HABITAT SELECTION BY MOOSE (*ALCES ALCES*) IN CLEAR-CUT LANDSCAPES

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ABSTRACT: Habitat selection by moose was studied over 4 years in two large sectors subject to intensive forest harvesting using a two-scale approach. At the coarser scale, i.e. location of the home range within the landscape, habitat selection did not appear to be influenced by the presence of clear-cuts. In one sector, moose preferred mature mixed stands, young coniferous, and mature coniferous stands. In the second sector, the highest preference was noted for cut areas and mature deciduous stands. Moose home ranges were located in areas with higher edge and interspersion among habitat patches. Home range size for females was positively related to the proportion of cuts, but movements were not. Habitat selection was more pronounced at the finer scale (animal locations within home range) and did not differ between sectors. Mixed stands were preferred in all seasons. Mature conifer stands were preferred in summer and in early winter while young conifer stands were preferred in late winter. Clear-cuts were avoided except in early winter. Moose were located in areas closer to edge between food and cover stands than were random locations, especially in late winter. A marked decrease in movements also was noted in late winter. This study shows differences in habitat selection pattern between the coarser and finer scales. For example, clear-cuts did not seem to markedly influence home range location at a coarser scale, and adaptations to minimize their impact seemed to operate at a finer scale. Coarser scale habitat selection was probably linked to a trade-off between predator avoidance and browse availability, whereas seasonal changes suggest behavioural adaptations of moose to maximize energy gain and counteract predation and other adverse environmental conditions at the finer scale.

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Keywords: *Alces alces*, clear-cuts, cover, food, forest management, habitat selection, mortality

RESUMÉ: La sélection d'habitat par l'orignal a été étudiée durant quatre ans dans deux grands secteurs comportant d'importantes coupes forestières. Deux échelles d'analyse ont été retenues. À l'échelle brute, correspondant à l'emplacement du domaine vital dans le paysage, la sélection d'habitat ne paraissait pas influencée par la présence de coupes totales. Dans l'un des secteurs, l'orignal préférait les peuplements mélangés matures ainsi que les résineux jeunes et mûrs. Dans le deuxième secteur, la préférence la plus grande était notée pour les coupes forestières, les feuillus matures et les mélangés matures. Les domaines vitaux de l'orignal étaient localisés dans des sites comportant plus de bordure et plus d'entremêlement entre les parcelles d'habitat. Chez les femelles, la superficie du domaine vital était positivement liée à l'importance des coupes, mais les déplacements ne l'étaient pas. La sélection d'habitat était plus prononcée à l'échelle plus fine (localisation des animaux à l'intérieur du domaine vital) et elle ne différait pas entre les deux secteurs. Les peuplements mélangés étaient préférés en toutes saisons. Les résineux matures l'étaient en été et en début d'hiver alors que les jeunes résineux étaient préférés en fin d'hiver. Les coupes étaient évitées, sauf en début d'hiver. Les localisations d'orignaux étaient situées plus près des bordures entre des peuplements d'alimentation et de couvert que ne l'étaient des localisations aléatoires. Une diminution marquée des déplacements était aussi notée en fin d'hiver. Cette étude montre que les préférences d'habitat diffèrent entre les échelles brute et fine. Ainsi, les coupes forestières ne semblaient pas influencer grandement l'emplacement des domaines vitaux à l'échelle brute, et les adaptations visant à diminuer leur impact semblaient opérer à fine échelle. À l'échelle brute, la sélection d'habitat semblait résulter d'un compromis entre l'évitement des prédateurs et la recherche de nourriture alors qu'à l'échelle fine, les changements saisonniers suggéraient des adaptations comportementales visant à maximiser les gains énergétiques et à contrer les effets de la prédation et des conditions environnementales adverses.

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Mots clés: *Alces alces*, aménagement forestier, coupes totales, couvert, mortalité, nourriture, sélection d'habitat

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Johnson (1980) suggested that habitat selection, i.e. the decision to choose a specific habitat, is a hierarchical process, with decisions being made at different spatial and temporal scales. For example, an animal can choose to establish its home range (HR) in an area dominated by dense conifer stands while preferring rare deciduous stands within its HR to fulfil nutritional requirements. At a coarser scale, animals are expected to select habitats that reduce main limiting factors such as predation (Rettie and Messier 2000). When animals have successfully overcome the more important limiting factors at the coarser scale, selection could diverge at a finer scale to meet more specific needs, for example adequate shelter during the calving period, food intake in summer, and protection against unfavourable environmental conditions in late winter.

Moose (*Alces alces*) thrive in young boreal forests originating from perturbations (Timmermann and McNicol 1988). The highest densities are recorded in mixed stands (Brassard et al. 1974, Joyal 1987, Crête 1988) and in areas disturbed by forest fires, insect outbreaks, forest harvesting, or windfall (Krefting 1974, Peek et al. 1976, Timmermann and McNicol 1988, Loranger et al. 1991). Such stands provide abundant deciduous shrubs that constitute the main food source for moose (Crête 1989).

