

INFLUENCE DE LA SYLVICULTURE INTENSIVE SUR L'UTILISATION À FINE ÉCHELLE DE
L'HABITAT HIVERNAL PAR LA MARTRE D'AMÉRIQUE (*MARTES AMERICANA*) DANS UNE
FORÊT INDUSTRIELLE DU NOUVEAU-BRUNSWICK

THÈSE PRÉSENTÉE À LA FACULTÉ DES ÉTUDES SUPÉRIEURES ET DE LA RECHERCHE,
EN VUE DE L'OBTENTION DE LA MAÎTRISE ÈS SCIENCES FORESTIÈRES

FRANÇOIS VILLENEUVE

UNIVERSITÉ DE MONCTON, CAMPUS D'EDMUNDSTON
FACULTÉ DE FORESTERIE
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AVANT-PROPOS

La présente thèse est présentée sous forme de deux articles qui seront soumis pour publication. Le premier chapitre et le second chapitre sont les manuscrits des articles suivants :

Villeneuve, F. & Samson, C. (en prép.). Winter foraging behaviour of American marten in an industrial forest of northwestern New Brunswick : a snowtracking analysis. *Journal of Mammalogy*.

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Ces articles sont aussi signés par le directeur de ce projet. Ce dernier a principalement contribué à l'organisation préliminaire du projet, la supervision lors de la prise de mesures et la révision des articles avant la publication, menant ainsi à l'ajout de plusieurs nouvelles idées afin de mieux compléter le tout.

Le premier chapitre de cette thèse se penche sur la comparaison du comportement de la martre dans les deux principaux types de peuplements de l'aire d'étude, et tente de faire un lien entre la sinuosité mesurée et les éléments rencontrés par l'animal au cours de ses déplacements. Le second chapitre de la thèse compare des inventaires d'habitat à fine échelle effectuée sur les pistes de martres aux inventaires effectués ailleurs dans le même peuplement. La combinaison de ces deux chapitres nous permet de mieux comprendre de quelle façon la martre utilise les différents habitats mis à sa disposition dans un paysage forestier aménagé de façon intensive.

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SOMMAIRE

La sylviculture intensive est l'une des solutions mises de l'avant par l'industrie forestière nord-américaine afin de combler l'augmentation de la demande en produits ligneux. Ces opérations ont plusieurs impacts sur le peuplement produit, notamment une réduction de la diversité des espèces végétales, la diminution des apports de bois morts ainsi que le raccourcissement voire la disparition du stade suranné. Ainsi, l'application à grande échelle de ces pratiques pourrait avoir un impact important sur les espèces vivant dans les vieilles forêts, comme la martre d'Amérique (*Martes americana*). Étant donné que la sylviculture intensive est une pratique récente en Amérique du Nord, peu d'études ont porté sur l'impact à long terme de ces pratiques. Au Nouveau-Brunswick, des travaux de recherche ont suggéré que la martre sous-utiliserait les plantations de 20 à 45 ans par rapport à leur disponibilité en hiver. Cette sous-utilisation serait liée à la faible quantité de bois mort dans les plantations, limitant l'accès de la martre à l'espace sub-nival où elle recherche des proies et s'abrite contre les prédateurs et le froid.

L'hypothèse de cette recherche était que la martre recherche les accès potentiels sous la neige lors de sa recherche de proies et d'abris. Si cette hypothèse est exacte, les déplacements de la martre seront alors moins sinueux dans les plantations âgées de 20 à 45 ans que dans les peuplements matures d'origine naturelle car elle aurait tendance à les traverser pour aller rejoindre d'autres sites plus propices à la quête alimentaire. De même, l'abondance d'éléments permettant l'accès sous la neige devrait être supérieure sur la piste de la martre que dans le reste du peuplement.

La cartographie de 15 kilomètres de pistes de martres au cours des hivers 2004 et 2005 dans un paysage forestier aménagé de façon intensive, a permis de mieux comprendre l'utilisation que fait la martre des plantations de 20 à 45 ans. Contrairement à ce qui était attendu, la sinuosité des déplacements est significativement plus grande dans les plantations que dans les peuplements matures d'origine naturelle. Les inventaires d'habitat effectués sur la piste et dans le reste du peuplement montrent que la martre recherche les portions résineuses, les débris ligneux grossiers et une plus grande

obstruction latérale lorsqu'elle se déplace dans les peuplements matures d'origine naturelle. Lorsqu'elle se déplace dans les plantations de 20 à 45 ans, la martre semble plutôt éviter les souches, les conifères à branches basses et recherche une obstruction latérale faible. Ces résultats suggèrent que les plantations sont un milieu de recherche de proies sur la surface de neige tandis que les peuplements d'origine naturelle seraient plutôt utilisés pour des déplacements rectilignes entre des sites d'alimentation sub-niveaux. La qualité des plantations en tant qu'aire d'alimentation semble influencée par l'abondance relative de proies, la sinuosité étant significativement supérieure lors de l'année de plus grande abondance de petits mammifères.

L'étude a montré que la martre utilise les plantations de 20 à 45 ans pour la recherche de proies à la surface de la neige, en particulier durant l'année où les proies sont abondantes. Les peuplements d'origine naturelle seraient plutôt utilisés pour la recherche de proies sous la neige, notamment à cause de leur faible couvert de protection hivernal (peuplements feuillus ou mixtes à dominance feuillue). La contribution des plantations âgées 20 to 45 ans au maintien de la martre dans l'aire d'étude reste encore à être évaluée.

Mots clés : Sylviculture intensive, *Martes americana*, Pistage sur neige, Sélection d'habitat hivernal à petite échelle, Sinuosité, Inventaire d'habitat multiressources, Plantations.

SUMMARY

Intensive management practices (IMP) have been proposed by the forest industry to meet growing North American demands for wood products. Those practices have major impacts on managed stands, including lower plant species diversity, decreased dead wood incomes and reduction of the duration of the overmature stage. Large scale IMP could have a major impact on species living in old-growth forests, like American marten (*Martes Americana*). Long-term impacts of IMP are largely unknown because this management strategy has not been used for a long time in North America. In New Brunswick, studies on marten's habitat selection suggested that 20 to 45 year-old plantations are being used less than their availability during winter. This underutilization is likely related to the lack of dead wood in plantations that provide subnivean access points where marten hunt preys and seek refuge against predators and cold weather.

The hypothesis of this study was that number of subnivean access points might be a limiting factor for marten's winter foraging and denning behaviour. If this hypothesis is valid, movements of martens should be less tortuous in 20 to 45 year-old plantations than in natural stands because the species will cross intensively managed stands to seek other sites more suitable for foraging and denning. Also, the amounts of subnivean access should be higher in the portion of the area used by marten than in the rest of the same stand.

We mapped 15 kilometers of marten tracks during winters 2004 and 2005, in an industrial forest of Northwestern New Brunswick. Contrary to the prediction, tracks were more tortuous in plantations than in mature natural stands. Habitat inventory plots in natural mature stands showed a selection for resinous portions of the stand, for higher amount of coarse woody debris and for higher visual obstruction. In 20 to 45 year-old plantations we found fewer stumps and low branches conifer stems as well as lower visual obstruction near marten tracks compared to the surroundings. Those results suggest that martens use plantations as foraging habitat over the snow cover and that natural stands are mainly used for subnivean foraging and denning. The quality of

plantations as foraging areas could be influenced by prey abundance, as tortuosity was significantly higher during the year of higher small mammals abundance.

This study showed that martens use 20 to 45 year-old plantations where they forage for prey on the snow surface. Mature natural stands (deciduous and mixed with deciduous dominance stands) appear to be used for subnivean activities, likely because of the poor protective cover during winter in those stands. The contribution of 20 to 45 year-old plantations to the maintenance of a marten population remains to be assessed.

Keywords : Silviculture, *Martes americana*, Snowtracking, Winter habitat selection, Track tortuosity, habitat inventory, Plantations.

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INTRODUCTION GÉNÉRALE

Plusieurs scénarios de modélisation prédisent une croissance de la demande mondiale pour les produits forestiers ligneux de 1 % par année jusqu'en 2040 (Sohngen, Mendelsohn, Sedjo & Lyon, 1997). Dans le contexte actuel de mondialisation, l'industrie forestière canadienne a de plus en plus de difficulté à répondre à cette demande, car elle est en compétition avec des pays où les coûts de production sont inférieurs. Afin de préserver l'important impact économique de cette industrie, les autorités gouvernementales doivent déployer plus d'effort pour accroître la productivité de l'industrie canadienne tout en tenant compte des enjeux environnementaux liés aux impacts de l'exploitation forestière (Gouvernement du Canada, 2005). Le Conseil canadien des ministres des forêts a donc appuyé les demandes de l'industrie visant une augmentation de la production de fibre de bois notamment par une intensification de la sylviculture (Gouvernement du Canada, 2002). Ainsi, en 2004, un total de 382 000 hectares ont été plantés ouensemencés au Canada, dont 70 000 hectares au Québec, 104 000 hectares en Ontario et 156 000 hectares en Colombie-Britannique (Gouvernement du Canada, 2005). Depuis 1987, plus de 300 000 hectares de forêt font l'objet d'aménagement sylvicole à chaque année au Canada, cette superficie ayant atteint 520 000 hectares en 1998 et 422 000 hectares en 2005 (Conseil canadien des ministres des forêts, 2005).

