sel** R function for the real moose: **forward.sel(Y, X, nperm =999, R2thresh = 0.7848816, adjR2thresh=0.6414693, Xscale = FALSE, Yscale = FALSE, Ycenter = FALSE),** where R2thresh and adjR2thresh are equal to the R² and adjusted R² of the **rdaTest** output for the real moose, the scaling and centering parameters are set to FALSE since these matrices were already

scaled and centered before the **rdaTest** was performed. The default R^2 more parameter is set to 0.001 and the α is set to 0.05.

I used the following parameters for the forward.sel R function for the model moose of

scenario #1:forward.sel(Y, X, nperm =999, R2thresh = 0.6788635, adjR2thresh=0.5825226, Xscale = FALSE, Yscale = FALSE, Ycenter = FALSE), where R2thresh and adjR2thresh are equal to the R² and adjusted R² of the rdaTest output for the model moose of scenario #1, the scaling and centering parameters are set to FALSE since these matrices were already scaled and centered before the rdaTest was performed.

I used the following parameters for the **forward.sel.par** R function for the real moose: **forward.sel(Y, X, R2thresh = 0.7848816, adjR2thresh=0.6414693, Yscale = FALSE)**, where R2thresh and adjR2thresh are equal to the R^2 and adjusted R^2 of the **rdaTest** output for the real moose, the scaling of matrix Y was set to FALSE but it was standardized during the process.

I used the following parameters for the **forward.sel.par** R function for the model moose of scenario #1:

forward.sel(Y, X, R2thresh = 0.6788635, adjR2thresh=0.5825226, Yscale = FALSE), where R2thresh and adjR2thresh are equal to the R^2 and adjusted R^2 of the rdaTest output for the model moose of scenario #1, the scaling of matrix Y was set to FALSE but it was standardized during the process.

Finally, I ran the **rdaTest** function on three other model scenarios that had all 36 roadside salt pools present, namely scenario #6 (road avoidance behaviour on, salt pool spatial memory off), scenario #11 (road avoidance behaviour off, salt pool spatial memory on),

and scenario #16 (road avoidance behaviour off, salt pool spatial memory off). I then compared the R^2 and adjusted R^2 values for the four model scenarios with all 36 roadside salt pools present, scenarios #1, #6, #11, and #16 and compared them to the R^2 and adjusted R^2 values of the real moose **rdaTest** results. The purpose of these tests is to see if these other scenarios produced similar R^2 and adjusted R^2 values to the real moose and the model moose of scenario #1, and similar tri-plots to the real moose and scenario #1.

6.4 Results

6.4.1 Redundancy Analysis graphs of real moose and scenarios #1, #6, #11, and #16

The tri-plots of the five RDA results for the real moose and scenarios #1, #6, #11, and #16 show quite a similar structure for the environmental and response variables, particularly, for the **FoodAvailable**, **FoodSelected**, **CoverAvailable** and **CoverSelected** arrows (Figures A.1 - A.5). As well, for the scenarios #1, and #11, with the salt pool spatial memory factor on, the **SaltPoolsAvailable** and **SaltPoolsSelected** arrows are in similar locations. When this factor is turned off in scenario #6 and #16, these arrows are reduced in size and are also in similar locations.

An analysis was performed on the tri-plots for the real moose and scenario #1's model moose, to determine for the 21 real moose (

Table A.1. For the RDA tri-plot of the 21 real moose, this table presents the response and explanatory variables that each real moose was closest to; in some cases the real moose has more than one arrow close to it. Table A.2. For the RDA tri-plot of the 40 model moose in Scenario #1, this table presents the response and explanatory variables that each real moose was closest to, in some cases, the model moose has more than one arrow close to it.

which shows explanatory and response variables were closest. The tri-plots for scenarios #6, #11 and #16 were not further analyzed.