The benefits of forest harvesting for moose, however, are restricted to the 15-40 year period following disturbance (Cowan et al. 1950, Crête 1977, Franzmann and Schwartz 1985). Over the short-term, clear-cutting leads to landscapes dominated by large openings separated by small strips of uncut forest. Such recently clear-cut landscapes seem much less favourable to moose than older cuts since previous studies have indicated low moose densities in these areas (Eason et al. 1981, Girard and Joyal 1984, Eason 1989). Increased moose mortality caused by hunting and predation following forest harvesting were suggested to explain these low densities (Eason et al. 1981, Girard and Joyal 1984, Dalton 1989, Eason 1989) and as shown by Rempel et al. (1997). Consequently, cutovers seem less favourable for moose survival. Whether or not moose avoid these areas in order to increase their survival and at which scale such an avoidance could occur is unknown.

In this study, we used radio-telemetry to evaluate habitat selection by moose in an area subject to intensive forest harvesting during the last 10-15 years. We used a two-scale approach to test (1) if moose avoid landscapes with clear-cuts, and (2) if they avoid clear-cuts and edges within their HR. At a coarser scale (HR within the landscape), we expected moose to select habitats that are believed to decrease their vulnerability to predation and hunting (Eason et al. 1981, Girard and Joyal 1984, Dalton

1989, Eason 1989). At that scale moose should exhibit low preference (disproportional use, Hall et al. 1997) for areas dominated by clear-cuts, and should increase their HR size and movements in cut areas as suitable habitats are more scattered. At a finer scale (within HR), we expected that habitat use would be oriented toward maximizing energy gains and would vary seasonally depending on the severity of environmental conditions. Habitat requirements are more easily fulfilled during the growing season and in early winter when high quality food is abundant and snow (< 60 cm) does not restrict movement. However, during the growing season, females must protect their calves from predation by wolves (*Canis lupus*) and black bears (*Ursus americanus*) (Ballard 1992). Consequently, in summer and early winter, moose should then look for stands offering both ample food supply to maximize nutritional intake (Schwartz 1992), and cover to keep predation risk at a moderate level (Edenius 1992), such a trade-off being more pronounced in females than males. Moose are sensitive to heat stress in late winter and their movements are hampered by snow depth and hardness (Timmermann and McNicol 1988). During this period, moose should reduce their daily movements, prefer cover to food supply, and be located closer to edges between food and cover than in other seasons (Peek et al. 1992).

METHODS

Study Area

The study was conducted in a 3,200 km^2 area located in northwestern Québec, Canada (Fig. 1). The study area is a typical boreal forest dominated by conifer stands that were intensively harvested (22% of the

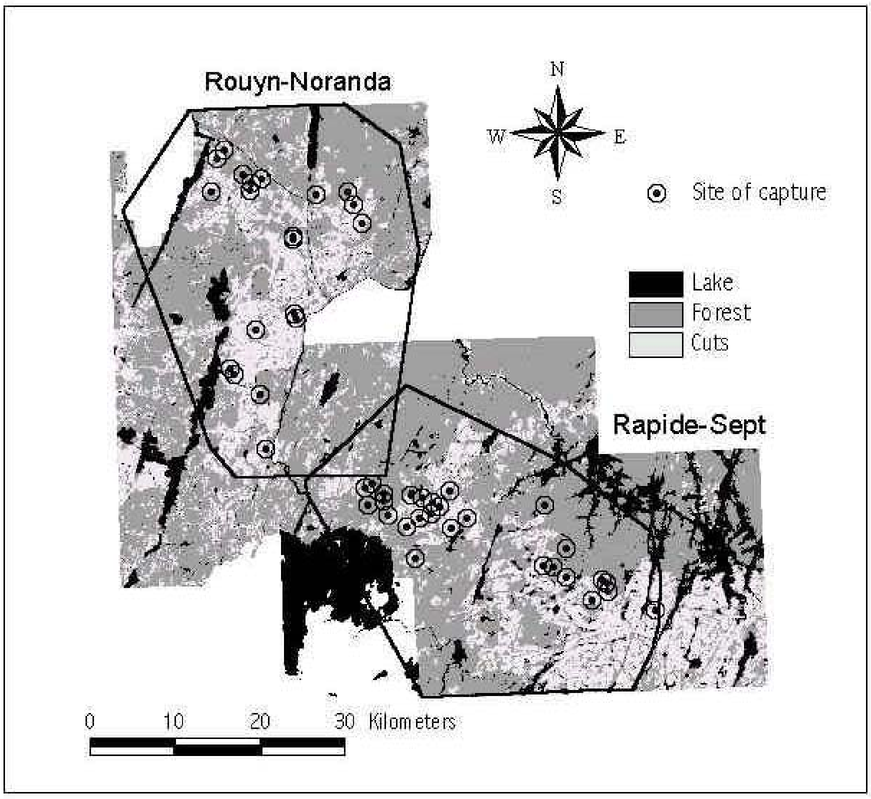

Fig. 1. Location of the study area in northwestern Québec (78° 40' W, 47° 50' N). Dots indicate sites of capture of marked animals.

area) between mid-1980 and 1994. At the end of the study, 31% conifer, 13% mixed, and 8% deciduous stands covered the area. Other habitat classes available include stands currently unproductive for forestry (12%, mostly alder, *Alnus rugosa*), conifer stands affected by the spruce budworm (*Choristoneura fumiferana*) outbreak (5%) during the 1980s, and water bodies or lakes (9%). Dominant trees are black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), jack pine (*Pinus banksiana*), paper birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Clear-cutting without protecting advanced regeneration was practiced in the study area 7 to 11 years (94% of all cuts) before the study. In areas cut between 1992 and 1994, feller-bunchers and skidders circulated in trails spaced 10-15 m apart to protect advanced regeneration.