Au Nouveau-Brunswick (N.-B.), l'industrie forestière a proposé que la coupe annuelle permise de résineux sur les terres de la Couronne soit augmentée d'ici 50 ans pour répondre à la demande, passant de 3,3 à 6,8 millions de m³ par année (Comité spécial de l'approvisionnement en bois, 2004). L'industrie propose de doubler la superficie plantée pour atteindre cet objectif, passant ainsi à 40 % des terres publiques du Nouveau-Brunswick (Jaakko Pörry Consulting, 2002). Suite à cette recommandation, le gouvernement provincial a décidé d'appuyer un aménagement intensif sur les terres privées industrielles (18 % des terres forestières productives de la province, incluant notamment le District de Black Brook) (Comité spécial de l'approvisionnement en bois, 2004). Le scénario d'aménagement intensif privilégié comprend principalement la mise

en terre de semis de résineux suivi d'une série d'opérations de contrôle de la compétition par des dégagements et des éclaircies commerciales. L'application d'un tel scénario à grande échelle entraînerait vraisemblablement des modifications à long terme du paysage forestier provincial. Dans ce contexte, l'acquisition de connaissances sur les impacts de l'aménagement intensif sur la faune et son habitat est donc plus que jamais d'actualité dans la province.

Le scénario d'aménagement élaboré par la compagnie J.D. Irving Ltd. (JDI Ltd) (Gaetan Pelletier, directeur forestier chez JDI Ltd, comm. pers., février 2002) pour les plantations de conifères est un bon exemple de sylviculture intensive pratiquée tout au long du développement du peuplement. À la suite de la coupe totale du peuplement originel, une préparation mécanique du site, comprenant notamment l'écrasement des déchets de coupe, visant à créer des microsites propices à la plantation. Ensuite, la plantation d'essences résineuses est effectuée, généralement l'année même de la coupe totale ou le printemps suivant. Des phytocides seront appliqués, si nécessaire, au cours des deux ou trois années suivant la plantation, là où la régénération artificielle est restreinte par la compétition d'espèces feuillues indigènes plus agressives. Ces premières opérations permettent de minimiser le temps d'implantation du nouveau peuplement tout en permettant la survie d'un maximum de semis.

Les interventions suivantes, consistant principalement en une série d'éclaircies mécaniques, varieront en fonction du développement particulier au peuplement et visent à gérer la compétition entre les plants pour optimiser la croissance des jeunes arbres. Un dégagement des tiges est d'abord effectué lorsque le peuplement est âgé d'environ 12 ans, laissant une grande quantité de débris ligneux de faible diamètre au sol. Par la suite, une série de deux ou trois éclaircies commerciales sont effectuées, dépendamment de la productivité du site, respectivement lorsque le peuplement atteint l'âge d'environ 25, 35 et 45 ans. Ces opérations d'éclaircies permettent de maintenir une densité optimale du peuplement tout au long de son développement afin de produire plus rapidement un plus grand nombre de tiges de dimension commerciale, sans toutefois augmenter la biomasse totale produite. Une coupe totale avec protection de la régénération viendra par la suite

compléter la révolution du peuplement entre l'âge de 55 et 75 ans, selon les conditions de croissance du et la qualité du site.

Selon Bunnell, Kremsater & Wind (1999), l'aménagement intensif d'un peuplement équiennne, similaire à celui pratiqué par la compagnie JDI Ltd, a deux principaux effets par rapport à la régénération naturelle du peuplement. En premier lieu, les stades d'établissement de la régénération sont raccourcis puisque la compétition par les espèces indigènes sur la régénération artificielle est contrôlée. En second lieu, les derniers stades de développement vont pratiquement disparaître puisque le peuplement est généralement récolté dès l'atteinte de la maturité commerciale de la strate dominante. Or, la diversité faunique et floristique des peuplements résineux équiennes est plus élevée au début et à la fin de leur développement (Bunnell *et al.*, 1999). Cette plus grande diversité est due à la présence d'espèces ayant des besoins spécifiques en habitat qui sont comblés dans les peuplements en début ou en fin de succession.

Thompson, Baker & Ter-Mikaelian (2003) présentent une revue de littérature exhaustive relative aux impacts des pratiques sylvicoles sur l'habitat faunique. Tout d'abord, la préparation mécanique de terrain effectuée avant la plantation a pour effet de réduire la quantité et la qualité (dimension et disposition) du bois mort au sol. De plus, la plantation de résineux et le contrôle chimique de la compétition augmentent la proportion de résineux présents dans le peuplement, réduisant ainsi la diversité végétale du peuplement. Aussi, les opérations de dégagement et d'éclaircies mécanique retirent généralement les arbres morts ou endommagés du peuplement, diminuant ainsi les apports futurs du peuplement en débris ligneux de forte dimension. Les principaux impacts susceptibles de diminuer la qualité de l'habitat forestier pour les espèces caractéristiques des vieilles forêts sont : la diminution de la diversité horizontale et verticale et le morcellement de l'habitat (Thompson *et al.*, 2003).

L'impact à court terme des pratiques sylvicoles peut être négatif pour certaines espèces non seulement par le raccourcissement des premiers stades de développement du peuplement, mais aussi par la modification de la structure du jeune peuplement. Les

opérations de préparation mécanique du site peuvent réduire la quantité de débris ligneux grossiers (Thompson *et al.*, 2003). De plus, l'utilisation d'herbicides empêche la prolifération d'espèces végétales indigènes qui procurent abris et nourriture aux espèces fréquentant les peuplements en régénération (Wedeles & Van Damme, 1995). Cette simplification de la strate arbustive affecterait l'abondance de nourriture pour des espèces tel que l'orignal (*Alces alces*), le cerf de virginie (*Odocoileus virginianus*), ainsi que les espèces d'oiseaux frugivores (Enns, 1994). L'aménagement intensif aurait aussi un impact important sur les espèces d'amphibiens par l'acidification du sol, la réduction de l'épaisseur de litière et la réduction d'abondance de débris ligneux grossiers (DeMaynadier & Hunter, 1995).

Les impacts à long terme de l'aménagement intensif sur la faune ont surtout été étudiés en Europe, où la sylviculture intensive y est pratiquée depuis beaucoup plus longtemps qu'en Amérique du Nord. Edenius & Elmberg (1996) rapportent que la réduction des superficies de forêts mixtes en Suède au profit de peuplements de pin (*Pinus* sp.) aménagés a entraîné une diminution de l'abondance et de la diversité des communautés aviaires par la diminution de la superficie d'habitat de ces espèces. Nilsson (1979) a, de son côté, comparé des vieilles plantations d'épinettes de Norvège (*Picea abies*) et de pins sylvestres (*Pinus sylvestris*) aux peuplements naturels composés d'épinette de Norvège et de chêne (*Quercus* sp.). L'auteur a rapporté que les plantations renfermaient en moyenne trois fois moins d'espèces d'oiseaux, en particulier les espèces nichant dans des arbres à cavité. Étant donné l'intérêt relativement récent de l'industrie forestière nord-américaine pour la sylviculture intensive, encore peu de travaux de recherche se sont penchés sur le cas des plantations ayant atteint des stades de maturité relativement avancés.

La martre d'Amérique (*Martes americana*) a longtemps été considérée comme une espèce dépendante de forêt mature ou surannée, particulièrement des vieux peuplements de conifères (Soutiere, 1979; Spencer & Zielinski, 1983; Clark, Anderson, Douglas & Strickland, 1987; Thompson, 1994, Thompson & Curran, 1995). Les premiers travaux ont surtout porté sur les effets de la coupe à blanc de grande superficie sur l'habitat et la

dynamique de population de cette espèce (Chapin, Harrison et Katnik, 1998 ; Payer & Harrison, 1999 ; Potvin, Bélanger & Lowell, 2000). Ces travaux ont montré que la martre délaisse les parterres déboisés, provoquant ainsi une diminution locale de l'abondance de la population. Récemment, certains auteurs ont suggéré que la martre était moins dépendante des vieux peuplements de conifères, mais rechercherait surtout des peuplements ayant une structure complexe (Payer & Harrison, 2003; Bissonette, Harrison, Hargis & Chapin, 1997). Ces conditions peuvent aussi se retrouver dans des peuplements mélangés et feuillus matures (Potvin, 1998), ainsi que dans des peuplements relativement jeunes, ayant subi des épidémies d'insectes (Poole *et al.*, 2004; Porter, St-Clair & deVries, 2005).

Les impacts à long terme et à grande échelle de la sylviculture intensive sur la martre et son habitat n'ont pas fait l'objet de beaucoup de travaux, principalement parce qu'il y a encore relativement peu de territoires qui ont fait l'objet de ce type d'aménagement à une échelle industrielle. Au Nouveau-Brunswick, JDI Ltd est reconnue pour pratiquer des techniques d'aménagement intensif à grande échelle depuis la fin des années 1950 sur ses terres privées. Le comportement et la dynamique de population de la martre d'Amérique sont étudiés depuis 2001 dans le District de Black Brook (Laurion, 2005; Pelletier, 2005). Cette propriété privée appartenant à la compagnie JDI Ltd est située dans le nord-ouest du Nouveau-Brunswick. Les résultats obtenus jusqu'à présent suggèrent que la densité de population de martres, dans les secteurs dominés par les plantations âgées de 20 à 45 ans, serait généralement plus faible que celles rapportées dans la littérature pour les territoires non aménagés et couverts par des peuplements matures (Laurion, 2005). De même, la population comporterait une proportion relativement faible de vieux individus, *i.e.* ceux qui sont âgés de plus de 2 ans, ce qui suggère un taux de mortalité et de dispersion relativement élevé (Pelletier, 2005).

Les plantations âgées de moins de 20 ans sont évitées par les martres en été (Pelletier, 2005) et en hiver (Laurion, 2005), tant à l'échelle du domaine vital (*i.e.* proportion de localisations télémétriques dans les plantations inférieure à la proportion

de la superficie du domaine vital couverte par ces mêmes plantations) qu'à l'échelle du paysage (i.e. proportion moins grande de plantations dans le domaine vital que dans le paysage forestier avoisinant). Cet évitement serait dû à l'absence d'un couvert arborescent suffisamment haut et dense. Les vieilles plantations, *i.e.* celles qui sont âgées de 20 à 45 ans sont quant à elles proportionnellement moins utilisées en hiver que les peuplements matures d'origine naturelle à l'échelle du peuplement (Laurion, 2005). Des inventaires comparatifs d'habitat suggèrent que la faible quantité de débris ligneux grossiers et la faible densité de conifères à branches basses limiteraient l'accès à l'espace sub-nival (Laurion, 2005). Ces éléments permettent à la martre un accès aux proies sous la neige tout en procurant un abri contre le froid et les prédateurs, ce qui pourrait être à l'origine de l'utilisation relativement plus faible des vieilles plantations par rapport aux peuplements d'origine naturelle (Laurion, 2005).

