

UNIVERSITÉ DU QUÉBEC

**Influence de la coupe forestière sur la sélection de l'habitat par
l'ours noir (*Ursus americanus*) en forêt boréale**

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AVANT-PROPOS

Ce mémoire est présenté sous la forme d'un manuscrit qui sera soumis à une revue scientifique. Le chapitre concernant le manuscrit est donc présenté en anglais. L'introduction et la conclusion générale sont rédigées en français et elles présentent le contexte de l'étude et résument l'essentiel des résultats sujets à des retombées appliquées dans la gestion de l'ours noir en forêt boréale.

RÉSUMÉ

L'exploitation forestière intensive modifie la structure d'âge de la forêt boréale à l'échelle continentale en rajeunissant un paysage autrefois dominé par des peuplements matures et surannés. Il est reconnu que dans les forêts septentrionales, l'écologie de l'ours noir (*Ursus americanus*) est principalement influencée par la productivité des arbustes fruitiers, généralement intolérants à l'ombre. Nous avons donc émis l'hypothèse que l'exploitation forestière influence la sélection de l'habitat par l'ours noir. Le suivi télémétrique VHF de 12 femelles dans la Réserve faunique des Laurentides (Québec, Canada) en 2004 et 2005 nous a permis d'analyser les patrons saisonniers de sélection d'habitat dans un paysage hétérogène à deux échelles spatiales (i.e. paysage et domaine vital). La caractérisation de la végétation d'intérêt pour l'ours en sept types de couvert forestier (Coupe récente (0-5 ans), Régénération ouverte (6-20 ans), Régénération fermée (6-20 ans), Jeune peuplement (20-50 ans), Mature mixte (> 50 ans), Mature résineux (> 50 ans) et Tourbière) a permis de comparer la productivité en petits fruits de peuplements de différents stades successifs suite à la coupe avec protection de la régénération et des sols (CPRS). Les peuplements de 6-20 ans, en régénération ouverte et fermée, supportaient la plus abondante couverture de végétation au sol, une plus forte densité de petits fruits et une biomasse élevée de petits fruits. Les ours ont préféré les couverts forestiers de type Régénération ouverte, aux échelles du paysage (34.7% de la composition du domaine vital vs. 26.1% de la composition de l'aire d'étude) et du domaine vital (42.3% des localisations vs. 34.7% de la composition du domaine vital) et ils évitaient le couvert forestier de type Mature résineux (> 50 ans) à l'échelle du domaine vital (21.7 vs. 30.0%). La taille des domaines vitaux était inversement proportionnelle à leur proportion en habitats âgés entre 6 et 20 ans suite à la coupe forestière. L'exploitation forestière intensive a influencé les patrons d'utilisation de l'espace et de l'habitat chez l'ours noir, et possiblement la dynamique des populations, en augmentant la capacité de support des habitats septentrionaux. La croissance des populations de ce prédateur opportuniste pourrait avoir des conséquences en conservation dans les paysages perturbés, notamment pour le caribou forestier.

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CHAPITRE I : INTRODUCTION GÉNÉRALE

L'ours noir (*Ursus americanus*) est un animal omnivore opportuniste présent dans une multitude de zones bioclimatiques en Amérique du Nord (Pelton 2003). La limite nord de son aire de répartition est étroitement liée au vaste biome de la forêt boréale, et sa présence est notée dans la toundra, sur la péninsule de l'Ungava. L'ours noir possède une capacité d'apprentissage élevée, la flexibilité de ses patrons d'activité et son régime alimentaire diversifié reflètent sa grande capacité d'adaptation (Stirling & Derocher 1990). La perte d'habitat a réduit de 40% l'aire de répartition historique de l'ours noir qui s'est graduellement confinée au nord du continent (Laliberte & Ripple 2004). La plus importante population d'ours est maintenant répartie à une densité relativement faible dans la forêt boréale Nord-Américaine (Samson 2001; Pelton 2003). Malgré de nombreuses études sur l'ours noir en forêt mixte, son écologie en forêt boréale reste méconnue (Samson 1996). À ce jour, notre capacité d'effectuer une gestion intégrée des populations septentrionales est donc limitée.

Outre les études menées en Alberta (Young & Ruff 1982) et en Alaska (Schwartz & Franzman 1991), les recherches sur l'ours noir en forêt boréale ont été réalisées en forêt boréale de transition (Jonkel & Cowan 1971; Rogers 1977; Obbard & Kolenosky 1994; Samson & Huot 1998) et sous l'influence du climat maritime (Chamberland 1999; Daigle *et al.* 1999; Deering 1999; Fortin *et al.* 1999). La diversité d'arbres et arbustes feuillus présents dans la zone de transition mixte offre une alimentation plus riche en protéines et gras végétaux ainsi que des contraintes environnementale moins sévères qu'en forêt de conifères. Comme l'écologie de l'ours noir est fortement reliée à l'abondance et à la diversité de la nourriture végétale, son comportement est susceptible de varier selon les différentes zones bioclimatiques (Jonkel & Cowan 1971). La rigueur et la longueur des hivers s'ajoutent à la faible diversité alimentaire ce qui fait de la forêt boréale un habitat contraignant pour l'ours noir.

La forêt boréale du centre du Bouclier Canadien a été perturbée sur plus de 50% de sa superficie (WWF 2006). L'exploitation forestière intensive est susceptible d'engendrer une modification importante de la disponibilité des ressources (Nielsen *et al.* 2004; Friedman & Reich 2005). En forêt mixte, l'ours utilise les peuplements jeunes de façon opportuniste et tend à préférer les peuplements matures qui offrent davantage de ressources protéiques sous la forme de noix (Litvaitis 2001). À l'opposé, il est possible qu'en forêt boréale, les peuplements jeunes supportent davantage de ressources énergétiques pour l'ours, principalement des petits fruits (Obbard & Kolenosky 1994). La variation importante de la composition végétale des différentes zones bioclimatiques est à l'origine de l'ambiguïté de la relation entre la qualité de l'habitat et l'âge des peuplements. En effet, des études démontrent que l'ours noir tend à la fois à préférer les coupes forestières (Jonkel & Cowan 1971; Lindzey & Meslow 1977; Samson & Huot 1998) et à les éviter (Unsworth, Beecham & Irby 1989; Koehler & Pierce 2003; Mitchell & Powell 2003). L'impact de la coupe forestière sur la qualité de l'habitat de l'ours est donc nuancé en fonction de l'origine du peuplement perturbé (Mitchell & Powell 2003), et selon l'importance des petits fruits dans sa diète automnale (Rogers 1976).

Plusieurs études soulignent l'importance de l'apport en nourriture à forte teneur protéique et lipide en fin de saison pour l'ours noir (Amstrup & Beecham 1976; Garshelis & Pelton 1981; Rogers 1987; Elowe & Dodge 1989; Costello & Sage 1994; Samson & Huot 1998). Bien que l'ours soit connu pour sa grande consommation de petits fruits (Rogers 1976), un pourcentage minimal en protéines animales et végétales est nécessaire pour la maximisation de son rendement métabolique (Rode & Robbins 2000). Or, la forêt boréale est dépourvue de la majorité des espèces végétales riches en protéines et lipides recherchées par l'ours. Face à cette difficulté, l'ours doit de surcroît être en mesure d'accumuler des réserves de graisse suffisantes pour une hibernation prolongée qui peut durer plus de six mois. La stratégie alimentaire végétale de l'ours noir vise à maximiser la taille des bouchées et le

rythme d'ingestion en sélectionnant les parcelles d'habitat de forte densité calorique (Welch 1997). Les peuplements où la nourriture est distribuée en parcelles de forte densité seraient préférés aux peuplements où la densité est plus faible ou homogène (Rogers 1987). La qualité d'un habitat d'alimentation pour l'ours noir dépendrait donc de l'agglomération et de la valeur énergétique des ressources.