For the 21 real moose, 8 moose were closest to the explanatory variable, **ProxSP** or proximity to salt pools, and 6 moose were closest to the explanatory variable and response variable, **FoodAvailable** and **FoodSelected**, respectively. There were three moose closest to the **CoverAvailable** and **CoverSelected** variables. All the other variables had just one or two variables closest to them. Thus, one can conclude that **ProxSP**, **FoodAvailable** and **FoodSelected** had the highest effect on the real moose. The p-value associated with the permutation tests was 0.001, thus highly significant. The first 4 of the five eigenvalues had a percentage variance of 36.89882, 25.75355, 10.14533, and 5.601632 for a cumulative total of 78.39934 compared to the R² of 0.7848816.

For the 40 model moose in scenario #1, 21 were closest to the **FoodAvailable** and **FoodSelected** variables, 9 were closest to the explanatory variable, **ProxWB**, or proximity to water bodies, and the response variable, **distance**, had 8 model moose closest to it and all of the explanatory variables had 6 moose each while the remaining response variables, **SaltPoolsSelected** and **Crossings** had 6 and 2 moose closest to them, respectively. Thus, one can conclude that **ProxWB**, **FoodAvailable** and **FoodSelected** had the highest effect on the model moose. Since the weight on the **FoodSelected** variable was set at 0.45, and there are 2,262 of 10,575 that have highest value of 5, that is not a surprising result and though, the weight on **ProxWB** was set to just 0.10, there are a

lot of water bodies in the study area, so a large number of forest polygons (2,836 of 10,575) would have a value of 5, representing that it is adjacent to a water body. The p-value associated with the permutation tests was 0.001, thus highly significant. The first 4 of the five eigenvalues had a percentage variance of 44.41253, 15.59495, 5.181138, and 2.258358 for a cumulative total of 67.44697 compared to the R^2 of 0.6788635.

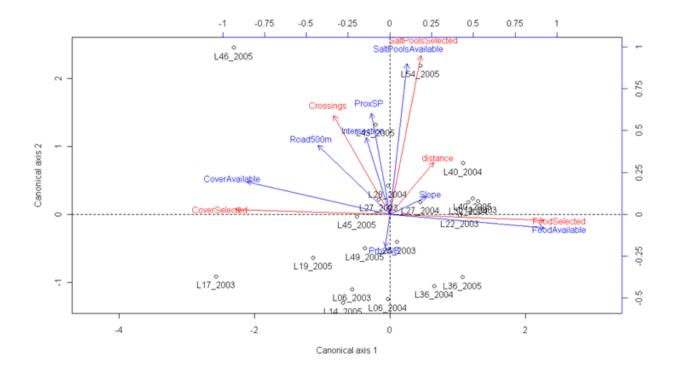


Figure A.1. Redundancy Analysis tri-plot of Real Moose. The red arrows and labels represent the 5 response variables: Food Selected, Cover Selected, Crossings distance, and Salt Pools Selected. The blue arrows and labels represent the 8 environmental variables: Food Available, Cover Available, Slope, ProxSP, ProxWB, Road500m, Intersection, and Salt Pools Available. The 21 real moose ids are positioned nearest to the variables that affected them the most. All of the environment (X matrix) and species (Y matrix) arrows in the 5 graphs were multiplied by 1.75 so that they could be more easily read.

Response Variables								
FoodSelected	L40_2005	L36_2005	L36_2004	L32_2004	L22_2003	L13_2003		
CoverSelected	L45_2005	L19_2005	L17_2003					
SaltPoolsSelected	L54_2005	L28_2004						
Crossings	L46_2005							
distance	L40_2004							
Explanatory Variables								
FoodAvailable	L40_2005	L36_2005	L36_2004	L32_2004	L22_2003	L13_2003		
CoverAvailable	L45_2005	L19_2005	L17_2003					
SaltPools Available	L54_2005	L28_2004						
ProxWB	L49_2005	L36_2005	L36_2004	L25_2003	L19_2005	L14_2005	L06_2004	L06_2003
ProxSP	L43_2005							
Road500m	L46_2005	L27_2003						
Intersection	L43_2005							
Slope	L27_2004	L13_2003						

Table A.1. For the RDA tri-plot of the 21 real moose, this table presents the response and explanatory variables that each real moose was closest to; in some cases the real moose has more than one arrow close to it.