Les travaux effectués par Laurion (2005) et Pelletier (2005) démontrent que la martre passe tout de même plus de 40 % de son temps dans les plantations de 20 à 45 ans pendant toute l'année. Les vieilles plantations de l'aire d'étude semblent donc avoir des caractéristiques relativement attirantes pour la martre. Les études de préférence d'habitat effectuées par Laurion (2005) et Pelletier (2005) ont été réalisées à l'aide de la radiotélémetrie, qui permet essentiellement de déterminer approximativement dans quel type de milieu un animal se trouve à un moment précis. Toutefois, cette technique ne permet pas d'obtenir des informations détaillées sur le comportement de l'animal lorsqu'il utilise un peuplement en particulier.

L'objectif de la présente étude est donc d'évaluer l'influence de la structure du peuplement sur les déplacements hivernaux à fine échelle de la martre d'Amérique afin de comparer le comportement de l'espèce dans les vieilles plantations et les peuplements matures d'origine naturelle. L'étude est basée sur l'hypothèse que, lors de ses déplacements hivernaux, la martre est attirée par les portions du peuplement contenant plus d'éléments permettant un accès sous la neige (débris ligneux grossiers, conifères à branches basses et masses racinaires exposées). Selon Edwards, Forbes & Bowman (2001), les déplacements plus sinueux d'un prédateur seraient un indicateur du

comportement de recherche et de capture de proies. Si l'hypothèse de l'étude s'avère exacte, les déplacements effectués par la martre seront moins sinueux dans les plantations que dans les peuplements d'origine naturelle. Les plantations, contenant proportionnellement moins d'éléments permettant l'accès sous la neige, sont un milieu moins favorable aux comportements de quête alimentaire et devraient donc être traversées sans montrer de comportements de recherche de proies. De plus, on peut s'attendre à retrouver plus d'éléments permettant un accès sub-nival le long des pistes comparativement au reste du peuplement parcouru et ce, peut importe le type de peuplement parcouru.

Le premier chapitre compare la sinuosité des déplacements hivernaux de martres dans les plantations et les peuplements d'origine naturelle et s'intéresse à la relation entre la sinuosité des déplacements et les éléments rencontrés par la martre. Le chapitre 2 compare l'habitat retrouvé le long du parcours effectué par la martre à celui retrouvé dans le reste du peuplement. Les résultats présentés dans chacun des chapitres de cette thèse devraient permettre une meilleure compréhension du comportement qu'adopte la martre dans ces deux types de peuplements très différents. Ces nouvelles connaissances permettront notamment de mieux interpréter les effets éventuels de l'aménagement forestier intensif sur la dynamique de la population de la martre.

CHAPITRE I

WINTER FORAGING BEHAVIOUR OF AMERICAN MARTEN (*MARTES AMERICANA*) IN AN INDUSTRIAL FOREST OF NORTHWESTERN NEW BRUNSWICK : A SNOWTRACKING ANALYSIS

1.1 Abstract

Intensively managed stands have a low structural complexity and thus they could be considered as low quality habitat for american marten (*Martes americana*). Indeed, martens are known to be attracted to stands with high abundance of structural features, such as coarse woody debris, snags, conifers with live low hanging branches, and a dense forest canopy. Many of those features enhance martens' foraging success and provide protection against cold temperature and predators in winter. Snow tracking was used to assess the way marten uses its habitat at fine scale. To determine how the relative abundance of structural features (CWD, understory conifer density, snags, stumps, exposed root masses) affects marten's foraging behaviour, 15 km of adult marten tracks were mapped in an industrial forest of northwestern New Brunswick, Canada. Information on habitat elements and prey encountered by marten were also noted. Tortuosity of tracks was significantly higher in 20 to 45 year-old plantations compared to natural mixed and deciduous mature stands. Also, the tortuosity of tracks was negatively correlated to habitat elements enabling subnivean access ($p = 0.01$), positively correlated to elements enabling canopy access ($p = 0.04$) and also positively correlated to prey tracks encountered ($p = 0.05$). Those results suggest that the martens hunt more frequently over the snow surface in 20 to 45 year-old plantations compared to natural mixed and deciduous mature stands, reacting to habitat elements and prey tracks encountered during its movements.

1.2 Introduction

Intensive Forest Management Practices (IFMP) are used primarily to increase the value and/or volume of desired fiber products (Bell *et al.*, 2000). Plantations are considered an essential component of IFMP (Thompson *et al.*, 2003). Indeed, stand yield could be maximized by planting desired species, followed by the control of competition

using successive chemical and mechanical thinning operations, up to a final clear cut where all the residual volume is harvested in an even-aged mature stand (Thompson *et al.*, 2003). In 2004, 382 000 hectares were planted in Canada (Government of Canada, 2005). In New Brunswick, plantations covered 9% of productive public forests in 2002, and this proportion may increase up to 17% by 2030 (Erdle & Pollard, 2002). Loss of structural diversity provided, in part, by deadwood features such as snags and woody debris, is an important and common effect of IFMP and is likely to reduce the diversity and abundance of species dependent on those features (Thompson *et al.*, 2003). Considering the predicted increase of IFMP in the near future in Canada and United States, the impacts of those practices on behavioural ecology and population dynamics of species that use late-successional forests, such as marten, need to be assessed.

In New Brunswick, Laurion (2005) and Pelletier (2005) reported that <20 year-old plantations are avoided by martens in winter and summer at both stand and landscape levels. This avoidance is probably due to the lack of a dense and high tree cover, and is similar to the avoidance of recent clear-cuts that have been reported for marten (Potvin, 1998; Potvin *et al.*, 2000). On the other hand, 20 to 45 year-old plantations provided a sufficient tree cover to be used by marten but they seem less preferred than mature and over-mature natural stands during winter at the stand level (Laurion, 2005). The relative lower winter use of 20 to 45 year-old plantations at the stand level suggests that low abundance of coarse woody debris (CWD) and of conifers with low branches (CLB) may be a limiting factor for marten when they search for subnivean access in those intensively managed stands (Laurion, 2005). Martens nevertheless tend to spend approximately half of their time in 20 to 45 year-old plantations (Laurion, 2005) indicating that these cover types have characteristics that attract this species. A smaller scaled study is needed to understand why and how marten use 20 to 45 year-old plantations despite to the low abundance of structural features in these stands.

Foraging activities largely determines how animals use their habitat (Benhamou, 1990). For carnivores, foraging is a large energy investment that has to be profitable at short term to allow an individual to survive. Pine marten possess an elongated body form

that allows them to follow their preys in narrow spaces, but highly increases their metabolic costs for homeothermy (Zielinski, 2000). Nevertheless martens have some behavioural strategies to optimize their thermal budgets, especially during winter (Drew & Bissonette, 1997). For example, the species reduced and synchronized its daily activity to periods of greater vulnerability of preys (Drew & Bissonette, 1997; Zielinski, 2000). Martens, as weasels (Edwards *et al.*, 2001), may also minimize distance travelled in their home range, which should result in relatively straight movements between foraging areas combined with more complex movements within foraging areas.

Time spent in a specific environment, typically obtained by radiotracking, is a crude measure of the fitness value of an habitat since animals may be performing different activities in this environment (Nams & Bourgeois, 2004). This method is often used when visual observations of behaviour are difficult to obtain. Observing paths left in the snow by the studied animal can be used to obtain a more detailed portrait of the animal activities without influencing its behaviour (Nams & Bourgeois, 2004).

The typical tortuous pattern of mustelid movements, resulting from zigzag search path and investigation of likely prey refugia, is the primary hunting technique of martens (Spencer & Zielinski, 1983). Indeed, when martens enter a foraging area, movements should become more tortuous, increasing the probability of encountering preys (Edwards *et al.*, 2001). The degree of tortuosity of a path may be a good indicator of the foraging opportunities, but also of cover against predator and harsh conditions provided by a specific environment (Nams & Bourgeois, 2004). Thus, a comparison of path tortuosity between two stand types should provide some insights of the activities performed in those environments.

Density and height of the trees are among the structural features that provide escape cover to marten from avian and terrestrial predators (Strickland & Douglas, 1987; Buskirk & Ruggiero, 1994). Because of its small size, the marten is vulnerable to predators such as the fisher (*Martes pennanti*), lynx (*Lynx canadensis*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*) and some raptors (Hargis & McCullough, 1984;

Strickland & Douglas, 1987; Bissonette, Fredrickson & Tucker, 1988; Thompson, 1994; Bissonette *et al.*, 1997; Hodgman, Harrison, Phillips & Elowe, 1997). Coarse woody debris, large snags, canopy cover and low-branched conifer stems also provide escape cover (Hargis & McCullough, 1984; Buskirk & Ruggiero, 1994; Thompson, 1994; Bissonette *et al.*, 1997; Hodgman *et al.*, 1997) in addition to resting and denning sites (Chapin, Phillips, Harrison & York, 1997; Ruggiero, Pearson & Henry, 1998; Bull & Heater, 2000).

Structural diversity also provides marten with access to various prey species such as shrews (*Sorex* sp.), mice (*Peromyscus* sp.), voles (*Microtus* sp. and *Clethrionomys gapperi*) and snowshoe hares (*Lepus americanus*) (Sherburne & Bissonette, 1994; Thompson & Curran, 1995; Watt, Baker, Hogg, McNicol & Naylor, 1996). The marten's elongated body allows it to catch shrews, mice and voles by crawling among debris. Additionally, low-branched conifer stems and shrubs allow martens to find larger prey like snowshoe hares (Laurion, 2005). Hunting behaviour also includes : following prey tracks, ambush, nest robbing, excavation and even use of hunting perches (Spencer & Zielinski 1983). Pine marten's foraging behaviour should therefore be influenced by the prevalence of one or more of those habitat features regardless of the stand type used.