Les besoins changeants et les différents aspects du cycle vital de l'ours peuvent engendrer un patron de déplacement saisonnier spécifique (Garshelis & Pelton 1981; Young & Ruff 1982; Elowe & Dodge 1989; Schwartz & Franzman 1991; Schooley *et al.* 1994; Samson & Huot 1998). L'analyse des déplacements à l'échelle du domaine vital révèle normalement la présence de secteurs d'intérêt particulier (Powell, Zimmerman & Seaman 1997; Samson & Huot 1998). Un patron typique d'utilisation de l'espace est caractérisé par un ou deux groupements de localisations distincts formant des zones d'utilisation intensive dans le domaine vital. Dans un milieu hétérogène, les déplacements se feraient en relation avec la phénologie des espèces comestibles (Unsworth, Beecham & Irby 1989; Schwartz & Franzman 1991). Cependant, une étude menée par Lindzey et Meslow (1977) démontre que les femelles matures utilisent l'ensemble de leur domaine vital indépendamment de la période de l'année. Ces auteurs stipulent cependant que la sélection saisonnière s'exercerait à une échelle plus fine, selon la disponibilité de la nourriture. La capacité d'interpréter les patrons de déplacements est limitée par l'échelle utilisée, les variables utilisées pour qualifier les catégories d'habitat, ainsi que par la fréquence et la précision des localisations télémétriques.

Certaines études démontrent que la distance journalière moyenne parcourue par l'ours noir est inférieure à 2 km (Amstrup & Beecham 1976; Young & Ruff 1982; Rogers 1987; Horner & Powell 1990). Cependant, une femelle aurait la capacité de parcourir plus de 50 km en une journée (observation personnelle). La faible disponibilité de nourriture au printemps est susceptible d'augmenter l'ampleur des déplacements de l'ours noir. Les déplacements semblent

ensuite diminuer graduellement au cours de l'été (Young & Ruff 1982), spécialement chez les femelles (Amstrup & Beecham 1976). L'ours noir a un patron d'activité normalement diurne (Amstrup & Beecham 1976; Larivière, Samson & Huot 1994; Hirsch, Bender & Haufler 1999) et présente généralement un pic d'activité crépusculaire (Lindzey & Meslow 1977; Larivière, Samson & Huot 1994). L'activité nocturne serait plus soutenue au printemps et à l'automne (Amstrup & Beecham 1976) ainsi qu'en présence de ressources anthropiques (Clark, van Manen & Pelton 2002). Notons toutefois que les patrons d'activité ont presque exclusivement été étudiés en milieux mixtes et feuillus. Leur lien étroit avec la qualité du milieu laisse croire qu'ils pourraient différer en forêt boréale.

Le degré de chevauchement des domaines vitaux est une mesure indirecte de la territorialité qui est largement répandue chez les mammifères (Maher & Lott 1995). Puisque l'ours se déplace généralement sur de grandes superficies et qu'il utilise certains secteurs plus intensivement, l'étude de la territorialité nécessite l'analyse temporelle des localisations dans les zones d'utilisation intensive (Samson & Huot 2001). Comparativement aux milieux riches, le domaine vital des femelles adultes présente généralement moins de chevauchement dans les habitats de productivité intermédiaire (Rogers 1987). En milieu productif, la territorialité chez les femelles adultes augmenterait lorsque la productivité du milieu diminue (Horner & Powell 1990), et serait aussi amplifiée en période d'œstrus (Garshelis & Pelton 1981; Horner & Powell 1990). Cependant, il semble que la variation de la territorialité suite à la modification de la productivité du milieu soit nuancée par la qualité initiale de l'habitat. En milieu peu productif, le chevauchement des domaines vitaux serait élevé, ce qui traduirait la difficulté à défendre l'exclusivité d'un vaste domaine vital (McLaughlin & Ferguson 2000). L'amélioration de la qualité d'un habitat pauvre pourrait donc accroître l'expression de la territorialité en réduisant la taille du domaine vital des individus. La territorialité chez l'ours deviendrait un facteur limitant de plus grande importance dans un habitat de qualité moyenne.

La disponibilité et la qualité des sites de tanière peuvent influencer la dynamique d'une population d'ours noir en agissant sur la survie des oursons (White *et al.* 2001). En forêt mixte, les femelles ont tendance à hiverner à l'intérieur de leur domaine vital estival (Schooley *et al.* 1994). La familiarité des sites d'alimentation à la sortie de la tanière serait un avantage lors de cette période critique (White *et al.* 2001). La préférence des cavités d'arbres comme site de tanières a été démontrée en présence d'arbres de diamètre suffisant (Oli, Jacobson & Leopold 1997; Powell, Zimmerman & Seaman 1997; White *et al.* 2001). En forêt boréale de transition, les arbres déracinés offrent un couvert de prédilection lors de l'hibernation (Daigle *et al.* 1999). En forêt exploitée, l'utilisation de débris de coupe en guise de couvert est fréquente (Hellgren & Vaughan 1989; White *et al.* 2001). Il est donc possible que les milieux récemment affectés par la coupe forestière procurent aussi des sites de tanière en forêt boréale, en complément aux forêts matures qui contiennent bon nombre de gros arbres renversés.

La disponibilité du couvert arborescent mature en tant que refuge serait d'importance pour l'ours. Bien que ce comportement soit peu documenté, il est reporté que les femelles accompagnées d'oursons utilisent la bordure forestière lorsqu'elles s'alimentent dans les milieux ouverts (Jonkel & Cowan 1971; Lindzey & Meslow 1977). Il est connu que les ourses incitent leurs oursons à grimper dans les arbres afin de les protéger du danger (Herrero 1972). La disponibilité d'un couvert de fuite pourrait donc influencer l'utilisation de l'habitat par l'ours (Young & Beecham 1983). En forêt boréale, l'habitat privilégié de l'ours serait similaire à celui de l'original (*Alces alces*), soit un entremêlement de milieux ouverts de faibles superficies et riches en nourriture, et d'un couvert forestier mature suffisant en guise de refuge (Claude Samson, communication personnelle).

La présence de nombreux aménagements forestiers en forêt boréale incite à un questionnement quant aux effets directs et indirects d'un habitat fortement perturbé sur les

relations trophiques. Ainsi, puisque l'ours noir est un prédateur efficace des jeunes ongulés (Schwartz & Franzman 1991; Ballard 1994), la dynamique de ses populations est susceptible d'influencer le taux de survie du caribou forestier (*Rangifer tarandus caribou*), une espèce désignée menacée par le *Comité sur la situation des espèces en péril du Canada* depuis 2001 (L.R.C., c. C-29), et désignée vulnérable par le gouvernement du Québec en février 2005 (L.R.Q.C., E-12.01).

Dans le cadre du projet de rétablissement de la population du caribou forestier de Charlevoix, une évaluation de la relation prédateur-proie est en cours dans la Réserve faunique des Laurentides (Lambert *et al.* 2006). Les résultats préliminaires de cette étude démontrent un lien important entre la prédation des faons par l'ours noir et le faible taux de recrutement de la population de caribous de Charlevoix. Une gestion intégrée prédateur-proie-habitat est envisagée afin de réduire les facteurs limitatifs de la croissance de la population de caribous (Sebbane *et al.* 2003). Cependant, l'utilisation de l'habitat et les patrons d'activité de l'ours noir dans l'aire de répartition du caribou de Charlevoix ne sont pas documentés.

Cette étude a pour objectif de documenter la sélection d'habitat de femelles ours noir en forêt boréale dans un habitat perturbé par l'exploitation forestière intensive. Nous avons émis l'hypothèse que l'exploitation forestière influence les patrons de sélection d'habitat et de déplacement de l'ours en augmentant la densité de nourriture par le rajeunissant du couvert forestier. Nous avons prédit de meilleures conditions alimentaires dans les peuplements âgés entre 6 et 20 ans suite à la coupe forestière. Ainsi, l'ours noir devrait préférer ces habitats, et éviter les peuplements d'âge mature et suranné qui offriraient de moins bonnes conditions alimentaires. Comme la taille des domaines vitaux est proportionnelle à la productivité du milieu chez l'ours, la proportion des habitats de 6-20 ans dans un domaine vital devrait être inversement proportionnelle à sa taille. Les aires de chevauchement entre les différents

domaines vitaux devraient contenir une proportion d'habitats de 6-20 ans supérieure à leur disponibilité dans l'aire d'étude.