The terrain is gently rolling with hills rarely exceeding 350 m above sea level. Temperature (mean ± SE (*n* years)), as measured at the nearby Belleterre meteorological station, was -16.2°C ± 0.6 (29) in January, and 17.3°C ± 0.2 (29) in July. Annual precipitation was 1013 mm ± 23 (24) including 291 mm ± 12 (26) that fell as snow. Maximum snow depth (66 cm ± 7 (17)) occurs in February and did not exceed 90 cm during the study. Wolf and black bear are found in the study area at approximately 1 and 14 individuals / 100 km^2 respectively (Lamontagne et al. 1999, Larivière et al. 2000).

Capture and Telemetry

Sixty-five moose (1991: 29; 1992: 16; and 1993: 20) were equipped with radio transmitters. Track networks in the snow were identified by aerial surveys, numbered and randomly selected to determine the collaring sequence. Males (14), females (37), and calves (14) were collared according to their proportion in the population of the hunting zone in which the study was conducted (Paré and Courtois 1990). All animals present in a chosen track network were collared provided they corresponded to the desired category. Moose were immobilized with succinylcholine chloride (Van Ballenberghe 1989, Delvaux et al. 1999), at a dosage of 5-6 mg / 100 kg of visually estimated body weight. Moose were equipped with LMRT-4 VHF transmitters (Lotek Engineering, Newmarket, Ontario) and ear tagged. To estimate habitat use and movements, moose were located from an aircraft (helicopter: 96%; fixed wing: 4%) in 3 seasons: summer and fall (15 April to 31 October), early winter (mid-December to late January: snow depth < 60 cm), and late winter (mid-February-end of March: snow depth > 60 cm). Each year, marked animals were located 3-4 times per season.

Transmitters included motionless sensors that allowed the identification of dead individuals. For dead animals, the cause of death was determined by inspection of the carcass and its surrounding area. Predation was presumed when the presence of wolves was obvious around the carcass. Animals killed by hunters were reported to mandatory registration stations.

Home Range Estimates

The minimum convex polygon (Eddy 1977) was retained to estimate HR size due to its widespread use in the literature (Aebischer et al. 1993). Post-capture outliers (distance > 10 km in < 3 days post-capture) were discarded to eliminate their effect on HR size, leaving 2,160 valid locations (1991: 297 locations; 1992: 626; 1993: 732; and 1994: 505). Most animals were followed for 2-3 years, yielding 32.6 locations per animal (SE = 2.1; *n* = 65 moose). The plot of multi-annual HR size against the number of locations per animal indicated an inflection point at 20 locations per animal, as noted by Courtois et al. (1998a). For moose collared at 0.5-year-old, only locations collected after they were 18 months old were used in analyses to avoid the influence of dispersing animals (Labonté et al. 1998) and to prevent pseudo-replication with the data of their mothers, which were also monitored. Consequently, analyses were conducted only for the 47 moose (11 males and 36 females ≥ 1.5 year-old) having ≥ 20 locations. Multi-annual HR sizes were calculated in ArcView GIS 3.1 (ESRI 1996) using the Animal Movement extension developed by Hooge and Eichenlaub (1997).

Habitat Composition

We used the term "habitat classes" to designate forest stands and unproductive areas identified on forest maps. Habitat composition was obtained from digitized 1:20,000 forest maps produced by interpretation of 1:15,000 aerial photographs (MER 1984). The minimum size of stands on these maps is usually 8 ha. This information was used to produce a 10 m × 10 m raster map imported into ArcView 3.1 and managed with the Spatial Analyst extension (ESRI 1996). To maximize the statistical power of comparisons (Alldredge and Ratti 1992) and to avoid having missing values in the availability data sets (Aebischer et al. 1993), habitats were grouped into eight classes according to their age (young: 20-60 years; mature: >60 years) and composition (Y_DEC, M_DEC, Y_MIX, M_MIX, Y_CON, M_CON, respectively, young and mature deciduous, mixed and coniferous stands; CUTS: clearcuts ≤ 11 years; OTHER: water (mainly) and unproductive stands). All cuts were grouped because those harvested between 1992 and 1994 were not available to all animals. Such grouping of habitat classes provides good correspondence between the forest maps and ground survey validations (Dussault et al. 2001). It also reflects the basic requirements of moose in terms of food (browse, leaves, and aquatics) and cover (heat stress, snow) (Thompson and Stewart 1998). CUTS can potentially provide summer and winter food as well as Y_DEC and M_DEC which could also offer summer cover against heat; OTHER was expected to give access to aquatics; Y_MIX and M_MIX could offer both food and cover all year long while Y_CON and M_CON were supposed to provide summer and winter cover. One habitat map per year (1 April to 31 March) was produced to take into account the chronology of cutting operations. Habitat composition of a given area (i.e., study area, HR) was computed as the percentage of that area covered by each habitat class.