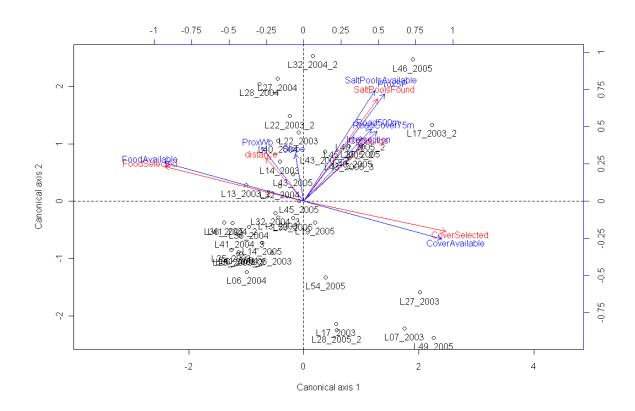


Figure A.2. Scenario #1. Redundancy Analysis tri-plot of Model Moose. The red arrows and labels represent the 5 response variables: Food Selected, Cover Selected, Crossings distance, and Salt Pools Selected. The blue arrows and labels represent the 9 environmental variables: Food Available, Cover Available, Slope, ProxSP, ProxWB, Road500m, RoadCover75m, Intersection, and Salt Pools Available. The 40 real moose ids are positioned nearest to the variables that affected them the most. All of the environment (X matrix) and species (Y matrix) arrows in the 5 graphs were multiplied by 1.75 so that they could be more easily read.

Response Variables									
FoodSelected	L53_2005	L45_2005	L43_2005	L41_2004_3	L41_2004_2	L41_2004	L36_2005		
	L36_2004	L32_2004_3	L32_2004_2	L32_2004	L28_2005	L25_2003_2	L25_2003		
	L14_2005	L14_2003	L13_2003_2	L13_2003	L06_2004	L06_2003_2	L06_2003		
CoverSelected	L54_2005	L49_2005	L28_2005_2	L27_2003	L19_2005	L17_2003	L07_2003		
SaltPoolsSelected	L46_2005	L45_2005_2	L43_2005_3	L43_2005_2	L40_2005_2	L40_2005			
Crossings	L45_2005_2	L17_2003_2							
distance	L45_2005	L43_2005	L40_2004	L32_2004	L28_2004	L27_2004	L22_2003_2	L22_2003	
Explanatory Variables									
FoodAvailable	L53_2005	L45_2005	L43_2005	L41_2004_3	L41_2004_2	L41_2004	L36_2005		
	L36_2004	L32_2004_3	L32_2004_2	L32_2004	L28_2005	L25_2003_2	L25_2003		
	L14_2005	L14_2003	L13_2003_2	L13_2003	L06_2004	L06_2003_2	L06_2003		
CoverAvailable	L54_2005	L49_2005	L28_2005_2	L27_2003	L19_2005	L17_2003	L07_2003		
SaltPools Available	L46_2005	L45_2005_2	L43_2005_3	L43_2005_2	L40_2005_2	L40_2005			
ProxWB	L45_2005	L43_2005	L40_2004	L32_2004	L28_2004	L28_2004	L27_2004	L22_2003_2	L22_2003
ProxSP	L46_2005	L45_2005_2	L43_2005_3	L43_2005_2	L40_2005_2	L40_2005			
Road500m	L45_2005_2	L43_2005_3	L43_2005_2	L40_2005_2	L40_2005	L17_2003_2			
Intersection	L45_2005_2	L43_2005_3	L43_2005_2	L40_2005_2	L40_2005	L17_2003_2			
Slope	L40_2004	L32_2004	L28_2004	L27_2004	L22_2003_2	L22_2003			
RoadCover75m	L45_2005_2	L43_2005_3	L43_2005_2	L40_2005_2	L40_2005	L17_2003_2			

Table A.2. For the RDA tri-plot of the 40 model moose in Scenario #1, this table presents the response and explanatory variables that each real moose was closest to, in some cases, the model moose has more than one arrow close to it.