CHAPITRE II : HABITAT SELECTION BY BLACK BEARS IN AN INTENSIVELY LOGGED BOREAL FOREST

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Abstract

Intensive logging is modifying the boreal forest age structure at the continental scale by rejuvenating a landscape once dominated by old-growth stands. Black bear (*Ursus americanus*) fitness and behavior are known to be primarily related to the abundance of shade intolerant soft mast species in northern forests. Therefore, we hypothesized that logging will influence habitat and space use patterns of black bears. We used VHF telemetry on 12 mature female black bears in the Reserve faunique des Laurentides (Québec, Canada) in 2004 and 2005 to investigate seasonal patterns of habitat selection in an exploited heterogeneous boreal landscape at two spatial scales (i.e. landscape and home range). Habitat characterization based on 7 forest cover types, taking into account time elapsed since disturbance (Recent clearcut (0-5 years), Open regeneration (6-20 years), Closed regeneration (6-20 years), Young stands (20-50 years), Mature mixed (> 50 years), Mature coniferous (> 50 years) and Bog), allowed us to compare the productivity of key forage species in various post-logging age classes. Open and closed regeneration 6-20 years old had the uppermost ground vegetation cover, providing both the highest density and a high biomass of berries. Female black bears preferred open regeneration 6-20 years old at both the landscape (34.7% of the home range vs. 26.1% of the study area) and home range scales (42.3% of locations vs. 34.7% of the home range), and avoided mature coniferous forests (> 50 years old) at the home range scale (21.7 vs. 30.0%). Home range size was inversely related to the proportion of 6-20 year old clearcuts. Intensive logging influenced black bear habitat and space use patterns, and presumably their population dynamics, by increasing the carrying capacity of northern habitats. Increasing populations of an opportunistic predator such as black bear poses great concern for conservation, especially for forest-dwelling woodland caribou.

Keywords: Black bear, boreal forest, habitat selection, home range, clearcut logging, berries.

Résumé

L'exploitation forestière intensive modifie la structure d'âge de la forêt boréale à l'échelle continentale en rajeunissant un paysage autrefois dominé par des peuplements matures et surannés. Il est reconnu que dans les forêts septentrionales, l'écologie de l'ours noir (*Ursus americanus*) est principalement influencée par la productivité des arbustes fruitiers, généralement intolérants à l'ombre. Nous avons donc émis l'hypothèse que l'exploitation forestière influence la sélection de l'habitat par l'ours noir. Le suivi télémétrique VHF de 12 femelles dans la Réserve faunique des Laurentides (Québec, Canada) en 2004 et 2005 nous a permis d'analyser les patrons saisonniers de sélection d'habitat dans un paysage hétérogène à deux échelles spatiales (i.e. paysage et domaine vital). La caractérisation de la végétation d'intérêt pour l'ours en sept types de couvert forestier (Coupe récente (0-5 ans), Régénération ouverte (6-20 ans), Régénération fermée (6-20 ans), Jeune peuplement (20-50 ans), Mature mixte (> 50 ans), Mature résineux (> 50 ans) et Tourbière) a permis de comparer la productivité en petits fruits de peuplements de différents stades successifs suite à la coupe avec protection de la régénération et des sols (CPRS). Les peuplements de 6-20 ans, en régénération ouverte et fermée, supportaient la plus abondante couverture de végétation au sol, une plus forte densité de petits fruits et une biomasse élevée de petits fruits. Les ourses ont préféré les couverts forestiers de type Régénération ouverte, aux échelles du paysage (34.7% de la composition du domaine vital vs. 26.1% de la composition de l'aire d'étude) et du domaine vital (42.3% des localisations vs. 34.7% de la composition du domaine vital) et ils évitaient le couvert forestier de type Mature résineux (> 50 ans) à l'échelle du domaine vital (21.7 vs. 30.0%). La taille des domaines vitaux était inversement proportionnelle à leur proportion en habitats âgés entre 6 et 20 ans suite à la coupe forestière. L'exploitation forestière intensive a influencé les patrons d'utilisation de l'espace et de l'habitat chez l'ours noir, et possiblement la dynamique des populations, en augmentant la capacité de support des

habitats septentrionaux. La croissance des populations de ce prédateur opportuniste pourrait avoir des conséquences en conservation dans les paysages perturbés, notamment pour le caribou forestier.

Mots-clés : Ours noir, forêt boréale, sélection de l'habitat, domaine vital, coupe forestière, petits fruits.

Nomenclature : (Marie-Victorin 1995; Prescott & Richard 1996)

Introduction

The boreal forest covers nearly 90 percent of Canada's productive forested land and most of interior Alaska. These forests were once dominated by old-growth stands where historically, the mosaic of seral types was mainly shaped by wildfire (Haggstrom & Kelleyhouse 1996; Brassard & Chen 2006). Over the past 30 years, intensive logging has changed the natural perturbation regime by rejuvenating boreal forests at the continental scale. The World Wildlife Fund reports that more than 50% of the Central Canadian Shield forests have been logged (WWF 2006). Clearcutting is the dominant harvesting technique in fir-spruce forests. This method is the most intensive and designed for exploitation of even-aged stands, naturally found throughout most of the boreal forests (Burton *et al.* 2003). The impact of clearcuts on seral habitats remains ambiguous although changes in resource availability and habitat structure may have strong consequences on many wildlife species (Thompson, Baker & Ter-Mikaelian 2003; Malcolm *et al.* 2004)

The boreal forest shelters the most abundant black bear (*Ursus americanus*) populations (Samson 2001; Pelton 2003), though these are poorly documented. Black bears have proven great adaptability by colonizing a variety of habitats throughout North America, mainly because of their opportunistic behavior (Stirling & Derocher 1990). However, the species distribution has considerably regressed northwards and has now lost approximately

40% of its historical range (Laliberte & Ripple 2004). Consequently, black bears are gradually being confined to less productive northern habitats even though their ecology is in close relation with the abundance of high energy foods (Jonkel & Cowan 1971; Rogers 1976; Schwartz & Franzman 1991). Survival rates and reproductive success are known to be closely related to the abundance of proteins and lipids in their fall diet, mainly comprised in hard mast food supplies (Amstrup & Beecham 1976; Costello & Sage 1994; Samson & Huot 1998). Boreal forests offer meagre hard mast species due to rigorous winters and short growing seasons.

Harvested stands now characterize most of the coniferous and mixed northern habitats (Fisher & Wilkinson 2005). Logging is commonly perceived as habitat loss through extreme modification of structural aspects, physical conditions and species composition. Still, the increased abundance and productivity of shade intolerant species and early succession edible deciduous trees (Moola & Mallik 1998; Bock & Van Rees 2002; Etcheverry, Ouellet & Crête 2005) could make harvested coniferous stands favourable to bears (Rogers 1976; Lindzey & Meslow 1977). However, stand level planning often generates extensive open clearcuts (Burton *et al.* 2003) that may not be fully exploited by black bears (Samson 1996). Some fruit-producing species can be more productive in forested conditions (Nielsen *et al.* 2004) or sensitive to important environmental change (Moola & Mallik 1998). Our knowledge of species composition and structure of post-logging seral types is limited by intensive logging's short history (Malcolm *et al.* 2004; Brassard & Chen 2006).

The foraging strategy of bears seems oriented towards high-grading, which consists of foraging mainly in high density berry patches to maximize bite size and in moving constantly to attain a profitable bite rate (Rogers 1987; Welch 1997). The distribution and productivity of key berry species throughout seral habitats becomes of great concern when considering black bear foraging behavior (Welch 1997). Even though black bears are known to be

efficient predators of cervids (Schwartz & Franzman 1991; Ballard 1994; Lambert *et al.* 2006), their meat consumption is highly variable (Jacoby *et al.* 1999) and a minimum of fruit abundance is necessary for their survival even in the presence of abundant animal prey (Côté 2005). The integration of behavioral aspects in habitat selection studies is important to extend and better understand the perceptual scales and movements of animals (Lima & Zolner 1996). The behavior of black bears in managed landscapes is complex and remains unclear (Koehler & Pierce 2003).

Studies have shown that black bear territoriality and spatial activity patterns are influenced by seasonal food availability (Garshelis & Pelton 1981; Horner & Powell 1990). Thus, habitat use and intraspecific interactions can vary at different latitudes (Jonkel & Cowan 1971; Garshelis & Hellgren 1994). In comparison to males, female black bears have smaller home ranges. Female home range size greatly depends on seasonal food availability, while ranging behavior of males is greatly influenced by polygamous mating strategies (Rogers 1977; Powell, Zimmerman & Seaman 1997). Female behavior is consequently closely related to habitat productivity. Home range overlap between individuals is a common measure of territoriality (Maher & Lott 1995) and can be related to habitat productivity (Rogers 1987; McLaughlin *et al.* 2003). The remodelling of the landscape and the seral environmental changes following clearcut can greatly influence the behavior of black bear females.