The objective of this study is to compare the winter foraging behaviour of adult (>1 year old) resident martens between naturally regenerated mature stands and intensively managed stands in an industrial forest of northwestern New Brunswick, Canada. More specifically, we will try to determine how the structural features met by marten influence its movements at a fine scale during winter. We hypothesize that the scarcity of structural features (CWD, understory conifer density, snags, stumps, exposed root masses) in intensively managed stands will affect marten's foraging behaviour in winter. If this hypothesis is valid, we predict that martens will travel in a straighter line when foraging inside intensively managed stands (i.e. more tortuous paths in natural stands) as plantations contains more subnivean access martens will travel right through those stands. We also predict that marten's tracks tortuosity will be positively related to

the number of structural features and number of preys tracks encountered during movements.

1.3 Methodology

1.3.1 Study area

The study area is located in the Black Brook District, an industrial forest owned by J.D. Irving Limited. This area is located about 35 km northeast from the city of Saint-Leonard, New Brunswick (47°18'44''N, 67°42'38''O). Weather conditions during the period the study was conducted (January to March 2004 and 2005) was typical of Atlantic Canada winter. Monthly temperature means was between -15.3°C in January and -4.9°C in March and monthly snowfall averaged between 54.4 cm in February and 103.1 cm in March. Snow accumulations reached 151 cm in mid March (weather report from Saint-Leonard airport 47°9'N, 67°49'O, Altitude : 241.7 m; Environment Canada, 2006). Most of Black Brook District is located in the Maritime Upland Ecoregion, characterized by the Acadian forest, which covers most of the Maritimes provinces of Canada (Mosseler, Lynds & Major, 2003). The forest composition of the Acadian Forest Region include the red spruce (*Picea rubens*), in association with balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*). These species grow in various proportions and associations depending upon local climate, soil fertility, and disturbance conditions within the region (Erdle & Pollard, 2002).

The Black Brook District surface area is 188 670 ha, but the study site, named Skin Gulch area, covers about 5 400 ha (figure 1). Nearly 95 % of this area is covered by productive forest stands, which include 49.5 % of naturally regenerated mature stands and 42.8 % of intensively managed plantations (Laurion, 2005). These plantations are composed primarily of white spruce (*Picea glauca*), but also include balsam fir, black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and Norway spruce (*Picea abies*) in various proportions. A dense forest roads network provided accessibility in the area.

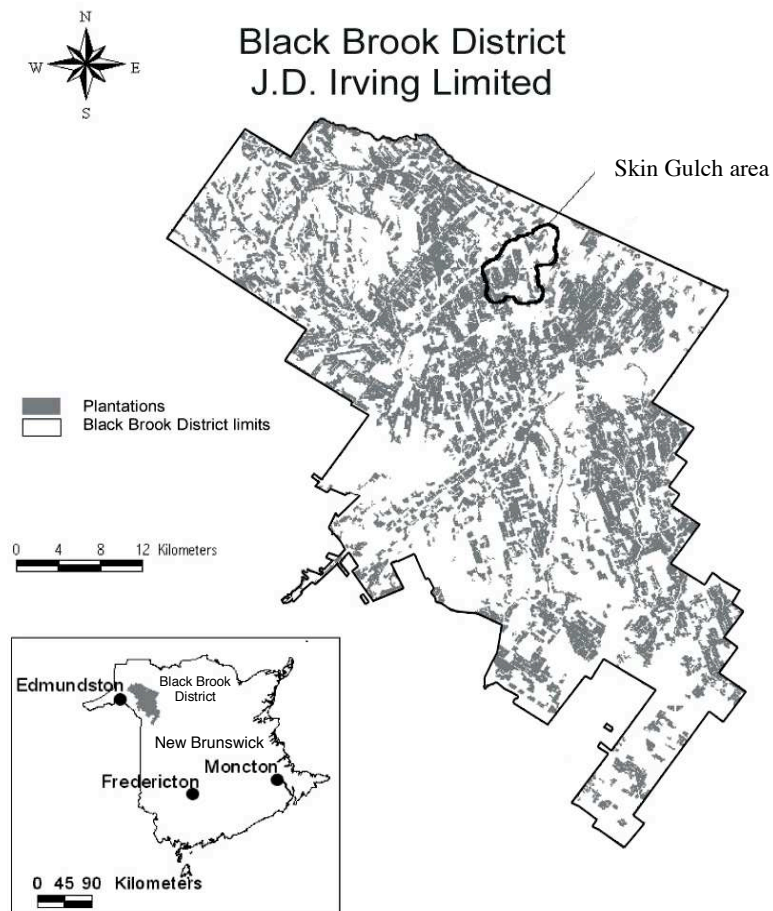


Figure 1. Location of the Black Brook District and the study area

1.3.2 Snow tracking

Fieldwork was conducted during January to March 2004 and 2005. Snow tracking was done on recent snow only, from a couple (>2) hours after snowfall up to 96 hours (4 days) after the last snowfall. Tracks were selected opportunistically by exploring the study area on snowmobile. Various areas were searched in alternance to maximize the chance of finding tracks of different individuals. All backtracked individuals were radiocollared adult resident martens (see Laurion, 2005; Pelletier, 2005). It was easy to recognize the track of a radiocollared animal since the transmitter antenna was long enough to leave a trace on the snow along the marten track. Unfortunately the followed tracks could not be associated without any doubt to a single individual as expected initially. The location of a signal by homing was difficult in deep snow conditions, often working several hours to locate a single animal. We therefore abandoned homing, which

allowed field crew to double or triple the length of marten tracks mapped for every day on the field. We mapped marten movement by backtracking and taking a location approximately every 5 m using a global positioning system (GPS) receiver (March II; CMT Inc.). To maximize the precision of each GPS point, locations were taken in static mode with an accumulation of 5 triangulations. A differential correction was also applied. The number and nature of structural features encountered by the individual during the last 5 m of track were also noted. These structural features include : > 10 cm of diameter at breast height (DBH) stumps, > 10 cm DBH snags, > 10 cm DBH live trees, low branches conifer pole-size stems (i.e. stems of 2-10 cm diameter with branches touching the snow surface), and > 10 cm diameter and > 1 m long CWD. The features must have clear evidence of use by marten to be considered “encountered”, i.e. the marten must clearly have changed direction toward the feature and appear to have at least inspected it. Martens are known to inspect most of prey tracks encountered (Spencer & Zielinski, 1983). The number of tracks of potential prey encountered by the marten (i.e. track of small mammals, snowshoes hare and red squirrel) during the last 5 m of tracking was noted, if there was clear evidence of inspection by marten.

1.3.3 Track tortuosity calculation

Various indices of path tortuosity have been proposed (Gillis & Nams, 1998; Nams & Bourgeois, 2004; Edwards *et al.*, 2001). However, we chose to use a tortuosity index derived from the straightness index from Batschelet (1981). This simple measure, very easy to compute and conceptualize, is equal to the total distance travelled by an individual (L) by the straight distance travelled (D) to obtain a proportional scale of the path tortuosity (L/D). This index has a value of 1 if the animal has travelled in perfect straight line and its value increases as the path gets more tortuous leading to an indefinite maximum. Path tortuosity is dependent on the scale of measure (Nams & Bourgeois, 2004). To prevent this bias, we chose an arbitrary scale of 50 m, i.e. 10 segments of 5 m each, for calculation. The type of index we used, increases the precision of the tortuosity measure by ignoring most of the GPS location error, using only the start and finish points of the 50 m. To minimize the error relative to location of start and finish point, every possible 50 m segment was calculated. A mean tortuosity index was

then calculated for each track mapped during backtracking, leading to a single tortuosity value for each track. Only one tracking segment was retained for analysis when the animal crossed different stand types (i.e. plantations vs. natural mature stands), avoiding pseudoreplication. To be included in the analysis, a track segment had to be at least 250 m in a continuous stand type. Some tracks or tracks segments could not be included in the analysis because of their small length and were simply eliminated.

1.3.4 Statistical analyses

All statistical analyses were performed using Systat, version 11.0. Student *t*-tests (Zar, 1999), using 95% confidence level, were calculated to compare tortuosity, number of subnivean access used per 5 m, number of canopy access used per 5 m and number of preys encountered per 5 m between stand types and between years. The significance level used in this study is $p \leq 0,05$. Because of the small sample size, relationships with a $p \leq 0,10$ were considered as non-significant strong tendencies and will be discussed in this paper. Comparisons were performed on data of each year separately and on pooled data. Tortuosity index and habitat variable measured in each cover type were also compared between each year. Equality of variance was assessed using a Levene's Test (Zar, 1999). Numbers of degree of freedom were adjusted when equality of variance could not be assumed (Zar, 1999).

Since we could not identify which individual was associated with the mapped tracks, we had to assume that each track was independent from the others. However, to increase the independence of samples and avoid pseudoreplication, we excluded some of the >250 m segments when the animal crossed different cover types. In those cases, since the sample size of natural mature stands was more limited, we excluded the segments located in plantations. Different field crews made backtracking in 2004 and 2005 but with the same protocol and the same field equipment. Data from those different years were kept separate to identify this potential bias but were also pooled together to get better sample size.

A Multiple Linear Regression (MLR) was performed (Systat, version 11.0) to evaluate the correlation between tortuosity and 3 selected habitat variables. Same kind of

analysis performed by Edwards *et al.* (2001) with short tailed weasel, except in this case we used the all-subset procedure instead of a stepwise approach (Quinn & Keough, 2002). The regressors included the mean number of subnivean access points (CWD, low branches conifer stems and stumps), of canopy access points (snags and living trees) and of prey tracks encountered on 5 m segments. Those regressors were transformed to fulfill MLR conditions. The response variable of this model is a mean tortuosity of the track, based on a 50 m distance. All data available were used for this analysis, whether or not the tracks crossed >1 cover types. Based on the assumption that the relationship between habitat variables and tortuosity remained the same over years, both years were pooled to increase the power of this analysis.