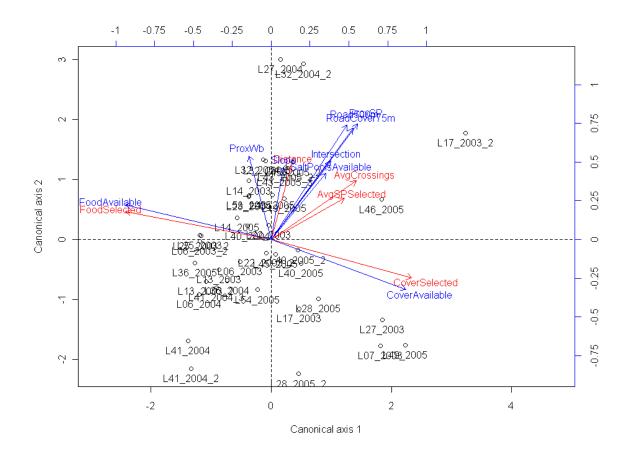


Figure A.3. Scenario #6. Redundancy Analysis tri-plot of Model Moose. The red arrows and labels represent the 5 response variables: Food Selected, Cover Selected, Crossings distance, and Salt Pools Selected. The blue arrows and labels represent the 9 environmental variables: Food Available, Cover Available, Slope, ProxSP, ProxWB, Road500m, RoadCover75m, Intersection, and Salt Pools Available. The 40 real moose ids are positioned nearest to the variables that affected them the most. All of the environment (X matrix) and species (Y matrix) arrows in the 5 graphs were multiplied by 1.75 so that they could be more easily read.

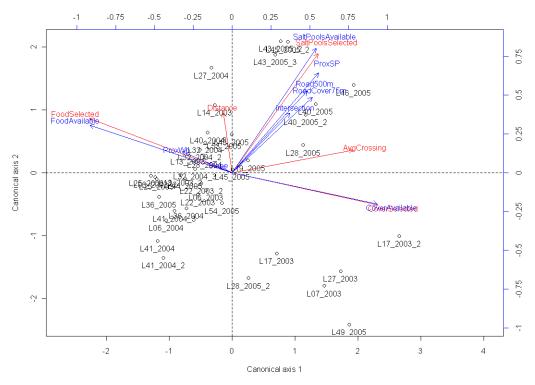


Figure A.4. Scenario #11. Redundancy Analysis tri-plot of Model Moose. The red arrows and labels represent the 5 response variables: Food Selected, Cover Selected, Crossings distance, and Salt Pools Selected. The blue arrows and labels represent the 9 environmental variables: Food Available, Cover Available, Slope, ProxSP, ProxWB, Road500m, RoadCover75m, Intersection, and Salt Pools Available. The 40 real moose ids are positioned nearest to the variables that affected them the most. All of the environment (X matrix) and species (Y matrix) arrows in the 5 graphs were multiplied by 1.75 so that they could be more easily read.

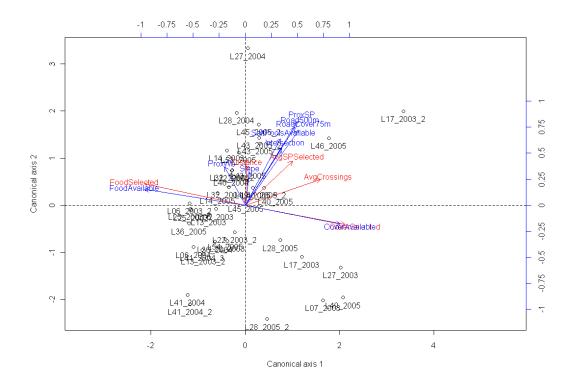


Figure A.5. Scenario #16. Redundancy Analysis tri-plot of Model Moose. The red arrows and labels represent the 5 response variables: Food Selected, Cover Selected, Crossings distance, and Salt Pools Selected. The blue arrows and labels represent the 9 environmental variables: Food Available, Cover Available, Slope, ProxSP, ProxWB, Road500m, RoadCover75m, Intersection, and Salt Pools Available. The 40 real moose ids are positioned nearest to the variables that affected them the most. All of the environment (X matrix) and species (Y matrix) arrows in the 5 graphs were multiplied by 1.75 so that they could be more easily read.

6.4.2 Forward selection results for real moose

The forward selection was performed on both the real moose's X and Y matrices for the RDA (TableA.3,TableA.4) and the model moose X and Y matrices for the RDA (TableA.5, TableA.6) using both the permutation test and parametric versions of forward.sel for the packfor library.