We hypothesised that black bear space and habitat use patterns are influenced by logging in the boreal forest through an increase in forage availability. We predicted that black bears would prefer habitats providing better foraging conditions. We expect that 6 to 20 years post-logging forest covers would provide these conditions. Further, if as expected the boreal habitat is of poor foraging quality, individual home ranges should overlap considerably (McLaughlin *et al.* 2003) and overlap areas should be comprised of high proportions of 6 to

20 years post-logging. Finally, home range size should be negatively related to the proportion of 6-20 years post-logging habitats.

STUDY AREA

This study was conducted in the réserve faunique des Laurentides, ca. 100 km north of Québec city ($47^{\circ} 34' N$, $71^{\circ} 12' W$), on the southeast region of the Central Canadian Shield in the balsam fir-white birch eastern sub-domain. The landscape is dominated by the Laurentian hills with elevations ranging from 500 m to 1100 m above sea level. The centennial logging history, becoming extensive during the past 25 years, has created a heterogeneous landscape and provided access to most of the Wildlife Reserve (7995 km^2) and surrounding areas. Due to the elevation of the Laurentian hills, the climate is relatively cold for this latitude with an average of 75 days without frost, limiting growth of most deciduous tree species. Depending on local weather, black bears can den from November to mid-May. The area is characterised by important precipitations ($\approx 1500 \text{ mm/year}$); snow accumulates to over 3 m.

The forest cover is dominated by black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), and sparsely distributed white spruce (*Picea glauca*). Trembling aspen (*Populus tremuloides*) becomes more abundant in lower altitudes and tamarack (*Larix laricina*) is also present on moist soils. The most abundant berry species found in the study area and prized by bears are: blueberry (*Vaccinium myrtilloides*), raspberry (*Rubus idaeus*), cloudberry (*Rubus chamaemorus*), currants (*Ribes sp.*), and small cranberry (*Vaccinium oxycoccus*), all of which are mostly shade intolerant. Bunchberry (*Cornus Canadensis*) and creeping snowberry (*Gaultheria hispida*) are also common edible fruits, and can be found even in shaded conditions. Weekly monitoring of plant maturation over the course of the two-year telemetry survey indicated that fruits ripen after July 20, allowing

bears to feed on higher energy sources in the late summer and fall. This was corroborated by scat analysis also performed during the study (unpublished data).

Methods

CAPTURE AND TELEMETRY

We used foot snares and tube traps (Lemieux & Czetwertynski 2006) to capture black bears during early summer 2004 (June 17-10 July) and spring 2005 (May 17 – 23 June). Animals were immobilized using tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, Ayerst Laboratories Inc., Montréal, Québec, Canada) from a projectile dart. Females that were over 5 years of age were fitted with a VHF collar (Lotek LMRT-4), modified for an extendable fit and wear-off release. All captures were made during spring-early-summer. Captured bears were measured, weighed and identified using numbered ear tags. We noted the presence of cubs and lactation to determine reproductive status. Dens were visited during winters of 2005, 2006 and 2007 between the end of February and the end of March for collar adjustments and information on reproductive status. Den location was taken on site and plotted on forest maps to ascertain the percentage of dens in each forest cover type. Handling procedures were approved by the Animal Care Committee of the ministère des Ressources naturelles et de la Faune (N° 04-00-02) and of the Université du Québec à Rimouski (N° 17-04-22) based on the Canadian Council on Animal care guidelines.

An attempt was made to locate each individual on a daily basis. Pick-up trucks and all-terrain vehicles gave access to most logging roads, non accessible terrain was covered by foot. The study area was made highly accessible by past and ongoing logging activities and maintenance of main roads for outfitting purposes. This allowed most localisations to be made within 1 km of the animal using a portable VHF receiver. On average, 5 bearings were used to obtain a location. A small aircraft or helicopter was used twice to locate individuals leaving

their usual area. Telemetry tracking was conducted in July and August in 2004 and covered most of the active period in 2005 from mid-May to October. Locations were taken at least 16 hours apart during daylight. Triangulation was calculated using LOAS® software (Ecological Software Solutions, CA.). Median radius localization error calculated from field tests of 20 known collar positions was 136 m.

FOREST COVER TYPES

Forest cover types were characterized using forest maps (smallest polygon = 4 ha) produced by the ministère des Ressources naturelles et de la Faune du Québec from 1:15 000 aerial photographs. Photographs were taken in 1990-91 and maps were updated to 2005 by including subsequent cut blocks. Habitats were then grouped into 7 forest cover types (Recent clearcut 0-5 years, Open regeneration 6-20 years, Closed regeneration 6-20 years, Young 30-50 years, Mature mixed >50 years, Mature coniferous >50 years, Bog), taking into account the limitations of forest maps (Dussault *et al.* 2001), the objectives of this study and the biology of the study species. The classification was intended to represent the forest succession following CPRS (clearcut with protection of regeneration and soils), the dominant logging method in Québec, and in the study area.

Post-perturbation forest was composed of early regenerating stands aged under 20 years after logging or natural perturbation. Recent clearcut (0-5years; 9.2% of the study area) were harvested in the past 5 years and were completely depleted of trees and poles but had important logging slash (unpublished data). Since the forest map showed that an important proportion (70%) of stands aged between 6 and 20 years after logging had poor tree stocking up to 20 years after intervention, we divided this seral type into Open regeneration and Closed regeneration forest covers. Vegetation surveys confirmed the forest map information. Open regeneration (6-20 years; 26.1% of the study area) was characterised by sites supporting

mostly black spruce seedlings, no tree, and were typically composed of poles that were less than 4.2 ± 0.7 meters in height. Closed regeneration forest covers (6-20 years; 7.9% of the study area) were composed of well regenerated stands and characterised by tree stocking of either coniferous or mixed species that were 6.9 ± 1.1 meters in height. Canopy closure was $15\% \pm 3$ for Open regeneration and $29\% \pm 3$ in Closed regeneration forest covers, respectively.

Established forest was composed of a variety of stands originating from post-logging and natural perturbations at least 30 years of age. Young forest covers (7.1% of the study area) represent seral types of between 20 and 50 years. They were mainly composed of conifers, dominated by black spruce and fir, with good stocking of poles and trees reaching over 11 m in height and forming a relatively dense canopy closure ($77\% \pm 3$). Mature mixed forests (7.7% of the study area) were aged between 50 and 120 years following anthropic or natural perturbations. Mature mixed forests were composed of paper birch with spruce and fir as co-dominates, resulting in a dense canopy closure ($80\% \pm 2$). Mature coniferous forests (32.6% of the study area) were over 50 years of age and included over-mature and old-growth forests. They were typically dominated by black spruce-moss stands and characterised by high canopy closure ($77\% \pm 2$). Bog forest covers (2.5% of the study area) comprised humid, non productive open areas ($10\% \pm 2$ canopy closure) covered by sphagnum species, shrubs, grasses and sedges, and stunted conifers. Non-forested areas (*e.g.* lakes, sand pits, etc.) were categorized as Other (7.0% of the study area).

FRUIT ABUNDANCE AND BIOMASS

Fruit abundance and biomass of the main forage species for bears were estimated on ten 100 m transects randomly located within each of the 7 forest cover types considered in this study. Because plant diversity was low, all common berry shrub species were considered

as main forage species; this assumption is supported by an analysis made on 226 scats that were sampled in the study area during the two-year study (unpublished data). Five 4 m² sample plots were regularly spaced along each transect to estimate ground cover and measure fruit production. Within each plot, all fruits were inventoried using a hand-held counter device. We also estimated canopy closure using a spherical densiometer (Robert E. Lemmon forest densiometers, Bartlesville OK, USA). A sub-sample of 20 fruits was picked according to its availability within transects in the different forest cover types. Wet weight was used to compare fruit biomass between forest cover types. We also estimated the suitability of forest covers for a high-grading foraging strategy using the same approach in another 4 m² plot that we felt contained the greatest fruit density along each transect.

STATISTICAL ANALYSES

We used one-way nested ANOVAs, nesting plots by transect to determine the effect of forest cover types on vegetation characteristics and *post-hoc* Tukey test to identify significant differences between forest cover types.