Habitat Structure

Habitat structure at the coaser scale was estimated with 7 Fragstats landscape pattern indices (McGarigal and Marks 1995) computed with the ArcView extension Patch Analyst (Elkie et al. 1999). We selected two indices to measure edge (the length of the interface) between habitat patches (ED: edge density, perimeter of all habitat patches per unit area [m/ha]; CWED: contrast-weighted edge density [m/ha], edge between deciduous or mixed vs. coniferous stands [weights = 1; other edges = 0]). One metric (CAD: core area density) was selected to estimate the density of core areas per 100 ha. Core area was defined as the interior of the patch exclusive of a band 100 m wide immediately inside the patch boundary. The size of the buffer was based on observations indicating that moose overused the 100 m zone on each side of food-cover edges (Dussault 2002). Two indices measured the diversity of the landscape (SDI: Shannon's diversity index, amount of information per habitat patch [without units]; IJI: interspersion and juxtaposition index, measure the extent to which patch types are equally adjacent to each other [percent]). Two other indices were selected to quantify the shape and size of stands (MSI: mean shape index, average perimeter-to-area ratio [without units]; TCAI: total core area index, relative importance (%) of the core areas). Finally, an index of edge preference was calculated as the mean distance (m) between moose locations and the nearest edge between deciduous or mixed vs. coniferous stand.

Data Analysis

Habitat components were ranked in order of preference, rather than classified as preferred or avoided, because preference and avoidance depend markedly upon the array of components assumed to be available (Johnson 1980). In all analyses, the level of rejection of the null hypothesis was set at $\alpha = 0.05$.

Conclusions drawn from habitat selection studies are critically dependent upon the delineation of available habitat (Aebischer et al. 1993, McClean et al. 1998, Wilson et al. 1998). To ensure that habitats deemed available were really accessible to each animal, we delimited two sectors (Rapide-Sept, 1,065 km^2, in the south eastern part of the study area; Rouyn-Noranda, 1,184 km^2, in the north western) using 100% convex polygons joining all the locations of moose frequenting each sector (Fig. 1). Each of these sectors were 13-15 times the size of the mean HR size, which seems sufficient to provide a precise estimate of availability outside a given HR. At the same time such an area remains potentially accessible to moose. For example, dispersal of yearlings is usually 10-30 km and some animals can travel up to 100 km before settling down (Labonté et al. 1998). Preference analyses (percent used/percent available) were conducted using the animal as the sample unit (Aebischer et al. 1993). Zero values in percent use were replaced by a small value (0.01%) about one order of magnitude smaller than the minimum encountered in the data set.

Analyses were conducted at two scales to identify: (1) preferences revealed by the multiannual HR location within the landscape (coarser scale); and (2) seasonal preferences within the HR (finer scale). At the coarser scale, habitat within the HR was defined as use while availability corresponded to habitat composition of the sector where each animal was collared. To test the influence of landscape pattern indices, each moose HR was paired with 30 areas of identical size and shape (random HR) randomly positioned (x and y coordinates of the centroid) and oriented (0-360 degrees of rotation from the observed orientation) in the sector frequented by that animal (Wilson et al. 1998, Potvin et al. 2001, Dussault 2002). The use of random HR facilitated the comparison of landscape pattern indices because it eliminates the influence of size and shape on landscape pattern indices of HR under comparison (McGarigal and Marks 1995). Preference at the coarser scale was studied using the 1994 habitat map. However, this will overestimate moose preference towards cuts since some stands that were frequented before cutting will appear to be cut in the analysis. Any conclusion that cutovers are avoided will therefore be conservative.

At the finer scale, habitat composition in a 100-m buffer zone around each moose location was compared to that of the total HR of that animal. The buffer minimized the influence of spatial imprecision of habitat map and telemetry locations (Rettie and McLoughlin 1999). The size of the buffer was relatively small because locations were precise (20-100 m; Potvin 1998) due to the use of a helicopter that permitted seeing most animals (69%) during telemetry locations. Habitat use was estimated using the annual forest map corresponding to each location. Data collected during a given season (summer, early winter, and late winter) and year were pooled per animal to avoid temporal pseudo-replication (thus giving one record per animal per season of each year). Edge preference (distance [m] from an edge) was evaluated by comparing moose locations with paired random locations (one per moose location) within the HR of each animal. Paired locations were retained to assure that habitat characteristics at the random locations were accessible to the animal under consideration.

Preference analyses (Aebischer et al. 1993) were preceeded by multivariate analyses of variance (Proc GLM, SAS Institute 1989) to evaluate the effect of independent factors (year, sector, sex, season, and their interactions) on habitat preference for all habitat classes taken simultaneously. In these analyses, percentage use and availability were transformed into log-ratios using OTHER habitats as the denominator to render habitat variables independent (Aebischer et al. 1993). Multivariate normality of the residuals was assessed with Mardia skewness and kurtosis (program multnorm.sas, available from SAS Institute). Potential outliers were identified with the program OUTLIER.SAS (M. Friendly, http://www.math.yorku.ca/SCS/sssg/outlier.html). Predicted preference indices were estimated by a posteriori univariate analysis (Proc MIXED, SAS Institute 1989) followed by a bootstrap procedure (available at gaetan.daigle@mat.ulaval.ca). The bootstrap technique with 500 samples was used in order to approximate the exact distribution of the estimation procedure, conditional on the observed data (Efron and Tibshirani 1993). Bootstrap technique allows estimating the statistic of interest with many subsamples drawn from the original data with replacement. The associated distribution of the estimates is an approximation of its true distribution, and thus can be used in statistical analyses.

