

## Linking moose habitat selection to limiting factors

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It has been suggested that patterns of habitat selection of animals across spatial scales should reflect the factors limiting individual fitness in a hierarchical fashion. Animals should thus select habitats that permit avoidance of the most important limiting factor at large spatial scales while the influence of less important factors should only be evident at fine scales. We tested this hypothesis by investigating moose *Alces alces* habitat selection using GPS telemetry in an area where the main factors limiting moose numbers were likely (in order of decreasing importance) predation risk, food availability and snow. At the landscape scale, we predicted that moose would prefer areas where the likelihood of encountering wolves was low or areas where habitats providing protection from predation were dominant. At the home-range scale, we predicted that moose selection would be driven by food availability and snow depth. Wolf territories were delineated using telemetry locations and the study area was divided into 3 sectors that differed in terms of annual snowfall. Vegetation surveys yielded 6 habitat categories that differed with respect to food availability, and shelter from predation or snow. Our results broadly supported the hypothesis because moose reacted to several factors at each scale. At the landscape scale, moose were spatially segregated from wolves by avoiding areas receiving the lowest snowfall, but they also preferentially established their home range in areas where shelter from snow bordered habitat types providing abundant food. At the home-range scale, moose also traded off food availability with avoidance of deep snow and predation risk. During winter, moose increased use of stands providing shelter from snow along edges with stands providing abundant food. Habitat selection patterns of females with calves differed from that of solitary moose, the former being associated primarily with habitats providing protection from predation. Animals should attempt to minimize detrimental effects of the main limiting factors when possible at the large scale. However, when the risk associated with several potential limiting factors varies with scale, we should expect animals to make trade-offs among these.

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Habitat selection is rarely analyzed in light of limiting factors, which limits our capacity to fully understand variation in habitat choice across individuals within and between populations of the same species. Studies of habitat selection should consider the spatial distribution

of critical resources and also environmental constraints that limit exploitation of those resources (Morrison 2001). Spatial scale is also a critical variable to consider when assessing habitat selection (Wiens 1989). Habitat selection must be viewed as a hierarchical process that

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implies selection or avoidance of habitat types at various spatial scales. Animals may pursue different goals at large and fine spatial scales because resource distribution, foraging costs and predation risks vary with scale (Senft et al. 1987, Bailey et al. 1996, Boyce et al. 2003). Senft et al. (1987) hypothesized that decisions at the large scale occur less frequently but are likely to have more influence on fitness than those at fine scales. Further, Rettie and Messier (2000) suggested that the pattern of habitat selection of animals across spatial scales should reflect the hierarchy of the factors that potentially limit individual fitness. In other words, animals should adopt selection patterns that permit avoidance of those factors most likely to limit individual fitness at large spatial scales (i.e. across the landscape) while the influence of less important factors should appear at fine scales only (i.e. within the home range). Herein we refer to limiting factors as those factors likely to influence fitness of individuals within a population.

In this study, we tested the hypothesis that hierarchy in habitat selection is linked to hierarchical influence of limiting factors (Rettie and Messier 2000) using moose *Alces alces*. Predation, food availability, climate, parasites and disease are the most important natural factors that can potentially limit moose populations across North America, in that order (Van Ballenberghe and Ballard 1998). Hunting is also a major limiting factor of moose populations in areas accessible to humans.

Terrestrial animals such as moose can escape the effects of limiting factors through habitat selection in two ways. First, they may directly avoid the effect of a limiting factor spatially (e.g. avoid areas where the likelihood of encountering a predator is high; Rettie and Messier 2000, Mahoney and Virgl 2003). Second, animals in a given area may select habitats where the effect of a limiting factor is reduced (e.g. use habitats where thermal conditions are enhanced; Dussault et al. 2004).

The moose population in the study area was at a moderate density ( $<5$  individuals  $10 \text{ km}^{-2}$ ) relative to similar habitats elsewhere (reaching ca 20 individuals  $10 \text{ km}^{-2}$ ; Crête 1989). Moose density, however, increased by ca 20% annually during the three years of this study (Dussault 2002). Hunting in the study area was prohibited but there are two potential predators of moose: the timber wolf *Canis lupus* and the black bear *Ursus americanus*. Whereas wolves are known to kill moose year-round (Tremblay et al. 2001), bears only prey on neonates for a couple of weeks following birth (Van Ballenberghe and Ballard 1998). We consider snow to be a major constraint to moose movements in the study area because annual snowfalls are among the highest encountered across moose winter range (up to 550 cm annually) and moose movements are known to

be impeded by snow depths  $>60$  cm (Renecker and Schwartz 1998).

Because in unharvested areas moose populations are limited mainly by wolf predation (Messier 1994, Van Ballenberghe and Ballard 1994), we predicted that habitat selection at larger spatial scales should be oriented towards avoiding exposure to predation risk. At the finer scale, we predicted that moose habitat selection should be primarily influenced by food availability and secondarily by snow. The influence of predation risk, food availability and snow on moose habitat selection was tested at two scales. We used a larger scale corresponding to the location of the home range within the landscape (thereafter referred to as landscape scale) and a finer scale corresponding to exact individual locations within the home range (home-range scale). Because calves are more vulnerable to predation than adults (Linnell et al. 1995, Hayes et al. 2000), we expected predator-escaping strategies to be more obvious in females accompanied by calves than in other adults.