1.4 Results

A total of 32 marten tracks were backtracked over the two years of field work (table 1). A total of 14.9 km of pine marten tracks were inventoried, i.e. 4 095 m in 2004 and 10 825 m in 2005. High standard errors obtained for subnivean access, canopy access and preys encountered originate from the large amount of zero value in database.

Table 1. Backtracking results for 2004 and 2005

| Year | Cover type ¹ | N | Tortuosity index | Nb. of subnivean access used /5 m | Nb. of canopy access used /5 m | Nb. of prey encountered/5m |
|-----------|-------------------------|----|---------------------|-----------------------------------|--------------------------------|----------------------------|
| | | | Mean \pm Std err. | Mean \pm Std err. | Mean \pm Std err. | Mean \pm Std err. |
| 2004 | Nat | 2 | 1.03 \pm 0.27 | 0.27 \pm 0.32 | 0.06 \pm 0.06 | 0 |
| | Pl | 8 | 1.09 \pm 0.24 | 0.12 \pm 0.13 | 0.03 \pm 0.04 | 0.02 \pm 0.06 |
| 2005 | Nat | 6 | 1.17 \pm 0.15 | 0.06 \pm 0.05 | 0.04 \pm 0.05 | 0.08 \pm 0.09 |
| | Pl | 16 | 1.45 \pm 0.25 | 0.04 \pm 0.04 | 0.10 \pm 0.08 | 0.12 \pm 0.11 |
| 2004+2005 | Nat | 8 | 1.13 \pm 0.17 | 0.11 \pm 0.16 | 0.05 \pm 0.05 | 0.06 \pm 0.09 |
| | Pl | 24 | 1.33 \pm 0.30 | 0.06 \pm 0.09 | 0.07 \pm 0.08 | 0.08 \pm 0.11 |

¹Nat : natural mature stands; Pl : plantations

The tortuosity index was higher in plantations at $p < 0.05$ in 2005 and at $p < 0.10$ when data were pooled between years (Table 2). None of the habitat variables were different between cover types (Table 2).

Table 2. Comparison of tortuosity index, subnivean access, canopy access and prey encountered between cover types during each year and for both years pooled

| Year | Variable | Between cover type comparison | | |
|-------------|---------------------------------|-------------------------------|-----------|-------------|
| | | <i>t</i> | d.f. | <i>p</i> |
| 2004 | Tortuosity index | 0.28 | 8 | 0.79 |
| | Nb. of subnivean access used/5m | -1.13 | 8 | 0.29 |
| | Nb. of canopy access used/5m | -0.82 | 8 | 0.44 |
| | Nb. of preys encountered/5m | 0.48 | 8 | 0.65 |
| 2005 | <i>Tortuosity index</i> | 2.57 | 20 | 0.02 |
| | Nb. of subnivean access used/5m | -0.94 | 20 | 0.36 |
| | Nb. of canopy access used/5m | 1.50 | 20 | 0.15 |
| | Nb. of preys encountered/5m | 0.73 | 20 | 0.47 |
| 2004 + 2005 | <i>Tortuosity index</i> | 1.74 | 30 | 0.09 |
| | Nb. of subnivean access used/5m | -1.02 | 30 | 0.31 |
| | Nb. of canopy access used/5m | 0.98 | 30 | 0.34 |
| | Nb. of preys encountered/5m | 0.61 | 30 | 0.55 |

In plantations, the tortuosity index, the number of canopy access used and the number of prey encountered were all higher in 2005 at $p < 0.05$ (Table 3). No difference between years was observed in natural stands.

Table 3. Comparison of tortuosity index, subnivean access, canopy access used, prey encountered between years for each cover type

| Cover type | Variable | Between years comparison | | |
|-----------------------|--|--------------------------|-----------|-------------|
| | | <i>t</i> | d.f. | <i>p</i> |
| Plantations | <i>Tortuosity index</i> | -3.39 | 22 | 0.00 |
| | Nb. of subnivean access used/5m | 1.65 | 22 | 0.14 |
| | <i>Nb. of canopy access used/5m</i> | -2.18 | 22 | 0.04 |
| | <i>Nb. of prey encountered/5m</i> | -2.73 | 22 | 0.01 |
| Mature natural stands | Tortuosity index | -0.94 | 6 | 0.38 |
| | Nb. of subnivean access used/5m | 0.93 | 6 | 0.52 |
| | Nb. of canopy access used/5m | 0.32 | 6 | 0.76 |
| | Nb. of preys encountered/5m | -1.12 | 6 | 0.30 |

The all-subset multiple regression approach retained all of the three predictive variables entered in the model (adjusted $r^2 = 0.356$; $F = 6.7$, d.f. 31, $p = 0.001$). This model shows a negative correlation between track tortuosity and number of subnivean access used (Table 4). Both number of canopy access used and number of preys encountered were positively correlated to tortuosity of the track (table 4).

Table 4. Results of the multiple linear regression relating tortuosity of marten tracks to habitat features

| Variable | Coefficient | Std Error | <i>t</i> | <i>p</i> |
|------------------|-------------|-----------|----------|----------|
| Constant | 1.217 | 0.070 | 17.305 | 0.00 |
| Subnivean access | -1.159 | 0.383 | - 3.024 | 0.01 |
| Canopy access | 1.278 | 0.587 | 2.176 | 0.04 |
| Prey tracks | 0.844 | 0.418 | 2.017 | 0.05 |

1.5 Discussion

Mysterud, Larsen, Ims & Ostbye (1999), working with roe deer (*Capreolus capreolus*), showed that animals often have to make a trade-off in habitat selection between food and cover. In our study area, the abundance of food and cover was very different between stand types. Natural stands of the study area are mostly deciduous or mixed with a deciduous dominance. Those stands had a significantly lower canopy closure during winter and higher density of subnivean access point than plantations (Laurion 2005, see also chapter 2). Martens are known to avoid open canopy during winter (Payer & Harisson, 2003). The lack of a dense conifer cover in natural stands could lead martens to rely more on subnivean access provided by the large amount of coarse woody debris and high density of low branches conifer stems. Martens would minimize exposure to cold weather and predators by making straight movements between subnivean accesses. This behaviour would be the best trade-off between foraging and safety for marten in natural stands, and could explain why tortuosity of tracks was lower in natural mature stands compared to 20 to 45 year-old plantations. Precision of the GPS locations is affected by a dense resinous canopy (Lejeune & Hellemans, 2000) thus, tortuosity measured in plantations may be exaggerated by the method used in this study. Further research using GPS radiolocations to study animal movements in similar field conditions should consider using GPS unit with a fixed ground station (dGPS) to increase precision and try to evaluate precision actually obtained in each stand type.

We observed that the tortuosity of marten tracks was negatively correlated to the number of subnivean access points used and positively correlated to the number of canopy access point used as well as number of preys encountered. Edwards *et al.* (2001) also reported a negative relationship between coarse woody debris and tortuosity of short tailed weasel tracks. Spencer & Zielinski (1983) also found that tortuosity of marten movements is related to the number of prey encountered. They suggested that martens are opportunistic predators who investigate most of the prey tracks encountered.

Martens may thus have adapted their foraging strategy to the scarcity of structural features in plantations, focusing their effort on prey encountered on the snow surface and canopy cover. Pelletier (2005) reported that scared martens typically flee by climbing in the canopy and jumping from a tree to another. The dense conifer canopy cover found in plantations may therefore also provide an easily accessible protection against ground and aerial predators, while they forage for prey on the snow surface.

The foraging behaviour of marten differed between years in plantations. We observed a higher tortuosity, as well as a higher number of canopy access points used and number of prey tracks encountered in 2005. Forget (in prep.), found a significantly higher density of small mammals in 20 to 45 year-old plantations of the study area during 2005 compared to 2004. Martens are known to inspect most of prey tracks encountered (Spencer & Zielinski, 1983), so the higher density of small mammals may explain the higher tortuosity index reported in 2005. Unfortunately, prey tracks inventoried during 2004 snowtracking were not identified but were only noted as presence or absence. Small mammals tracks encountered by martens could not be compared between years. It is also difficult to relate an higher tortuosity of marten tracks to a higher density of small mammals, since marten are known to hunt small mammals in the subnivean space.

Forget (in prep.) also reported a significantly higher number of small mammals in 2005 in natural stands, although we found no significant difference in the tortuosity index. The absence of significant difference can probably be explained by a low sample size ($n = 8$) and relatively high variability, which limits the power of the statistical test, and by the subnivean oriented behaviour displayed in this stand type.

The relationship between foraging behaviour of pine marten and habitat features is complex and seems to be driven by many factors including canopy cover, prey vulnerability, canopy access points and subnivean access points. When in a foraging situation, a trade-off has to be made by the animal between protective cover and foraging efficiency. In our study area, we found a higher tortuosity of tracks in 20 to 45

years old plantations than in natural stands. This result shows that marten uses plantations as a foraging habitat but with a different strategy than in natural stands. The high canopy closure of those stands may allow marten to travel on the snow surface relatively safer from predators than in deciduous mature natural stands. The lower tortuosity of tracks in natural stands, as well as the significant negative correlation between tortuosity and subnivean access points suggests that martens seem to rely more on subnivean oriented behaviour when using an open stand.