Total and seasonal individual home ranges were estimated using the 100% minimum convex polygon method. A least-squares linear regression was used to assess the relationship between home range size and their proportion of 6-20 years forest cover; we pooled Open regeneration and Closed regeneration forest covers because of their similarity in fruit density and biomass. A comparison between the percentage of 6-20 years forest cover in home range overlap areas and annual ranges was made using a *t*-test.

The study area consisted of the 100% minimum convex polygon encompassing all individual home ranges. First we tested habitat selection at the landscape scale by comparing the home range forest cover type composition to availability within study area. To test habitat selection at the home range scale, we compared forest cover type at bear locations to

availability within home ranges. We tested the null hypothesis of no difference between habitat use and availability using the Hotelling's T² test (Rouleau, Crête & Ouellet 2002), a multivariate approach similar to the one proposed by Aebischer *et al.* (1993) but without log-ratio transformation of the data which is controversial in the literature (McClean *et al.* 1998). When a significant difference between use and availability was detected, we tested selection for each forest cover type using univariate *t*-test.

Habitat preference of den sites was tested with a G-test to distinguish mature (by pooling Mature mixed and Mature coniferous forest covers) and 0-20 years forest cover (by pooling Recent clearcut, Open regeneration and Closed regeneration forest covers). We used the composition of the study area to determine the expected occurrence of dens in each forest cover type. Significant threshold was set at 0.05 for acceptance of null hypothesis. We used SYSTAT 11.0 (SPSS 2004) for statistical analyses. Means \pm 1 SE are presented.

Results

CAPTURE AND DEN VISITS

A total of 12 mature females were tracked in 2004 and 2005; 8 females were tracked for the 2-year duration of the study and 4 others in 2005 (Table I). Bear no. 2, 5 and 21 died during the study, the last being struck by a truck in late-fall, the others were shot during spring and fall hunting of 2005. The average age of collared females in 2004 was 6.6 ± 0.7 , when omitting bear no. 5 that was an especially old individual at 29 years of age, and of 8.0 ± 0.7 in 2005. Collared females had an average body mass of 51.8 ± 2.3 kg at capture. No females were accompanied by a cub or a yearling during the two years of tracking. However, during the 2006 winter, 7 out of the remaining 9 females had cubs. In 2007, 3 out of the 6 remaining females had cubs and two were accompanied by yearlings. The mean litter size was

of 2.3 ± 0.2 cubs for the 10 females that reproduced. The body mass of the 7 females that had cubs averaged 55.1 ± 2.5 kg during the 2006 den visits; no measures were taken during the 2007 den visits.

FRUIT ABUNDANCE AND BIOMASS

Shrub vegetation cover ($F_{6, 63} = 13.462; p < 0.001$), fruit density ($F_{6, 63} = 11.440; p < 0.001$) and fruit biomass ($F_{6, 63} = 3.192; p = 0.008$) differed among forest cover types (Table II). In high-grading plots, shrub cover ($F_{6, 60} = 4.796; p < 0.001$), fruit density ($F_{6, 60} = 6.202; p < 0.001$), and biomass ($F_{6, 60} = 3.732; p = 0.003$) also differed significantly according to forest cover type.

In random plots (Table II), shrub cover was higher in Closed regeneration and Open regeneration forest covers compared to other forest covers ($p \leq 0.008$), except for Bog ($p = 0.298$). Open regeneration and Closed regeneration forest covers had higher fruit densities than other forest covers ($p \leq 0.007$). Except for Open regeneration forest cover, which had a higher biomass than Young ($p = 0.05$), no significant difference in biomass was detected among forest covers; high variability and the relatively small sample size likely explain this result.

In high-grading plots (Table II), shrub cover was higher in Open regeneration and Closed regeneration forest covers than in Young and Mature mixed forest covers ($p \leq 0.011$). Fruit density was similar in Open regeneration and Closed regeneration forest covers, but higher than in other forest covers ($p \leq 0.032$). Fruit biomass was higher in Open regeneration forest cover than in Young, Mature mixed, Mature coniferous, and Bog forest covers ($p \leq 0.048$).

HABITAT SELECTION

Bears had well established home ranges; individual annual home ranges of the 8 bears followed for two years overlapped by $86\% \pm 5$. We therefore pooled the two years of tracking data and obtained an average of 75 ± 11 locations per bear for habitat selection analyses (Table I).

The Manova test suggested that habitat selection at the landscape scale was random ($F_{1, 7} = 2.39, p = 0.20$). Nevertheless, *t*-tests show that bears seem to prefer Open regeneration and to avoid Young forests (figure 1a).

At the home-range scale (figure 1b), habitat selection was not random ($F_{1, 7} = 5.35, p = 0.04$). However, no seasonal effect was detected between spring-early-summer and late-summer-fall ($p > 0.3$). Bears preferred Open regeneration ($F_{1, 11} = 5.77, p = 0.02$) and Closed regeneration forest covers ($F_{1, 11} = 7.46, p = 0.02$) and avoided Mature coniferous forests ($F_{1, 11} = 8.48, p = 0.01$) and Recent clearcuts ($F_{1, 11} = 7.8, p = 0.02$).

Dens were located in post-perturbation (0-20 years) forest covers in a proportion of 33% ($n = 21$), and in established forest covers (> 30 years) in a proportion of 67%. Taking into account habitat availability, females preferred established forest covers for den sites ($G = 10.5, p < 0.05$).

HOME RANGE SIZE AND OVERLAP

Average multi-annual home range size was $65.1 \text{ km}^2 \pm 20.0$ (Table I). However, a bootstrap analysis revealed that asymptotic home range size was not attained and suggested that over 120 locations were needed. Locations inside home ranges were spread in a non clustered fashion. All bears made 1 to 5 sallies that lasted between one to three weeks during the survey, this generated triangular shaped home ranges for some individuals. Due to important inter-individual variability, we did not detect any significant difference between

spring-early-summer and late-summer-fall seasonal home range sizes although they were $26.3 \text{ km}^2 \pm 3.3$ during spring-early-summer and $46.9 \text{ km}^2 \pm 17.8$ during late-summer-fall ($p = 0.266$). Within each of the 12 individual home ranges, the spring-early-summer and late-summer-fall seasonal home ranges overlapped by $37\% \pm 6$. Since Open regeneration and Closed regeneration forest covers are of the same seral stage (6-20 years post-logging) and showed similar foraging quality, we pooled them for the analysis of home range size and overlap. Least squares linear regression shows a negative relationship ($y = -3.2x + 198.8$; SE = 55.09, $r^2 = 0.368$, $p = 0.022$) between the multi-annual home range size and the pooled percentage of Open regeneration and Closed regeneration forest covers.

We observed 7 areas where the home ranges of the 12 collared females overlapped; 4 females had their home range overlapping with 1 other collared female, and 5 females had home ranges overlapping with 2 other collared females. The average proportion of home ranges that was shared with other radio-collared females was $34\% \pm 9$ for individuals sharing the area with one other female, and $51\% \pm 11$ for those sharing with two others. The proportion of the 6-20 years post-logging forest covers did not differ significantly ($p = 0.235$) between overlap areas ($50\% \pm 4$) and multi-annual home ranges ($42\% \pm 4$).

Discussion

This study supports the hypothesis that logging influences the behavior of black bears by increasing the forage abundance of boreal forests. Female black bears preferred open regeneration 6 to 20 years post logging forest cover at both landscape and home range scales and avoided mature coniferous stands at the home range scale. The highest density of fruit was found in 6-20 years post-logging forest cover. Further, home range size was negatively related to the proportion in 6-20 years post-logging forest cover. These findings echoed those obtained in a Western coastal coniferous rain forest (Lindzey & Meslow 1977) and on the

Atlantic Coastal Plain (Hellgren, Vaughan & Stauffer 1991), indicating that logging activities increase overall habitat quality for black bears.