Univariate analyses (Proc GLM) were used to test the effect of independent factors on HR size, female productivity, and distance between successive locations. We used the same factors as in the multivariate analyses but time interval between two successive locations was added in analyses involving distance. The normality and homoscedasticity of the residuals were evaluated respectively with the Shapiro-Wilk's test and the plot of the residuals against predicted values. Paired *t*-tests were used to compare (1) landscape pattern indices between moose HR and the mean value of the 30 paired random HRs, and (2) the distance from an edge between moose and random locations. This last analysis was followed by an univariate analysis to assess the influence of independent factors on that variable.

To test the influence of clear-cuts on moose mortality, animals were partitioned into 2 groups according to the proportion of cuts within their HR (few: < 35%; many: $\geq$ 35%; based on the mean proportion found in HR). Proc LIFETEST (SAS Institute 1989) was then used to compare equality of survival curves over these two groups using the non-parametric log-rank test.

RESULTS

Habitat Preference at the Coarser Scale

At the coarser scale, two outliers were removed to respect the multinormality of the residuals. No transformation of the data permitted reaching multinormality with these two outliers. We detected a sector effect in habitat preference ($F[_{7,35}] = 9.25$, $P < 0.0001$) but no sex ($F[_{7,35}] = 0.31$, $P = 0.9461$) or sector*sex effect ($F[_{7,35}] = 1.25$, $P = 0.3009$). Consequently, preferences were estimated by sector. Important differences were noted between the two sectors (Fig. 2). In the Rapide-Sept sector, the highest preference was noted for mature mixed stands followed by mature coniferous and young coniferous. The rank order for all habitat classes was: M_MIX > M_CON = Y_CON > M_DEC = CUTS = Y_MIX = OTHER > Y_DEC. In

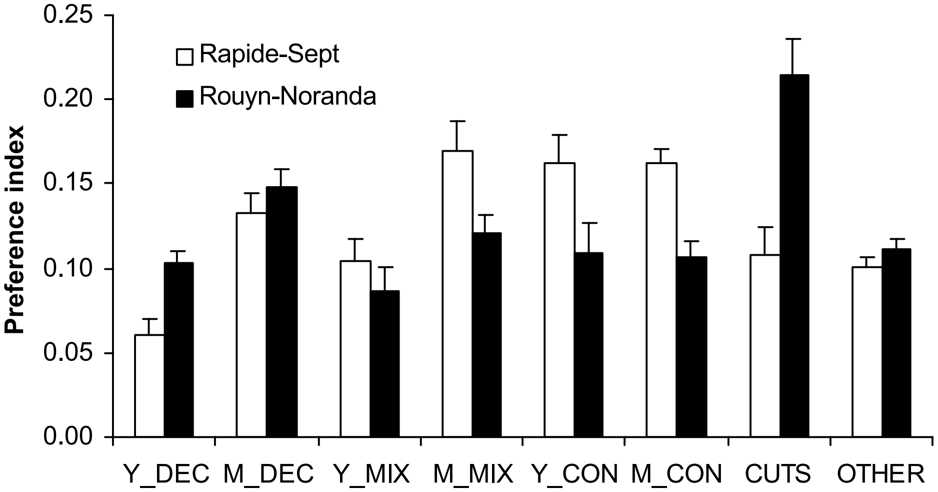

Fig. 2. Habitat preference (mean ± SE) by moose at the coarse scale in the two sectors of the study area in northwestern Québec, 1991-1994. Preference indices (% used/% available) were standardized to sum to unity.

the Rouyn-Noranda sector, the most preferred habitat classes were clear-cuts followed by mature deciduous, and all other habitat classes (CUTS > M_DEC > M_MIX = OTHER = M_CON = Y_CON = Y_DEC = Y_MIX).

Six of the seven habitat pattern indices differed between moose and random HR (Table 1). Moose HR had higher total edge and number of core areas per surface area, higher interspersion and diversity (IJI and SDI), and lower perimeter-to-area ratio, and core areas size than random HR within the landscape. The difference between moose and random HR was particularly important for the number of core areas (7.1 vs. 5.1 core areas/ha) and total edge (81 vs. 69 m/ha). Other significant differences were low (<9%).

Habitat Preference at the Finer Scale

Habitat preference within the HR varied among seasons ($F[_{14,566}] = 2.24$, $P < 0.0059$) without any sector ($F[_{7,37}] = 1.80$, $P < 0.1156$), sex ($F[_{7,37}] = 0.50$, $P < 0.8266$) or year ($F[_{21,813}] = 1.43$, $P < 0.0960$) influence, and no significant interactions. Preference analyses indicated that mature mixed and coniferous stands, and mature deciduous stands, were the most preferred habitat classes in summer and fall (M_MIX = M_CON > M_DEC > Y_CON = OTHER > CUTS = Y_DEC = Y_MIX). In early winter, moose preferred mature mixed stands, and cuts and mature coniferous (M_MIX > CUTS = M_CON > M_DEC > Y_CON = OTHER = Y_DEC = Y_MIX). In late winter, only M_MIX and Y_CON were preferred over other habitat classes (M_MIX = Y_CON > M_CON = Y_MIX = Y_DEC = OTHER = M_DEC = CUTS). Globally, the highest preferences were noted for mature mixed in all seasons (Fig. 3). The major seasonal changes were an important increase in the preference for CUTS in early winter, and Y_CON in late winter. Young and mature deciduous, and OTHER habitats were more preferred in summer-fall than in the two other seasons.