CHAPITRE II

FINE SCALE WINTER HABITAT SELECTION OF AMERICAN MARTEN (*MARTES AMERICANA*) IN AN INDUSTRIAL FOREST OF NORTHWESTERN NEW BRUNSWICK

2.1 Abstract

American marten (*Martes americana*) prefer mature and overmature forest stands that contain a high and dense canopy cover, coarse woody debris (CWD), and snags. Intensively managed coniferous stands contain little dead wood, which may reduce their use by marten. We examined fine-scale winter habitat selection to understand how marten used 20-40 year-old conifer plantations compared to mature stands. We hypothesized that within a stand, marten would select areas containing features that would provide subnivean access, such as CWD and low branching conifer stems (LBCS). Snowtracking was conducted in January-March 2004 and 2005. Habitat surveys were afterward conducted during summer 2005 to compare stand characteristics found near marten tracks with those of the surrounding stand. In mature mixed and deciduous stands ($n = 5$), marten tracks were located in areas with lower canopy ($p < 0.05$), higher CWD ($p < 0.10$), higher coniferous basal area ($p < 0.10$), and higher visual obstruction ($p < 0.10$). In plantations ($n = 12$), marten tracks were located in areas with fewer stumps ($p < 0.05$), a lower density of LBCS ($p < 0.05$), and lower visual obstruction ($p < 0.05$). We conclude that in mature mixed and mature deciduous stands, martens select areas with a high amount of cover from predators and with a large availability of subnivean access. Inside intensively managed stands, martens may prefer to forage over the snow cover.

2.2 Introduction

In order to meet the world's increasing demand in wood products, public forests will be more intensively managed in the future (Binkley, 1997; South, 1999; Sedjo,

2001). Intensive forest management practices (IFMP) are known to have important impacts on the habitat of many late-successional wildlife species, including a reduction in the amount of snags and woody debris, a reduction of tree species diversity, and a shortage or elimination of the overmature stage of stand development (Bunnell *et al.*, 1999; Bell *et al.*, 2000; Thompson *et al.*, 2003). Species, such as American marten (*Martes americana*), that requires some amount of snags and CWD in their habitat to fulfill their foraging and breeding needs, can therefore be affected by intensive forest management practices.

Martens have shown a preference for highly structured stands such as mature and overmature conifer stands (Burnett, 1981), young mixed and coniferous stands regenerating from spruce budworm defoliation (Potvin, 1998; Payer & Harrison, 2000) and young deciduous-dominated stands regenerating from mixed agricultural and timber productions (Poole *et al.*, 2004; Porter *et al.*, 2005). Martens have a preference for late-successional stands because the density and height of the canopy of these stands provide escape cover against avian and terrestrial predators (Strickland & Douglas, 1987; Buskirk & Ruggiero, 1994). Marten is vulnerable to many predators including fisher (*Martes pennanti*), lynx (*Lynx canadensis*), coyote (*Canis latrans*), red fox (*Vulpes vulpes*) and some raptors (Hargis & McCullough, 1984; Strickland & Douglas, 1987; Bissonette, *et al.*, 1988; Thompson, 1994; Bissonette *et al.*, 1997; Hodgman *et al.*, 1997). Like most small mustelids, martens will seek a refuge against predator and cold weather (Hargis & McCullough, 1984; Buskirk & Ruggiero, 1994; Thompson, 1994; Bissonette *et al.*, 1997; Hodgman *et al.*, 1997) as well as resting and denning sites (Chapin *et al.*, 1997; Ruggiero *et al.*, 1998; Bull & Heater, 2000) in coarse woody debris, snags, dense canopy cover and low-branches conifer stems. Marten's elongated body allows the species to catch various prey species such as shrews, (*Sorex* sp.), mice (*Peromyscus* sp.), and voles (*Microtus* sp. and *Clethrionomys gapperi*). They also hunt red squirrels (*Tamiasciurus hudsonicus*) in the canopy cover and search for snowshoe hares (*Lepus americanus*) in dense shrub layer (Sherburne & Bissonette, 1994; Thompson & Curran, 1995; Watt *et al.*, 1996).

The ecology of American martens in intensively managed forest has not been extensively studied, in part because IFMP are relatively recent in North America (Laurion, 2005). Most studies focus on the effects of clearcuts (Chapin *et al.*, 1998; Potvin *et al.*, 2000; Payer & Harrison, 1999) or partial harvesting (Steventon & Major, 1982; Soutière, 1979).

In northwestern New Brunswick, 20 to 45 year-old plantations seem avoided by martens in winter and summer at both stand and landscape scales as a result of the lack of a dense and high tree cover (Laurion, 2005; Pelletier, 2005). Plantations 20 to 45 year-old appear to be used but are less preferred compared to mature and over-mature stands during the winter at the stand level. Laurion (2005) established that intensively managed stands such as 20 to 45 year-old conifer plantations meet the minimal threshold of live-tree basal area, height and canopy closure proposed for marten by Payer & Harrison (2003). However, snags and coarse woody debris (CWD) abundance is low in plantations due to site preparation, pre-commercial and commercial thinning operations (Thompson *et al.*, 2003; Laurion, 2005). The lower CWD abundance and understory coniferous stem density found in those stands may then limit subnivean access for marten in intensively managed stand (Laurion, 2005).

Most studies of habitat selection by marten have been conducted at the stand and landscape scales (Taylor & Abrey, 1982; Smith & Schaefer, 2002; Wynne & Sherburne, 1984; Thompson & Curran, 1995; Poole *et al.*, 2004; Potvin *et al.*, 2000; Laurion, 2005; Pelletier, 2005). Studies at these spatial scales help to determine the factors that influence the second and third order of selection defined by Johnson (1980), i.e. selection of a specific landscape to install the home range and preference of specific cover types within the home range. However, studies at these scales are likely to miss some fine scale habitat selection (Porter *et al.*, 2005). Resources that are used infrequently or for a specific purpose may not be identified (Johnson, 1980; Mysterud & Ims, 1998; Mysterud *et al.*, 1999) especially when only radiotracking is used in a behavioural study. Finer scale studies are thus necessary to understand the mechanism of fourth order habitat selection, i.e. the preference of feeding and resting sites within cover

types. Studies such as those conducted by Porter *et al.* (2005) that compare the habitat structure along snow tracks with the habitat structure in the surrounding area can help to identify some habitat features important to the animal at fine scale (Johnson, 1980).

The aim of this study was to assess fine scale winter habitat selection of martens. We hypothesise that the scarcity of structural features (CWD, understory conifer density, snags, stumps, exposed root masses) in intensively managed stands will affect marten's foraging behaviour in winter. Martens would therefore select areas containing more CWD and a high density of low branches coniferous stem, both in plantations and in natural mature stands.

2.3 Methodology

2.3.1 Study area

The Black Brook District is an industrial forest owned by J.D. Irving Limited and is located approximately 35 km northeast from the city of Saint-Leonard, New Brunswick (47°18'44''N, 67°42'38''O). Weather conditions during the snowtracking (January to March 2004-2005) were typical of the Atlantic Canada winter. Monthly temperature means were between -16.7°C and -4.2°C and monthly snowfall averaged 21.6 cm to 103.1 cm. Snow accumulations reached up to 151 cm in mid March 2005 in weather reports from Saint-Leonard airport 47°9'N, 67°49'O, altitude : 241.7 m (Environnement Canada, 2006). Most of the Black Brook District is located in the Maritime Upland Ecoregion, characterized by the Acadian forest, which covers most of the maritime provinces of Canada (Mosseler *et al.*, 2003). The tree composition of the Acadian Forest Region includes red spruce (*Picea rubens*) in association with balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*), and American beech (*Fagus grandifolia*). These species grow in various proportions and associations depending upon local climate, fertility, and disturbance conditions within the region (Erdle & Pollard, 2002).

The Black Brook District surface area is 188 670 ha, but the study site, the Skin Gulch area, covers approximately 5 400 ha (Figure 2). Nearly 95% of this area is covered by productive stands, which include 49.5% of naturally regenerated mature and overmature stands and 42.8% of intensively managed plantations (Laurion, 2005). These plantations are composed of white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and Norway spruce (*Picea abies*). A dense forest roads network provided accessibility in the area.

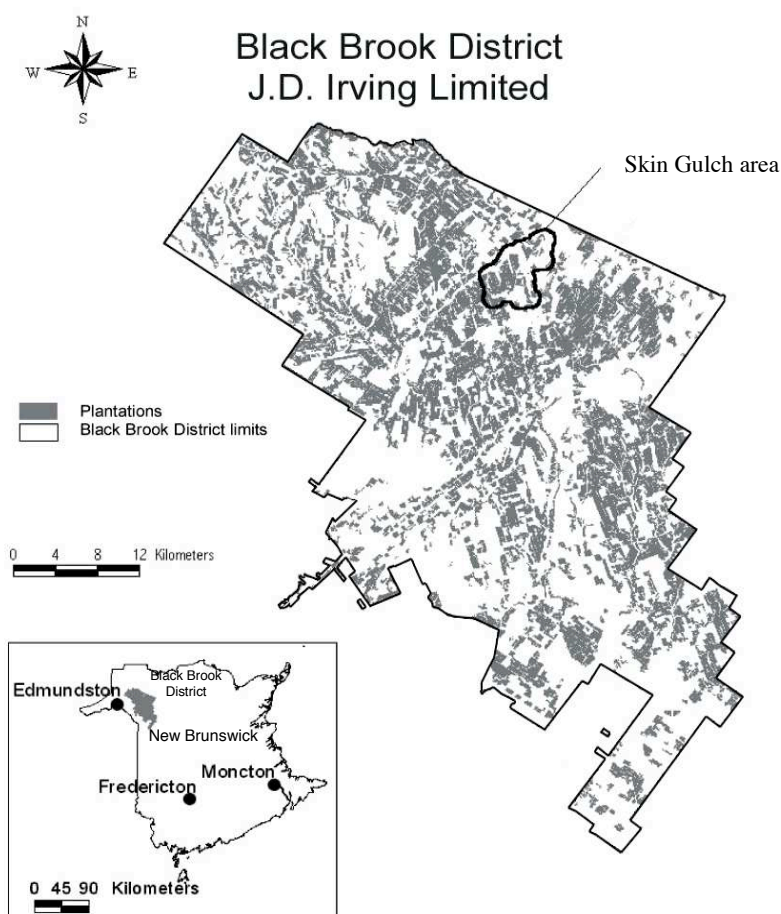


Figure 2. Study area and its localisation in the Black Brook District

2.3.2 Snowtracking

Marten snow tracks were chosen for study by travelling on the study area and by selecting tracks of radiocollared individuals from previous studies in the same area (see Laurion, 2005; Pelletier, 2005 for details on capture methods). The track of a radiocollared animal was easily recognizable because the transmitter antenna was long enough to leave a trace on the snow along the marten track. Selecting those marked individuals confirmed that the tracked animal was a resident non-juvenile marten. We mapped marten movements by backtracking and taking a location approximately every 5 m using a global positioning system (GPS) receiver (March II; CMT Inc.; see Chapter 1). To maximize the precision of each GPS point, locations were taken in static mode with the accumulation of 5 triangulations and a differential correction was afterwards applied.