IMPACT OF LOGGING ON HABITAT QUALITY

Our results suggest that the habitat created by clearcuts likely increased the foraging efficiency of black bears by creating higher fruit density patches than found in mature forests. Nevertheless, the most productive forest covers (Open regeneration; 49.8 berries / m²) supported a relatively low fruit density. Bears observed in mixed-wood forests of Alberta experienced loss of body mass in presence of 66 berries / m² (Pelchat & Ruff 1986). Above all, the efficiency of energy intake in a fruit diet can be 2 to 3 times lower when in an environment poor in vegetal fats and proteins (Rode & Robbins 2000). Bears of the boreal forest must therefore maximize their foraging behavior in the absence of nuts. Their most efficient fruit foraging strategy consists in high-grading fruit patches (Welch 1997). Our results suggest that in our study area bears should select patches with the highest fruit density to maximize bite size while moving continuously to maximize bite rate (Rogers 1987; Welch 1997). Open regeneration and Closed regeneration forest covers were the only ones offering close to suitable high-grading conditions, estimated to be over 50 berries / m² by Welch (1997). The higher fruit density found in post-logging habitat is therefore crucial for energy acquisition by black bears in boreal forests. Although bears efficiently digest berries, they need to eat tremendous amounts to store adequate energy and meet minimum protein requirements (Pritchard & Robbins 1990; Welch 1997). Even though post-logging forest covers are abundant, the relatively low fruit densities necessitate extensive movements to maintain an appreciable intake rate.

The reproductive success of females is closely related to nutritional conditions (Jonkel & Cowan 1971; Rogers 1976; Schwartz & Franzman 1991; Samson & Huot 1995). The

relatively small size of females captured in the réserve faunique des Laurentides could be a response to the poor habitat quality of the area. The environmental stress linked to low resource availability can influence the growth and development of bears (Badyaev 1998). It is interesting to note that all captured females aged over 8 years had a body mass ranging between 51 and 62 kg. Schwartz & Franzman (1991) also observed low body mass (56 kg) in Alaska for bears located far from American devilsclub patches, the main bear late summer food. Smaller bears have lower energetic costs and can consequently have better foraging efficiency in less productive habitats (Welch 1997). This allows a small individual to gain a higher proportion of its body mass as fat reserves with fewer resources. Therefore, smaller females can afford the energetic expense of having larger litters in less productive habitats. Rogers (1976) noted that females with body mass inferior to 67 kg when entering dens failed to reproduce. Samson and Huot (1995) observed that all females weighing more than 77 kg reproduced and those under 56 kg failed to reproduce. Despite their small size, females reproduced during the second year of the study and had a mean reproductive success of two cubs, which is the average litter size for the species (Pelton 2003). The improvement in habitat quality could allow an unusual increase in reproductive success due to the adaptive traits of small females. Logging in northern latitudes could therefore lead to an increase in black bear population densities.

HOME RANGE SIZE AND OVERLAP

Although our estimates were conservative, bears had relatively large home ranges ($65.1 \text{ km}^2 \pm 20.0$) when compared to 2-23 km^2 in the deciduous forest of the Great Smoky Mountains (Garshelis & Pelton 1981). Bears' movements were extensive in northern coniferous forests; shorter travel distances are more usual where resource distribution and availability are a lesser constraint (Garshelis & Pelton 1981; Rogers 1987). However, logging

seemed to have a positive effect on black bear space use patterns by reducing home range sizes. It is possible that movements remained extensive in an intensively logged landscape because bears may not fully exploit stands with low forest edge to perimeter ratios (Samson 1996; Nielsen, Boyce & Stenhouse 2004). Even though mature coniferous forest covers were avoided, they are useful when it comes to sheltering cubs and escaping danger (Herrero 1972). It has been reported that females with cubs tend to stay close to forest edges when foraging in open habitat (Jonkel & Cowan 1971; Lindzey & Meslow 1977). Further, our results demonstrate that mature forest covers offer important attributes for the establishment of dens. The availability of high-quality den sites can be crucial to cub survival (White *et al.* 2001). Although clearcuts decreased home range size, extensive movement by female black bears in the boreal forest are still needed to fulfill energy requirements and mature forest covers may be essential to complete their life cycle.

We found no statistical difference in habitat selection between spring-early-summer and late-summer-fall. A substantial overlap between seasonal ranges suggests homogeneity in seasonal habitat selection patterns as discussed by Lindsey & Meslow (1977). Early successional forest covers (6-20 years) seem to offer higher foraging quality throughout the bear activity period. In mixed forests, excursions to highly productive old stands of nut producing trees explain the large size of fall home ranges (Rogers 1987; Samson & Huot 1998). Furthermore, where hardwood stands occur, locations tend to be clumped in more intensively used areas (Horner & Powell 1990; Samson & Huot 1998). However, bears in a coniferous habitat seem to move continuously to forage on berry patches that are distributed more evenly in the landscape.

The study of territoriality requires regular and close monitoring of all individuals in a defined study area (Samson & Huot 2001). Our results did not meet these requirements. Food is considered the main limiting resource that induces territoriality in black bear populations

(Rogers 1976). Territoriality is expressed in diverse avoidance and aggressive behaviors, and can result in the exclusion of potential competitors (Horner & Powell 1990; McLaughlin & Ferguson 2000). Territoriality reaches a threshold when the costs of defending a large home range surpass the benefits. Despite our incapacity to monitor all individuals on a regular basis, we observed relatively large home ranges that overlapped considerably, which suggests the low quality of the exploited boreal forest habitat (McLaughlin & Ferguson 2000).

MANAGED VS. NATURAL FORESTS

Sparse tree regeneration created advantageous shrub distribution patterns for black bears by favouring large patches of diverse shade intolerant species and greater fruit densities. Although Open regeneration and Closed regeneration 6-20 years forest covers shared the same logging history, an important proportion (70%) of harvested stands demonstrated poor tree stocking up to 20 years after harvesting. Clearcutting (CPRS), the main exploitation method used in boreal forests, is known to generate low forest edge to surface ratios, and prolong the natural tree regeneration process (Green *et al.* 1999; Pothier 2000; Burton *et al.* 2003). In the long term, clearcuts can simulate stand characteristics of large scale wildfires (Reich *et al.* 2001). However, the short term regeneration characteristics differ (Carleton & MacLellan 1994), chiefly by substantial plant community disparities (Nguyen-Xuan *et al.* 2000). Plant diversity can also be higher in harvested stands than in undisturbed forests (Peltzer *et al.* 2000). The shrub regeneration process can also be faster in clearcuts when compared to burnt areas, as fire destroys most of the established ericaceous shrub layer, while harvesting allows established vegetation to rapidly form the new shrub layer (Potvin & Bertrand 2004).

Although located in the balsam fir-white birch domain, the Laurentian hills elevation creates weather conditions of the spruce-moss domain. It has been shown that large wildfires

in humid black spruce forests were of limited occurrence and of varying burn severity; this natural perturbation regime generates an uneven-aged stand structure (Bergeron *et al.* 2001). Forestry planning has had little consideration for the natural occurrence of mature stands at the landscape scale (Bergeron *et al.* 2002). In fact, clearcuts were designed to be of similar size to large wildfires and their spatial distribution was intended to mimic the 100 year cycle seen with severe wildfires. Conversely, the rejuvenation of humid coniferous forests is naturally driven by small scale disturbances that generate gaps in a landscape dominated by old mature coniferous stands (Pham *et al.* 2004). As a result, the natural age structure and stand composition in humid boreal forests has been distorted by ongoing forestry management practices (Hunter 1993; Bergeron *et al.* 2002). By planning forestry with broad scale even-aged silviculture, our industry has created a favourable habitat for the black bear. The boreal forest now offers black bear habitat that far exceeds in size and productivity its natural state. This process may have raised the boreal forest's carrying capacity for black bears to a historical high.

MANAGEMENT IMPLICATIONS

Intensive logging management in the past 30 years is now modifying black bear behavior and possibly its population dynamics in northern boreal forests. We demonstrated that clearcut logging influences black bear habitat selection in coniferous boreal forests by influencing the distribution and abundance of soft mast shade intolerant species. The rejuvenation and even-aged planning through clearcutting seems to have caused an increase in the boreal forest carrying capacity of black bears. The accepted view that bear habitat quality is greater in old stands (Litvaitis 2001) does not hold true in northern coniferous forests as Open regeneration stages take on a capital importance. Restoration of the natural forest structure by less intensive forest management and preservation of large mature to old-growth

stands (Bergeron 2004) would limit the influence of logging on black bear behavior and population dynamics.