In both the permutation and parametric versions, the two variables first selected in the real and model moose cases were **Food Available** and **SaltPoolsAvailable**. Both of these variables had high weights in the travelling process, 0.45 and 0.30, respectively, so

it could be expected that these two variables would be selected. An additional variable,

ProxWB, was selected for the model moose in the permutation test case. For the real

moose, two additional attributes, ProxSP and Road500m were selected for the

parametric case.

Permutation tests

Procedure stopped (alpha criteria): p-value for variable 3 is 0.063 (superior to 0.05)

variables	\mathbf{R}^2	R ² Cum	um AdjR ² Cum		p-value
FoodAvailable	0.318	0.318	0.282	8.867	0.001
SaltPoolsAvailable	0.223	0.541	0.490	8.731	0.001

Table A.3. Forward selection on 21 real moose using the permutation test version of the forward.sel function.

Parametric test

Procedure stopped (alpha criterion): p-value for variable 4 is 0.0942368

Variable	R ²	R ² Cum	AdjR ² Cum	F	p-value
FoodAvailable	0.318	0.318	0.282	8.867	6.162e-07
SaltPoolsAvailable	0.223	0.541	0.490	8.731	8.815e-07
ProxSP	0.062	0.602	0.532	2.634	2.904e-02
Road500m	0.072	0.674	0.594	3.559	5.881e-03

Table A.4. Forward selection on 21 real moose using the parametric version of the forward.sel.par function.

6.4.3 Forward selection results for model moose in scenario #1.

Permutation Tests

Procedure stopped (alpha criteria): p-value for variable 4 is 0.096 (superior to 0.050)

variables	\mathbf{R}^2	R ² Cum	AdjR ² Cum	F	p value
FoodAvailable	0.397	0.397	0.382	25.058	0.001
SaltPoolsAvailable	0.149	0.547	0.522	12.173	0.001
ProxWb	0.053	0.600	0.567	4.806	0.011

Table A.5. Forward selection on 40 model moose using the permutation test version of the forward.sel function.

Parametric Test

Procedure stopped (alpha criterion): p-value for variable 7 is 0.05073346.

Variable	\mathbf{R}^2	R ² Cum	AdjR ² Cum	F	p value
FoodAvailable	0.397	0.397	0.382	25.058	2.316e-19
SaltPoolsAvailable	0.149	0.547	0.522	12.173	3.310e-10
ProxWb	0.053	0.600	0.567	4.806	3.781e-04

Table A.6. Forward selection on 40 model moose using the parametric version of the forward.sel.par function.

6.4.4 Comparison of R² and adjusted R² for scenarios 1, 6, 11, and 16 and the real moose for the all 36 roadside salt pools present

For scenarios #1, #6, and #16, the R^2 and R^2 adjusted are very similar to each other but scenario #11 and the real moose have a more similar R^2 but not so much the R^2 adjusted value which is closer but higher to the R^2 adjusted of scenarios #1, #6, and #16 (TableA.6).

rdaTest	Model M				
all 36 roadside salt pools present					
Scenario	1	6	11	16	Real
R ²	0.679	0.680	0.796	0.677	0.785
adjusted R ²	0.583	0.583	0.735	0.580	0.641
RAB	on	on	off	off	Not applicable
SPSM	on	off	on	off	Not applicable

Table A.7. Comparison of R2 and adjusted R2 for scenarios 1, 6, 11, and 16 and the real moose.

6.5 Discussion

The redundancy analysis of the real moose and the scenario #1 with all roadside salt pool present, showed that for most of the moose, **FoodAvailable**, and **ProxWB** were the most important explanatory variables and **FoodSelected** was the most important response variable. Though, the forward selection procedure demonstrated that **FoodAvailable** and **SaltPoolsAvailable** were the explanatory variables that contributed the most to the variance in R², particularly, in scenarios #1 and #11. The forward selection procedure is used for guidance for definitely determining the most important variables. As well, the forward selection parametric test for the real moose produced the same first three variables as the RDA's most important variables, namely, **FoodAvailable**, **FoodSelected** and **ProxSP** as well as the **Road500m** variable. The forward selection parametric test for the model moose produced the same first three variables, as the RDA's most important variables, namely, **FoodAvailable**, **FoodSelected** and **ProxWB**.