2.3.3 Habitat sampling

Between June and August 2005, we characterized the habitat used by martens along the mapped tracks and compared it to the characteristics in the surrounding stands. We sampled each track with a minimum length of 250 m in a given stand type ($n = 12$ in plantations, $n = 5$ in mature natural stands, including 2 shade tolerant deciduous stands and 2 mixed stands with a deciduous dominance, and 1 coniferous stand). Tracks were imported in a Geographical Information System using ArcGIS (ESRI) and divided in 4 equal segments using Hawth's analysis tool (Spatial ecology.com, 2005). A sampling plot, representing the "used habitat", was positioned at the 3 intersections of those track segments. We established a 50 m buffer line around each of these sampling plots, and another sampling plot, representing the "available habitat", was positioned along this buffer line in North direction. When the plot was located outside the stand, we selected the nearest point in the stand along a 50 m buffer line. All sampling plots were required to be at least 50 m within the stand and at least 50 m away from any forest road to minimize edge effects and positioning imprecision. We obtained 51 "used" and 51 "available" plots along 17 snow tracks. We were able to position these sites in the stand using real-time, differentially corrected GPS (March II, CMT Inc.), allowing a possible

inaccuracy of 5 m for the initial location plus 5 m for the subsequent relocation of the site. This approximate 10 m of inaccuracy does not exceed the radius of the survey plot (22.6 m).

We used a marten habitat survey method developed by Laurion (2005), which was elaborated based on the work of Potvin (1998) and Payer & Harrison (2000). We placed one 11.3 m transect from the center of the plot heading North, and a second heading South. On this transect, every CWD (< 45 degrees of angle with the ground and > 7.6 cm in diameter at the intersection with transect; see Payer & Harrison, 2000) was recorded. To exclude CWD that would not have been used by martens during winter (Potvin, 1998; Payer & Harrison, 2000), we excluded debris that did not have at least one point > 50 cm above ground and all parts of the debris buried in the soil. Total length and diameter at both ends were measured (Payer & Harrison, 2000). Volume of CWD was calculated as the portion of a cone, and the variable width transect methodology (de Vries, 1986) was used to calculate CWD volume per hectare.

Canopy closure was also visually estimated, using 10% categories, at both ends and at the center of the CWD transect. Lateral visual obstruction was measured at 11.3 m from the center of the plot to both ends of the CWD transect using a profile board split vertically into four sections of 50 cm (Higgins, Oldemeyer, Jenkins, Clambey & Harlow, 1994). To measure the winter lateral visual obstruction, the proportion of deciduous and coniferous shrubs was assessed independently, and the lower 50 cm section was not considered to account for the snow accumulation (Laurion, 2005). We also counted every understory coniferous stems with living branches at a minimum height of 1.5 meter located within 1 m on each side of the transect (Payer and Harrison, 2003). Larch (*Larix laricina*) stems were excluded because of their winter defoliation.

The height (by 50 cm category) and mid-height diameters of every stump (from 0.5 to 2.0 m), in an 11.3 m radius from the center of the plot, were recorded and used to calculate the volume of stumps per hectare. Volume of individual stumps was calculated as a cylinder (Corn & Raphael, 1992). Snags (i.e. dead trees > 2 m high with an angle of

45 to 90 degrees to the ground) were noted in the same 11.3 m radius. Again, the volume of snags was calculated as a cone (Payer & Harrison, 2000), using approximate height. Exposed root masses were counted in the same circular plot and the diameter of the mass, diameter at the base of the tree trunk and the exposed proportion of the root mass were noted. The volume of each root mass was calculated as a trunked cone, adjusted with the exposed proportion.

Mean tree height was measured with a clinometers on a representative tree of the canopy height inside the 11.3 m radius plot. Finally, the basal area, density and volume of trees were measured using a wedge prism (Higgins *et al.*, 1994). We used a factor two prism and trees with a DBH < 7.5 cm were excluded. Trees were identified at the specie level.

2.3.4 Statistical analysis

The marten track was considered as the sample unit in the statistical analyses. Values for each habitat variable were averaged over the three plots sampled for each used and available track. The difference between the characteristics of the habitat used and the available habitat, as well as between stand types characteristics were analyzed using paired sample *t*-tests (Zar, 1999). Normality of the difference was tested using a Shapiro-Wilk test, and when not normal, a Wilcoxon paired-sample test was used (Zar, 1999). All statistical analyses were performed with SPSS 11.0 for Windows (SPSS Inc., 2003). The significance level used in this study is $p \leq 0,05$, but because of the small sample size relationships with a $p \leq 0,10$ are considered as non-significant strong tendencies and will be discussed in this paper.

2.4 Results

Available habitat in natural stands significantly differed ($p < 0.10$) from intensively managed stands in the following habitat characteristics (Table 5) : higher snag, stumps, exposed root masses, CWD, understory conifer density, canopy height and

deciduous basal area. Also, natural stands had lower winter canopy closure, coniferous and total basal area. These results are consistent with inventories previously made by Laurion (2005) on the same study area.

Table 5 : Forest inventory for available habitat plots and stand type comparisons

| Variable | Nat (n = 5) | | Pl (n = 12) | | Student's <i>t</i> -test | |
|----------------------------|-------------|-------|-------------|------|--------------------------|------------------|
| | Mean | S.D. | Mean | S.D. | <i>t</i> value | <i>p</i> value * |
| Canopy height | 19.22 | 2.42 | 16.50 | 1.35 | 3.007 | 0.05 |
| Snags | 4.29 | 0.97 | 2.07 | 0.75 | 5.149 | 0.00 |
| Stumps | 2.45 | 0.35 | 1.25 | 0.54 | 4.584 | 0.00 |
| Roots mass | 2.35 | 1.02 | 1.00 | 0.92 | 2.697 | 0.10 |
| CWD | 4.05 | 0.47 | 1.74 | 0.93 | 5.203 | 0.00 |
| Understory conifer density | 3.09 | 3.09 | 2.08 | 2.70 | 0.682 | 1.00 |
| Coniferous basal area | 10.33 | 8.01 | 40.40 | 5.52 | 9.92 | 0.00 |
| Deciduous basal area | 23.03 | 4.57 | 2.08 | 1.84 | 7.67 | 0.00 |
| Total basal area | 33.37 | 4.38 | 42.49 | 4.70 | 3.82 | 0.01 |
| Winter canopy closure | 18.00 | 10.95 | 62.08 | 6.20 | 8.45 | 0.00 |

*Bonferroni adjusted *p* value

In both stand types, the habitat characteristics along snow tracks differed from the characteristics of the surrounding stand (Table 6). In mature natural stands (n = 5), the mean tree height was lower ($p < 0.05$), while CWD as well as the coniferous basal area and visual obstruction were higher ($p < 0.10$) on the snow tracks compared to the surrounding stand composition. In plantations (n = 12), the stump volume was lower ($p < 0.05$) and the density of conifers with low branches and the visual obstruction were lower ($p < 0.10$) along the tracks.

Table 6. Comparison of the habitat characteristics found near (< 10 m) marten tracks and in the surrounding mature stands and conifer plantations in the study area. Variables that are different at $p \leq 0.10$ are indicated in bold and italics