The black bear management plan currently in place in the province of Québec (Lamontagne, Jolicoeur & Lefort 2006) proposes an increase in sport hunting and trapping based on the assumption of a province-wide increase in bear habitat quality. Great concern arises from conservationists because bears are known to be efficient opportunist predators. Predation by black bears becomes especially problematic in boreal coniferous forests because of its potential impact on endangered woodland caribou populations (*Rangifer tarandus caribou*) (Ballard 1994; Lambert *et al.* 2006). Management of black bear populations in the boreal forest should focus on the maintenance of historical population levels. However, harvest levels should remain conservative as managers must take into account the eventual recovery of the forest. An important proportion of the landscape consists of early successional post-logging stands that will become unfavourable to black bears as they mature to over 30 years. In extensively managed regions, black bear habitat quality should gradually reduce in the next 20 years, during which the proportion of mature forest covers should increase. The implementation of uneven-aged forestry practices in future forestry planning should contribute to lessen the effect of logging on habitat quality by maintaining natural stand attributes and favouring regeneration processes (Bergeron 2004).

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Tables and Figures

Table I. Information on individual bear age (years) in 2005, capture body mass (kg), number of radiolocations and mean home range size (mean \pm 1 SE). Bears no. 2 through 22 were followed both in 2004 and in 2005 whereas other bears were followed only in 2005.

Bear	Age	Mass	Number of locations			Home range size (km ²)		
			Spring-early-summer	Late-summer-fall	Total	Spring-early-summer	Late-summer-fall	Total
2	10.5	54	33	27	61	39.9	21.8	43.1
3	6.5	40	64	59	123	23.5	32.4	46.6
5	28.5	62	39	7	47	42.1	11.0	57.4
7	10.5	51	63	34	98	29.4	236.4	280.7
10	6.5	55	48	38	87	34.4	14.5	35.6
17	7.5	56	54	54	109	40.9	28.7	62.1
21	6.5	62	42	65	108	27.9	28.9	33.9
22	5.5	42	47	57	105	22.3	35.1	39.6
31	7.5	40	25	32	56	13.0	22.2	32.2
32	11.5	59	15	15	29	20.1	41.7	57.2
36	9.5	51	18	34	51	13.3	21.5	24.4
38	5.5	50	14	34	47	8.6	68.7	68.7
Total			462	456	921			
$\bar{x} \pm SE$	8 ± 1	51.8 ± 2.3	39 ± 5	38 ± 5	77 ± 9	26.3 ± 3.3	46.9 ± 17.8	65.1 ± 20.0

Table II. Shrub ground vegetation cover, fruit density and biomass of the main foraging species present in the 7 forest cover types considered in the black bear habitat selection analyses. Distinct letters indicate significant differences among forest cover types for a given parameter; forest covers without a letter do not differ significantly from any other forest cover for a given parameter (*post-hoc* Tukey test; $p \leq 0.05$).

Forest cover type	Shrub ground cover (%)				Fruit density (fruits / m ²)				Fruit biomass (kg / ha)			
	Random		High-grading		Random		High-grading		Random		High-grading	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Recent clearcut (0-5 yrs)	26.5 ^{a,c}	3.7	59.5	12.7	11.3 ^a	4.8	55.7 ^{a,c}	28.1	71.5	29.1	316.2	168.4
Open regeneration (6-20 yrs)	55.1 ^b	4.5	91.5 ^a	15.9	49.8 ^b	7.3	175.0 ^b	51.0	145.1 ^a	22.4	501.6 ^a	137.4
Closed regeneration (6-20 yrs)	57.9 ^b	3.3	95.5 ^a	6.9	43.8 ^b	5.5	133.7 ^{a,b}	31.4	104.9	14.1	247.7	35.8
Young (30 yrs)	8.7 ^c	1.4	33.0 ^b	7.5	1.0 ^a	0.6	21.7 ^{a,c}	10.1	2.5 ^b	1.0	71.1 ^b	23.6
Mature mixed [†] (50-120 yrs)	9.9 ^c	2.6	31.3 ^b	6.7	2.0 ^a	1.0	7.3 ^c	2.9	7.0 ^b	2.6	36.0 ^b	7.2
Mature coniferous (≥ 50 yrs)	19.5 ^{a,c}	2.7	58.0	14.1	2.7 ^a	0.9	16.4 ^c	5.3	8.8 ^b	2.7	64.9 ^b	20.9
Bog [†]	37.8 ^{a,b}	4.6	61.7	10.7	8.6 ^a	1.6	22.2 ^{a,c}	7.2	61.1 ^b	15.5	113.0 ^b	37.9

Note: High-grading values were calculated from plots ($n = 10$) selected for their highest fruit availability along random sampling transects (see methods for further details).

[†] $n = 9$ for high-grading plots.

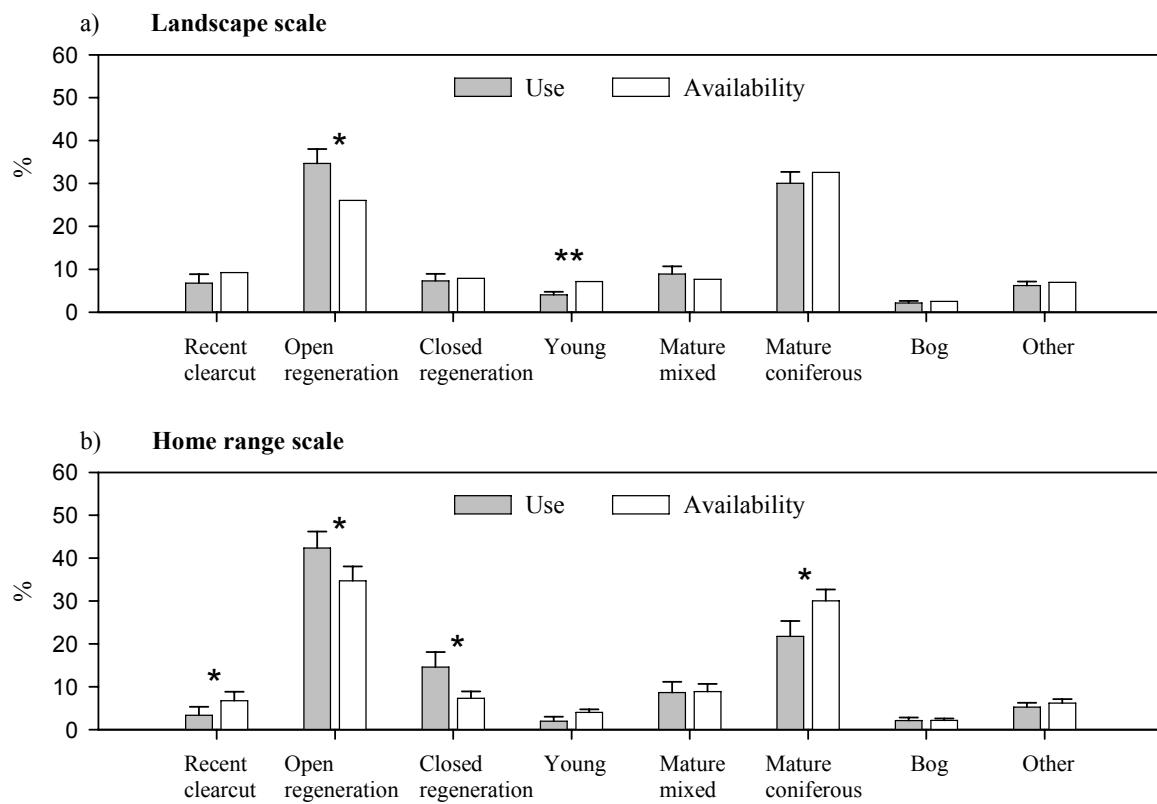


FIGURE 1: Habitat use by black bears compared to habitat availability a) at the landscape level where use is the percentage of each forest cover type inside the multi-annual home ranges and availability is the percentage of forest cover types inside the study area and b) at the home range level where use is the percentage of bear locations in each forest cover type and availability is the percentage of forest cover types inside the multi-annual home-ranges. Selection or avoidance occurs when use differs significantly from availability (mean values \pm 1 SE for 12 females; *, $p \leq 0.05$; **, $p \leq 0.01$).