Moose were located closer to edge between deciduous or mixed stands and coniferous stands (food-cover edge) than random locations within the HR (mean difference = 52 ± 16 m; $n = 297$; $t = 4.63$, $P < 0.001$; Fig. 4). Changes were noted among seasons ($F[_{2,296}] = 9.39$, $P = 0.0001$) but not between sex ($F[_{1,296}] = 0.55$, $P = 0.4615$), sectors ($F[_{1,296}] = 1.91$, $P = 0.1736$), year

Table 1. Mean value ± SE of seven landscape pattern indices in moose ($n = 47$) and random ($n = 30$ per moose) home ranges in northwestern Québec, 1991-1994.

Landscape pattern indices	Moose HR	Random HR	Paired Student's t	P
ED: total edge (m/ha)	80.6 ± 1.5	68.8 ± 0.8	7.40	<0.0001
CWED: food-cover edge (m/ha)	16.3 ± 0.7	16.5 ± 0.5	-2.27	0.7874
CAD: *n* core areas beyond 100 m/100 ha	7.1 ± 0.3	5.1 ± 0.1	7.17	<0.0001
MSI: perimeter to area ratio (without units)	1.84± 0.01	1.92 ± 0.01	-6.19	<0.0001
TCAI: importance (%) of core areas beyond 100 m	88.1 ± 0.2	89.6 ± 0.1	-6.80	<0.0001
JI: interspersion of habitat patches (%)	80.0 ± 1.2	75.5 ± 0.7	3.81	<0.0004
SDI: Shannon's diversity index (without units)	1.75 ± 0.03	1.61 ± 0.02	4.94	<0.0001

($F[_{3,296}] = 2.31$, $P = 0.0767$), or any interactions among factors. The difference was greater in late winter (80.9 m) than in the two other seasons (30.0 and 33.5 m). Moose were closer to an edge in late winter (254.2 ± 22.9 m, $n = 118$ moose-season) than in summer-fall (279.4 ± 14.5, 120) or in early winter (282.1 ± 17.9, 124).

Effects of Clear-Cuts on Space use, Mortality and Productivity

Mean multi-annual HR size was related to sex (87.7 km^2 ± 20.3 and 73.7 ± 10.9 for males and females respectively; $F[_{1,44}] = 4.68$, $P = 0.037$) and the interaction between sex and the proportion of cuts within the HR ($F[_{1,44}] = 9.23$, $P = 0.004$); HR size increased with the proportion of cuts for females ($r = 0.44$, $P = 0.009$, $n = 34$) (Fig. 5) but not for males. However, the proportion of cuts within HR, or sex, sector, and interactions among these variables did not influence the mean distance travelled between two successive locations ($F[_{4,44}] = 1.38$, $P = 0.2573$). Movements depended on season ($F[_{2,346}] = 32.59$, $P < 0.001$), interaction

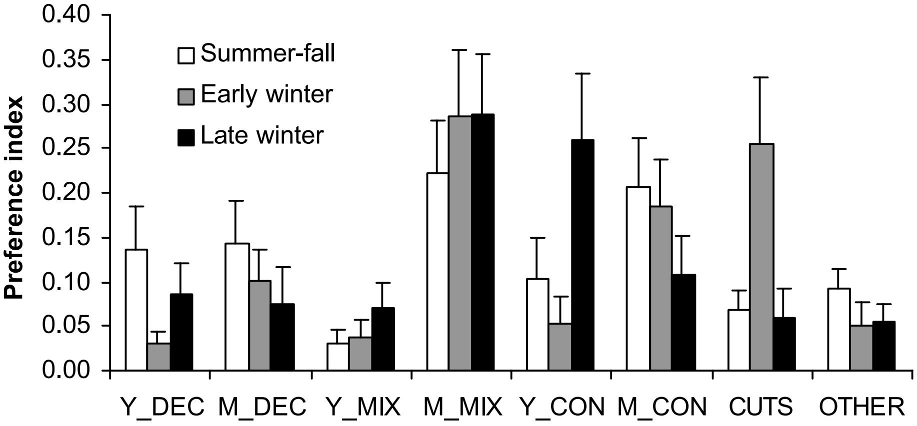

Fig. 3. Seasonal changes in habitat preference (mean ± SE) within the home range by moose in northwestern Québec, 1991-1994. Preference indices (% used/% available) were standardized to sum to unity.

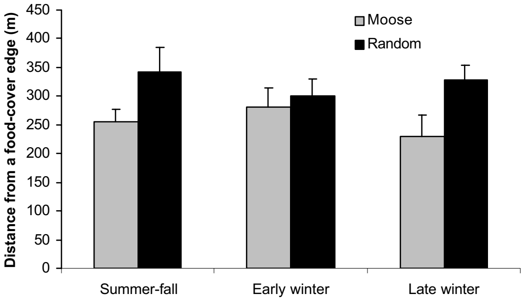

Fig. 4. Distance (mean ± SE) between moose locations or random locations and the proximal limit of the nearest edge between deciduous or mixed stands vs. coniferous stands in northwestern Québec, 1991-1994.

between year and season ($F[_{6,346}]$ = 2.48, P= 0.024), sector*year ($F[_{2,346}]$ = 5.06, P= 0.0069), and time interval between locations ($F[_{1,146}]$ = 3.99, P= 0.047). Mean distance travelled by moose was lower in late winter during all the years of the study (Fig. 6).