| Habitat variable | Natural stands (n = 5) | | | | | | | Plantations (n = 12) | | | | | | | | |
|--|------------------------|--------------------|--------------------|--------------------|--------------------|---------------------|-----------------|----------------------|--------------------|--------------------|--------------------|---------------------|----------|---------------------|------------------|--------------------|
| | Track | | Stand | | Stat. ¹ | Value | df | p | Track | | Stand | | Stat. | Value | df | p |
| | Mean | Std. Err. | Mean | Std. Err. | | | | | Mean | Std. Err. | Mean | Std. Err. | | | | |
| Snag (m ³ /ha) | 106.3 | 32.8 | 84.3 | 31.1 | <i>t</i> | 0.59 | 4 | 0.59 | 9.7 | 1.7 | 10.1 | 3 | <i>Z</i> | -0.47 | - | 0.64 |
| Stumps (m ³ /ha) | 12.2 | 3.4 | 12.0 | 2.0 | <i>t</i> | 0.04 | 4 | 0.97 | <i>3.1</i> | <i>0.5</i> | <i>4.8</i> | <i>0.7</i> | <i>t</i> | <i>-2.91</i> | <i>11</i> | <i>0.01</i> |
| Exposed mass roots (m ³ /ha) | 19.2 | 9.8 | 10.6 | 5.4 | <i>t</i> | 1.37 | 4 | 0.24 | 3.1 | 1.2 | 3.4 | 1.8 | <i>t</i> | -0.36 | 11 | 0.73 |
| Coarse woody debris (m ³ /ha) | <i>84.3</i> | <i>31.2</i> | <i>30.5</i> | <i>10.2</i> | <i>t</i> | <i>2.15</i> | <i>4</i> | <i>0.10</i> | 4.7 | 1.8 | 9.3 | 4.3 | <i>Z</i> | -0.39 | - | 0.70 |
| Understory conifer density (stems/ha) | 213.3 | 180.6 | 306.7 | 259.6 | <i>t</i> | -1.12 | 4 | 0.33 | <i>33.3</i> | <i>27.8</i> | <i>200</i> | <i>121.7</i> | <i>Z</i> | <i>-1.63</i> | - | <i>0.10</i> |
| Canopy height (m) | <i>18.2</i> | <i>1.0</i> | <i>20.2</i> | <i>1.2</i> | <i>t</i> | <i>-3.09</i> | <i>4</i> | <i>0.04</i> | 16.3 | 0.4 | 16.7 | 0.4 | <i>t</i> | -0.97 | 11 | 0.35 |
| Deciduous basal area (m ² /ha) | 22.8 | 3.3 | 23.3 | 1.7 | <i>t</i> | -0.14 | 4 | 0.89 | 1.3 | 0.4 | 2.9 | 0.9 | <i>Z</i> | -1.53 | - | 0.13 |
| Coniferous basal area (m ² /ha) | <i>13.1</i> | <i>4.6</i> | <i>7.5</i> | <i>2.8</i> | <i>t</i> | <i>2.16</i> | <i>4</i> | <i>0.10</i> | 40.7 | 1.6 | 40.1 | 1.8 | <i>t</i> | 0.38 | 11 | 0.71 |
| Total basal area (m ² /ha) | 35.9 | 2.1 | 30.8 | 3.1 | <i>t</i> | 1.46 | 4 | 0.22 | 41.9 | 1.6 | 43 | 1.4 | <i>t</i> | -0.82 | 11 | 0.43 |
| Canopy closure (%) | 15.8 | 4.0 | 18.4 | 6.2 | <i>Z</i> | 0.00 | - | 1.00 | 63.7 | 2.2 | 61.5 | 2.5 | <i>t</i> | 0.68 | 11 | 0.51 |
| Visual obstruction (%) | <i>32.3</i> | <i>6.2</i> | <i>26.2</i> | <i>4.5</i> | <i>t</i> | <i>2.11</i> | <i>4</i> | <i>0.10</i> | <i>30.0</i> | <i>2.3</i> | <i>35.2</i> | <i>2.3</i> | <i>t</i> | <i>-1.79</i> | <i>11</i> | <i>0.10</i> |

Note : *t* = paired samples Student t-test; *Z* = Wilcoxon test for related samples

2.5 Discussion

The selection by martens of features that provide subnivean access was not as strong as expected, especially in natural stands. However, the sample size for natural stands was low, resulting in low power to significantly detect relatively small differences. In naturally regenerated mature stands, martens nevertheless seem to prefer lower stands, as well as higher coniferous basal area and higher visual obstruction. The composition of the stands sampled was mostly deciduous and mixed stands, with a high proportion of shade tolerant hardwood species. These tree species usually reach a higher height than coniferous species in mature stands. The apparent preference made by marten for lower tree height and higher coniferous basal area could then represent a selection for coniferous portions of the stand. In mixed and deciduous mature stands, martens may prefer coniferous areas as they could find a better cover against predator, especially raptors (Hodgman *et al.*, 1997). Marten may also select areas with higher visual obstruction for the same reason. The apparent preference for areas with higher abundance of coarse woody debris could be related to a preference for areas with a large availability of subnivean access, where they can forage for small rodents and where they are less exposed to cold temperatures (Wilbert, Buskirk & Gerow, 2000; Sherburne & Bissonette, 1994; Thompson & Curran, 1995; Buskirk & Harlow, 1989).

In plantations, martens seemed to prefer portions of the stands with lower abundance of stumps and conifers with low branches, as well as lower visual obstruction. Most of the stumps in 20 to 45 year-old plantations originate from commercial thinning operations. Commercial thinning needs parallel trails to circulate in the stand and cut selected stems from this trail. Those trails appear to have more stumps and wood debris (<10cm in diameter) than the rest of the stand and the opening in the canopy they produce allows some shrubs to grow. The selection for lower stump, lower understory conifer density and lower visual obstruction, could illustrate movements between commercial thinning trails remaining inside the stand several years after thinning. This hypothesis could not be tested since we did not collected information on habitat characteristics related to commercial thinning trails.

Marten are probably less exposed to avian predators and they can also probably escape more easily their terrestrial predators in plantations. Indeed, when martens feel threatened, they usually climb in the canopy and escape by jumping from tree to tree (Pelletier, 2005). This escape behaviour is particularly efficient in plantations because the canopy cover is dense and dominated by conifers. This generalized protection in plantations may allow marten to forage in plantations relying on opportunistic prey encountering without risking exposure of open area.

The selection of the available habitat plot on a constant bearing instead of the perpendicular direction of the path could potentially have lead to some correlation between used and available habitat. Some available habitat plots from a north-south oriented path were located inside 10 meters of used habitat plot from the same path. Also, because we conducted the habitat survey several months after having marten tracks mapped, we may have introduced some imprecision in the characteristics of used habitat due to the imprecision of the GPS localisation, particularly in plantations because of the dense resinous canopy (Lejeune & Hellemans, 2000). Thus, the difference we observed between used and available habitat may therefore be conservative, and some preference or avoidance could have been undetected.

Those results contribute to demonstrate that the marten is actually using plantations (20-45 years old) as foraging habitat. American marten is a very polyvalent predator and needs to use most of the available resources to survive throughout winter. In the present study martens showed different foraging behaviour based on the protective cover available in the habitat used.

CONCLUSION GÉNÉRALE

La présente étude avait pour but d'évaluer l'influence de la structure du peuplement sur les déplacements hivernaux à fine échelle de la martre d'Amérique au moyen du pistage sur neige. L'hypothèse principale de ce travail était que, lors de ses déplacements hivernaux, la martre recherche des éléments permettant un accès sous la neige (débris ligneux grossiers, conifères à branches basses et masses racinaires exposées). Si cette hypothèse était valide, la sinuosité des déplacements de martres devait être supérieure dans les peuplements d'origine naturelle à celle des déplacements dans les vieilles plantations, et les éléments permettant un accès sous la neige devaient être plus abondants le long de la piste que dans le reste du peuplement.

Le comportement de la martre était sensiblement différent dans les deux types de peuplement comparés. Les résultats obtenus indiquent que les déplacements hivernaux, contrairement à ce qui avait été prévu, étaient plus sinueux dans les plantations que dans les peuplements d'origine naturelle. Ces résultats suggèrent que les plantations sont vraisemblablement un milieu utilisé pour la recherche de proies et d'abris sur la surface de la neige. Dans les peuplements d'origine naturelle, un milieu relativement ouvert en hiver, la martre semble se déplacer de façon rectiligne, d'un accès sub-nival à l'autre, minimisant ainsi son exposition aux prédateurs et au froid. De même, la martre recherche les secteurs où les débris ligneux sont abondants, où la surface terrière en résineux est plus élevée, et où l'obstruction visuelle est plus grande. Par contre, lorsque la martre se déplace dans les plantations, elle semble éviter les endroits où les souches et les conifères à branches basses sont abondants, tout en recherchant les portions du peuplement ayant une obstruction visuelle inférieure. Grâce à la protection offerte par la densité et la hauteur du couvert arborescent dans les plantations, la martre peut chasser sur la surface de la neige et inspecter à sa guise les pistes de proies rencontrées dans un type de peuplement où les proies sont présentes sur la surface de la neige. La faible quantité d'accès sous la neige dans les plantations diminue la valeur de ce type de peuplement pour la protection contre le froid. Mais le couvert forestier résineux dense procure une protection contre le vent et un couvert de fuite des prédateurs, permettant

une quête alimentaire opportuniste basée sur l'inspection de pistes de proies à la surface de la neige.

Les résultats suggèrent aussi que la martre chasse ses proies principalement au-dessus de la surface de neige et dans la canopée lorsqu'elle se déplace dans les plantations de l'aire d'étude. Dans les peuplements d'origine naturelle, le comportement de recherche de proies de la martre semble plutôt orienté vers les éléments permettant l'accès sous la neige, vraisemblablement à cause de la plus grande exposition au vent et aux prédateurs à la surface de la neige. Ce comportement est plus conforme au comportement alimentaire généralement associé à la martre dans la littérature scientifique.

Il est difficile d'évaluer l'effet de ce changement de comportement sur le maintien de la martre dans un paysage où l'on retrouve une forte proportion de plantations. Pour ce faire, il faudrait comparer le succès de capture de proies par les martres dans les deux types de peuplements, ce qui est très difficile à déterminer lorsque la martre se déplace sous la neige. Néanmoins, les résultats suggèrent que la martre utilise les plantations âgées de 20 à 45 ans pour se nourrir, et l'espèce ne fait pas que traverser les plantations pour se rendre d'un peuplement d'origine naturelle à un autre. Ces plantations contribuent donc, dans une certaine mesure, à fournir à la martre des proies et un refuge arboricole contre les prédateurs. Une analyse plus approfondie de la dynamique de la population dans des paysages couverts par différentes proportions de plantations permettrait de déterminer si une population de martre arrive à se maintenir dans un territoire aménagé de manière intensive.

L'impact de l'aménagement intensif sur les espèces fréquentant les vieilles forêts demeure un sujet très peu connu. Il est difficile d'évaluer la portée des résultats de cette étude étant donné la grande variabilité régionale des résultats d'études de sélection de l'habitat de la martre. Néanmoins la modification de comportement observée dans les plantations démontre l'importance de ce type de recherche. De plus, les plantations étudiées n'avaient toujours pas atteint leur maturité, et encore deux éclaircies

commerciales devraient y être effectué. De nombreuses questions se posent toujours sur l'impact que ces opérations d'éclaircies à grande échelle auront sur la martre dans le futur. Les résultats obtenus dans la présente étude suggèrent que les peuplements issus de la sylviculture intensive puissent avoir une valeur pour certaines espèces traditionnellement associées aux vieilles forêts de conifères.

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