6.6 Future Research

In my future research, I will apply some more individual variability to the model moose mainly based on sex and age using the following properties:

- good cover stands are less desired by males than females during spring, summer and early winter. Females selected and avoided these stands at day and night respectively from summer to early winter to avoid predation, predation being a limiting factor (Franzmann and Schwartz. 2007),
- in the winter at the home range level, moose trade off food availability with avoidance of deep snow and predators. During winter, moose increase use of stands with good cover next to stands with good food (Franzmann and Schwartz. 2007),
- females with calves differ from solitary female moose in that they seek protection from predation by choosing better cover (Franzmann and Schwartz. 2007),
- yearlings kicked out just 2 weeks before birth of new moose to find their own home ranges, thus there is much dispersal, lots of travelling, and MVCs, in order to find a home range near their mother (Franzmann and Schwartz. 2007),
- 5. females search for isolated sites for birthing with good cover to reduce stress and avoid predation, (islands, close to water, forest patches in large forest

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cuts: they use these sites for several days to several weeks) (Franzmann and Schwartz. 2007),

6. in the rut season from September to October: male moose leave wetlands gradually, and become less wary of roads during rut. Most male moose gradually stops eating during rut, and they fight with other males to see which will dominate and have most of the access to the females. Moose use larger travel steps up to doubling their rate of movement per day (Leblond *et al.* 2010). Males can travel more than 250 to 700 m/day but females reduce movement and wait for the males to arrive (Franzmann and Schwartz. 2007).

Other processes that will be added to all scenarios are: yearling dispersal, birth, hunting by humans and predators such as wolves and bears, reduced highway maintenance budgets, gates left open and increased human traffic in large wildlife underpasses.

When the time-steps are between May 15th and May 31st, if a female has one or more yearlings then she kicks them out. The yearlings then disperse using the square root of their mother's home range as their daily travel distance, and, after some time, find new home ranges next to their mother's. Males tend to disperse farther than females from their mother's home range, particularly after the first year of abandonment by the mother (Cederlund and Sand 1992).

When the time-steps are between June 1st and June 15th, the females with an age greater 3 years and apply a random generator so that the final births equal the birth rate for that year (4.5%). The percentage of males, females and calves in the population is

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32%, 52%, and 16% respectively and the total number of moose in LWR is about 3,283 according to a 2009 winter aerial survey (MRNF 2010).

When the time-steps are between Sept. 1st and Sept. 30th, the males with an age greater than three years and apply a random generator so that the final hunting deaths equal the hunting rate for that year (9.9%) with 4.5% for the females and 5.4% for the males (MRNF 2010). As well, predation by wolves and bears that mainly attack the very young moose will be added to the ABM.

Changes will be introduced in Transports Québec maintenance budgets of the fences and underpasses. Bissonette and Cramer (2008) found that, across North America, that the maintenance budgets for fencing and wildlife passages were too low. The Transports Quebec maintenance budget will be varied upwards and downwards per year and if the budget is too low then it will cause certain fences and passages to deteriorate. This will cause gaps between the fences and the underpasses and holes in the fence, either, caused by wear and tear or by humans cutting the fences deliberately. Neither of these two situations will receive the required maintenance if the budgets are too low.

The possibility will be added that pedestrian and road access gates along the Highway 175 are left open occasionally by hunters and fishermen and fisherwomen who use them, thus, increasing the probability that moose can enter the Highway 175 right-of-way and then wander on the Highway 175 itself. I will also add the double one-way-escape gates that have been constructed into the fences and analyze their frequency of use by the model moose and also measure the number of MVCs that that moose will be involved in. Too much human traffic in an underpass causes the wildlife to use the underpass less often as observed in the Florida Everglades, BNP and LWR (Foster and Humphrey

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1995; Clevenger and Waltho 2000; AECOM Tecsult 2010). Human traffic will be increased in certain underpasses thus causing the model moose to avoid these underpasses and perhaps use other ones instead.