Twenty-three collared moose died during the study from hunting (17), predation (4), and other causes (2). Survival rate of adults was similar for both sexes (χ^2 = 1.84, df = 1, P = 0.1746; males: 83.2% ± 5.8 [12,364 collar-days]; and females: 86.9% ± 3.3 [33,340 collar-days]). Similarly, no significant difference was found between survival for moose with many or few cuts in their HR (χ^2 = 0.50, df = 1, P = 0.4812). Female productivity depended on the sector ($F[_{1,34}]$ = 5.29, P = 0.0284) but not on the proportion of cuts within the HR ($F[_{1,34}]$ = 0.56, P = 0.4615), and no interaction was detected.

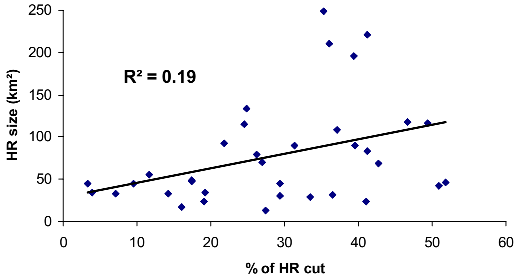

Fig. 5. Influence of the proportion of cuts within the home range (HR) on female moose HR size in northwestern Québec, 1991-1994.

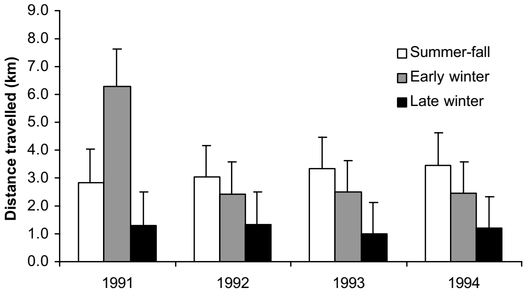

Fig. 6. Seasonal changes in distance (mean ± SE) travelled by moose between two successive locations in northwestern Québec, 1991-1994.

DISCUSSION

Johnson (1980) suggested a four-order scale to explain habitat selection by an animal: the geographic range of the species, the HR, the specific habitats within the HR, and the micro-habitat (e.g., feeding sites). Further, Rettie and Messier (2000) suggested that differences in selection pattern among the scales could reflect the importance of limiting factors with animals escaping the most important limiting factors at the coarser scales.

Habitat Selection at the Coarser and Finer Scales

Habitat selection patterns of moose differed between the coarser and finer scales in an area subject to intensive forest harvesting, suggesting that moose resource selection at the level of HR and within HR may reside in different domains (sensu Wiens 1989). However, our results do not support the hypothesis that moose avoid clear-cuts at the coarser scale. In the Rapide-Sept sector, moose preferred forested habitats over clear-cuts, but the reverse trend was noted in the Rouyn-Noranda sector. Females increased HR size, but not movements, in the presence of cuts.

Differences in habitat preference between sectors could not be related to different availability since both sectors comprised similar proportions of clear-cuts (24.4 vs. 23.6%) of similar age (≤ 11-year-old). The use of the 1994 habitat map and multi-annual HR could have over-represented the proportion of clear-cuts within moose HR, but the same situation prevailed for both sectors. Moreover, annual HRs were examined and the general trend was a propensity to stay in the same area despite the presence of clear-cuts. Only 3 of the 47 animals seemed to gradually shift HR following the progression of the cuts.

Preference at the finer scale was more pronounced than at the landscape scale. In both sectors, a marked preference was noted for mature over young stands, principally mixed and coniferous ones. In early winter, however, there was an increase in preference for cuts. Mixed stands and regenerated clear-cuts could provide significant browse availability (Courtois et al. 1998b). During the summer-fall period, there was an increased preference for young and mature deciduous, and for OTHER habitat class. Deciduous trees can provide food and thermal cover while unproductive areas and water give access to aquatics.

Preference for cover slightly increased in late winter. According to Thompson and Euler (1987), in cut areas, moose preferably choose young cutovers in early winter before moving to older ones, and finally leave clear-cuts to use undisturbed areas in late winter. During that period, between mid-March and mid-April, they also reduce their movements (Courtois and Crête 1988) probably because snow accumulation > 65 cm and crust impede movements (Peek et al. 1976). Also, moose are in poorer physical condition in late winter and can be heat stressed when temperatures reach -5 to 0°C (Renecker and Hudson 1986, Timmermann and McNicol 1988). Many authors have concluded that moose seek coniferous shelter in late winter (Desmeules 1964, Brusnyk 1983, Thompson and Euler 1987), whereas Crête (1988) doubted its necessity when deciduous browse is abundant. Our results showed that moose reduced their movements during that period, used cover in a greater proportion, and clear-cuts in a lesser proportion, than in summer or in early winter, but they still preferred mixed stands. Consequently, we suggest that dense cover is not a major component of late winter habitat, at least in regions where snow depth is usually < 90 cm as in our study area (Paré and Courtois 1990). Similar findings were made in an agro-forested site and in black spruce clear-cuts near our study area (Girard and Joyal 1984, Joyal and Bourque 1986) and also on the North Shore of the St. Lawrence River (Courtois et al. 1993). Moose decrease movements in deep snow but do not necessarily confine themselves under dense coniferous cover stands. For example, they can take advantage of small conifer patches within mixed stands.