CHAPITRE III : CONCLUSION GÉNÉRALE

Cette étude démontre que l'exploitation forestière en forêt boréale influence le comportement de l'ours noir en augmentant la capacité de support de son habitat. Les femelles ours noir ont préféré les peuplements en régénération, âgés de 6-20 ans suite à la coupe à blanc. La plus forte densité de petits fruits fut observée dans ce type de couvert forestier. L'ours noir s'alimente prioritairement dans les parcelles de forte densité de nourriture, cette stratégie alimentaire lui permet de maximiser son efficacité (Welch 1997). Nos résultats démontrent que les couverts forestiers créés par la coupe totale favorisent l'efficacité alimentaire de l'ours noir en augmentant la densité de la ressource sur une période d'environ 20 ans. La rareté des graisses et protéines végétales en forêt boréale diminue l'efficacité énergétique d'une diète riche en sucres (Rode & Robbins 2000). L'augmentation de la densité de fruits sur les parterres de coupe s'avère avantageuse pour l'ours. Cependant, la faible teneur des fruits en lipides et protéines limite la croissance de l'ours ainsi que sa capacité à accumuler des réserves énergétiques.

Le succès reproducteur chez l'ours est étroitement lié à la qualité de son alimentation. L'abondance de nourriture à forte teneur énergétique et protéique détermine le gain de masse corporelle au début de la gestation. La faible taille corporelle des femelles de la Réserve faunique des Laurentides pourrait être une réponse adaptative à un milieu de faible qualité nutritionnelle. Malgré leur faible masse corporelle, les femelles qui se sont reproduites ont eu en moyenne deux oursons, ce qui correspond à la moyenne pour cette espèce (Pelton 2003). Une plus faible taille corporelle pourrait donc permettre un meilleur succès reproducteur dans un milieu pauvre en ressources alimentaires. L'amélioration de l'habitat de l'ours par l'exploitation forestière pourrait donc engendrer une augmentation de la densité de la population, causée en partie par une augmentation du succès reproducteur.

Les parterres de coupe réalisés au cours des 20 dernières années constituent des milieux favorables à la croissance de petits fruits, une ressource importante pour l'ours. Une alimentation basée sur les petits fruits nécessite des déplacements constants et sur de grandes superficies afin de combler un besoin énergétique élevé. En effet, la taille des domaines vitaux en forêt boréale est supérieure à celle des ours vivant en forêt mixte (Garshelis & Pelton 1981). Cependant, nous avons observé que la taille des domaines vitaux diminuait lorsque leur proportion en couverts forestiers de 6-20 ans augmentait. L'exploitation forestière permettrait donc une meilleure efficacité alimentaire et pourrait avoir une influence positive sur la densité des populations. Cependant, l'ampleur de la superficie des domaines vitaux et l'importance de leur chevauchement suggèrent un habitat pauvre dans l'aire d'étude (McLaughlin & Ferguson 2000). Malgré l'importance des superficies perturbées par une exploitation forestière intensive, la forêt boréale demeure un habitat relativement pauvre pour cette espèce.

Nos résultats ne démontrent pas de différence significative entre les patrons saisonniers de sélection d'habitat (printemps-début-été et fin-été-automne). Les couverts forestiers âgés entre 6 et 20 ans suite à l'exploitation forestière semblent offrir une qualité alimentaire acceptable sur l'ensemble de la période active de l'ours noir en forêt boréale. En forêt mixte, l'ours adopte un comportement saisonnier distinct (Samson & Huot 1998). À l'automne, les peuplements de feuillus matures offrent une alimentation riche en lipides et protéines végétales. La faible qualité alimentaire des forêts de conifères matures explique en partie la modification du comportement saisonnier de l'ours en fonction de la latitude. Les jeunes stades successionnels seraient par conséquent d'importance majeure pour l'ours en forêt boréale. L'exploitation forestière constitue donc une perturbation qui permet d'accroître la qualité de l'habitat printanier, estival et automnal en forêt de conifère.

La coupe totale (CPRS) constitue la méthode principale de récolte de la matière ligneuse en forêt coniférière. Nos résultats démontrent que ce type de récolte favorise la croissance du couvert arbustif fruitier. Bien qu'à long terme la coupe totale se régénère pour créer un habitat semblable à celui créé par la succession végétale suite au feu (Reich *et al.* 2001), son effet à court terme diffère de la dynamique naturelle (Carleton & MacLellan 1994; Nguyen-Xuan *et al.* 2000). De plus, il est connu que les feux de grande superficie sont naturellement de faible occurrence en forêt coniférière humide (Bergeron *et al.* 2001). La structure de ces peuplements serait donc en partie régie par une dynamique de trouées qui permet le maintien d'importantes superficies de forêt matures (Pham *et al.* 2004). En appliquant une planification équienne et une récolte sur de grandes surfaces, l'industrie a artificiellement créé un habitat favorable à l'ours. Le paysage boréal est aujourd'hui dominé par des forêts aménagées (WWF 2006), ce constat permet d'envisager que la capacité de support de la forêt boréale pour l'ours noir a atteint un sommet historique.

La récente incidence de l'exploitation forestière intensive nous place aujourd'hui à l'avant plan pour évaluer les répercussions sur les populations d'ours noir. Or, les forêts septentrionales de conifère offrent plusieurs contraintes écologiques associées à la rigueur des hivers. Il est donc difficile d'estimer l'influence qu'aura l'amélioration des conditions alimentaires sur la dynamique des populations d'ours noir en forêt boréale. En tant que prédateur opportuniste, l'ours noir suscite l'intérêt des gestionnaires responsables du caribou forestier (*Rangifer tarandus caribou*), cet écotype est désigné vulnérable en vertu de la *Loi sur les espèces menacées ou vulnérables du Québec*. En tant que principal prédateur des faons caribous (Lambert *et al.* 2006), un accroissement de la densité d'ours noir s'avère une menace additionnelle à la survie du caribou forestier. La compréhension des dynamiques intra et interspécifique nécessite une acquisition de connaissance approfondie. Cette étude démontre que l'ours noir préfère les couverts forestiers créés par l'exploitation forestière intensive aux

peuplements qui dominaient autrefois un paysage naturel. Cependant, l'impact de l'amélioration de l'habitat sur la dynamique des populations d'ours noir en forêt boréale reste à être démontré. Une analyse de l'influence de l'habitat sur le taux de reproduction et le taux de survie des différents segments de la population serait hautement pertinente.

Au cours du siècle dernier, l'étalement urbain a causé une régression importante de l'aire de répartition de l'ours noir. Bien qu'il ait une grande capacité d'adaptation, l'essentiel de l'effectif de la population à l'échelle mondiale se retrouve désormais en faible densité en forêt boréale. L'importante proportion des superficies en régénération à l'échelle continentale reflète l'intensité des opérations forestières des trente dernières années. L'agglomération des parterres de coupe résulte aujourd'hui en de vastes régions dont le couvert forestier est considérablement rajeuni. Le régime forestier québécois est aujourd'hui en crise (Coulombe *et al.* 2004), le calcul des possibilités annuelles de coupes à rendement soutenu résulte présentement en une baisse de l'attribution des bois. Cette conjoncture devra mener à la réduction des opérations d'exploitation forestière en attente de la maturation du couvert forestier. La maturation des forêts issues du régime forestier intensif transforme graduellement les couverts forestiers propices pour l'ours en forêts défavorables à la croissance des petits fruits. Ainsi, la qualité de l'habitat pour l'ours noir est susceptible de diminuer au cours des deux prochaines décennies dans les régions qui subiront une baisse de leur possibilité forestière.

Le plan de gestion 2003-2013 de l'ours noir (Lamontagne, Jolicoeur & Lefort 2006) propose une augmentation des quotas de chasse sportive afin d'accroître la récolte de ce gibier. L'ours possède un double statut particulier, étant à la fois considéré en tant qu'animal à fourrure et gros gibier. Le plan de gestion actuel vise aussi mettre davantage l'ours en valeur en augmentant le quota associé aux activités de piégeage. Des indicateurs issus du suivi des récoltes et la présomption que l'aménagement des forêts augmente la qualité de l'habitat à

l'échelle provinciale justifient ces nouvelles modalités d'exploitation. Cette stratégie est en accord avec l'objectif d'optimisation de la récolte faunique dans une optique de gestion durable des ressources renouvelables. Cependant, la faible capacité de résilience de l'ours noir nécessite l'application du principe de précaution dans la gestion des activités de prélèvement. La présence de ce prédateur dans nos forêts ajoute à la richesse de notre patrimoine naturel, mais à court terme, elle représente aussi une menace potentielle pour certaines composantes de l'écosystème boréal.

RÉFÉRENCES DE L'INTRODUCTION ET DE LA CONCLUSION GÉNÉRALES

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