Forbes and Theberge (1993) also noted differences in habitat preference at different scales in Algonquin Park in Ontario. At a regional scale (>1,000 km^2), moose preferred sites with at least 33% of their area disturbed by spruce budworm epidemics or cuts (mainly uniform shelterwood and selection cutting). At a finer scale (<100 km^2), they preferred conifer stands, mostly hemlock (*Tsuga canadensis*), presumably because their study area was dominated by deciduous stands providing low cover. In our case, mature mixed stands were the most preferred habitat class both at the coarser and the finer scales in all seasons. Moreover, moose searched for diversified landscapes with high edge, interspersion and number of cores areas per surface area, and a lower size of core areas relative to habitat patch size. Consequently, preference at the coarser scale could result from a trade-off between predator avoidance and access to ample food supply (Dussault 2002). At the finer scale, habitat selection seemed to be oriented towards maximizing energy gains and counterbalancing adverse effects of the environment (Dussault 2002).

Presumed Relationship Between Habitat Selection and Limiting Factors

We expected that moose would avoid clear-cut areas at the coarser scale because they are considered more vulnerable to hunting and predation in these environments (Eason et al. 1981, Girard and Joyal 1984, Dalton 1989, Eason 1989). However, clear-cuts were not avoided in either sector, and mortality and productivity were not related to the abundance of clear-cuts.

Establishment of HR within the landscape may be more tightly related to sociological behaviour, namely philopatry for juvenile females and dispersal for males (Cederlund et al. 1987, Labonté et al. 1998) than habitat constraints. However, adopting philopatry as opposed to a more flexible strategy overcoming the influence of the factors affecting survival and reproduction could not be evolutionarily stable. Habitat selection probably has some portion of genetic programming. Our results suggest that avoidance of clear-cuts acts at the finer scale rather than at the coarser scale. It is also possible that moose may have tried to reduce the impact of several limiting factors at both scales. For example, it would not necessarily be a good strategy for a moose to choose a home range with very adverse environmental conditions even if there is no predator in that area.

Our approach of coarser scale habitat selection presupposes a top-down driven process due to limiting factors such as predation (Rettie and Messier 2000). An alternative hypothesis may be a bottom-up process where the establishment of the home range is the result of daily decisions in locating food patches and encounters with conspecifics and potential predators, like wolves and hunters, along with other variables such as daily and seasonal weather patterns. Our data could support this second interpretation since analyses demonstrate equivocal results for clear-cut avoidance at the coarser scale, and the fact that moose are unlikely to explore large landscapes before selecting a home range.

Behavioural changes that could diminish the impact of clear-cuts seemed to operate mainly at the finer scale, i.e., within the HR. Many studies have shown that moose, and particularly females with calves, avoid open habitats (Peek et al. 1987, Courtois and Crête 1988, Dalton 1989, Eason 1989, Hundertmark et al. 1990, Dussault 2002). In late winter, females with calves rarely go 60 m beyond the forest cover, whereas other moose browse up to 80 m from the forest fringe (Thompson and Euler 1987). Remaining close to cover could reduce predation risk. At the finer scale, cuts were one of the less preferred habitat classes, except in early winter. Moose preferred the forested part of their HR which probably contributed to minimizing the influence of clear-cuts on mortality. It is not known whether the impact of clear-cuts depends on moose density. At a higher density and particularly near to carrying capacity, the impact of habitat modifications may have been higher. In such situations, more animals would have been forced to frequent marginal habitats and would have been exposed to higher mortality risks (Sinclair and Arcese 1995).

MANAGEMENT IMPLICATIONS

Our work adds more evidence that moose and forest management can co-exist. However, recent clear-cuts are avoided except in early winter. The type of stands and the magnitude of forest harvesting determine the impact of logging (Joyal 1987).

Limited - diameter cuttings carried out in shade-tolerant hardwood stands are usually favourable to moose (Crête 1977). Openings created by such forest harvesting techniques, in which usually 40% of the basal area of the deciduous trees and 75% of the conifers are removed, rapidly stimulate the growth of browse. In shade-intolerant hardwood, > 75% of the basal area of deciduous and conifers is usually removed. In coniferous stands where all commercial trees (≥ 9 cm) are harvested; the influence of cuts is more pronounced and depends on the time lag between cutting and regeneration of browse species and re-establishment of cover.

An acceptable threshold for the proportion of cuts in the landscape can be estimated from the examination of the HR composition. In this study, moose HR comprised on average 30-40% of mixed, deciduous and spruce budworm-affected stands, 30-35% of coniferous stands, 20-25% of clear-cut areas, and 10-15% of other habitats. In northeastern Minnesota, Peek et al. (1976) suggested creating landscapes comprising 40-50% of cutovers and only 5-15% of conifers in order to favour moose.

The spatial organization of the landscape has been studied on some occasions. Considering the area of track networks seen during aerial surveys, residual blocks < 20-50 ha should be unattractive to moose (Courtois et al. 1998b). Eason (1989) suggested 70 ha as the minimum size for an attractive block of forest, with observed moose densities increasing with the size of residual blocks. Courtois et al. (1998b) and Potvin et al. (1999) suggested alternating 50-100 ha cut and leave blocks. Based on landscape pattern indices, this study shows that small cuts regularly interspersed with residual stands should be beneficial.

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