In boreal forest, avoidance of deep snow or predators could also have significant energetic implications because the habitat type providing the best shelter (coniferous stands) also offers the lowest food availability (Dussault 2002). In such a situation, one would expect individuals to trade off (Stearns 1989) access to food with exposure to other limiting factors. As an alternate hypothesis, we therefore considered the possibility that moose habitat selection at both scales consisted of a trade-off between food availability, predation risk and cost of locomotion in deep snow. We therefore included in the analyses habitat variables quantifying the proximity of food on the one hand and cover against snow or predation risk on the other hand.

## Study area

This study took place in the Jacques Cartier Park (665  $\text{km}^2$ , 71% of the entire study area) and part of the adjacent Laurentides Wildlife Reserve (274  $\text{km}^2$ , 29% by area), Québec, Canada. All moose were captured within the park but some used the adjacent areas. For this reason, the study area was delimited by the park boundaries and extreme moose locations in a convex polygon. The Jacques Cartier Park (47°15'N, 71°20'W) is a conservation area located 50 km north of Quebec City, Canada, where hunting and forest harvesting have been prohibited since 1981. In the Laurentides Wildlife Reserve, controlled hunting occurs from mid-September to mid-October and forest exploitation is allowed. There was no large scale forest disturbance (e.g. large burnt areas or clearcuts) in the study area that might have influenced our habitat selection analyses. We considered hunting not to be an important factor in our study area

because the majority (63%) of our collared moose never ventured outside the park and all but 3 individuals had >70% of their annual home range within the park. Moreover, hunting is marginal in that part of the reserve and no animal was harvested by hunters.

The forest in the study area is composed of balsam fir–white birch *Abies balsamea*–*Betula papyrifera* associated with balsam fir–black spruce *Picea mariana* stands. Some balsam fir–yellow birch *B. alleghaniensis* stands occupy the river valleys. In coniferous and mixed stands dominated by intolerant hardwoods, the most common understory species are balsam fir, white birch, black spruce and American mountain ash *Sorbus americana*. In deciduous and mixed stands with tolerant hardwoods, the understory is more diversified with maples *Acer* spp., yellow birch, beaked hazelnut *Corylus cornuta*, mooseberry *Viburnum alnifolium*, balsam fir and white spruce *P. glauca*.

Moose densities within the park varied from 0.21 to 0.45 km<sup>-2</sup> during this study (Laurian et al. 2000). Wolf and black bear densities in the Laurentides Wildlife Reserve during the 1990s were estimated at 0.44 individuals 100 km<sup>-2</sup> (Jolicœur 1998) and 22 individuals 100 km<sup>-2</sup>, respectively (Jolicœur et al. 1993). During this study, snow always began to accumulate on the ground in mid-November and increased until mid-April (101 cm in 1996) or in late February or March (165 cm in 1997, 79 cm in 1998 and 146 cm in 1999) (Dussault 2002).

## Methods

### Assessment of habitat use

Global Positioning System (GPS) telemetry was used to obtain data on habitat use of moose. Thirty individual moose were monitored with GPS telemetry collars between winter 1996 and winter 1999. Ten moose were captured between late March and late May in 1996 and monitored for one year. Collars were removed and installed on 10 new moose between late March and mid-April in 1997 and again in 1998. All moose were adult females ( $\geq 2.5$  yr-old), except in 1996 (7 females and 3 males), that were randomly selected among individuals seen during an aerial census conducted prior to capture. Moose were immobilized with carfentanil and xylazine (Delvaux et al. 1999). Collars were programmed to record a location every 4 h and GPS locations were differentially corrected to provide a horizontal position error of <35 m, 95% of the time (Dussault et al. 2001a).

We visually located moose by helicopter every 3 d during the calving period to determine whether females had given birth to a calf or not (Chekchak et al. 1998). During 1996 and 1997, we also visually located moose daily during the rut (early September to early Novem-

ber) and on average every 3 weeks for the rest of the year (Laurian et al. 2000). Whenever possible, the observer determined if the moose was accompanied by a calf. In 1998, we visually located moose only 4 times outside the capture period but all females that gave birth that year were accompanied by their calf during the recapture operations in March 1999. The 3 males captured in 1996 were combined with females without calves because they reacted similarly and removing them from the analyses did not qualitatively alter any conclusions (Dussault 2002, but see also Edwards 1983, Miquelle et al. 1992). Individuals not constrained by the feeding and protection of a calf were referred to as “solitary moose”.

### Assessment of predation risk and snow conditions at the landscape scale

A study of wolf population dynamics was underway in the Laurentides Wildlife Reserve during our moose study (Jolicœur 1998). From 1995 to 1998, at least one wolf per pack in the reserve was equipped with a VHF telemetry collar and located on a regular basis. Wolf territories were delineated using telemetry locations and other signs collected during field operations (captures, trappers' reports, aerial surveys, etc., Jolicœur 1998). The territories of 3 wolf packs overlapped our study area and predation risk for moose at the landscape scale was considered to be relatively higher in the areas overlapping wolf territories compared to the rest of the study area.

Snow conditions were not homogeneous across the study area. Jolicœur (1998) created a map showing the spatial variation of annual snowfall across the Laurentides Wildlife Reserve by interpolating snow precipitation data collected over the past 20 yr at the 47 weather stations found within a 50-km buffer zone around the study area. Interpolation was performed using the inverse distance weighting method. The relative harshness of snow conditions at the landscape scale was assessed using Jolicœur's (1998) map of annual snowfall. Snow precipitation is a good index of the harshness of snow conditions (Telfer and Kelsall 1984). In our study site, annual snowfalls were low (351–450 cm; 11.4% of the study area), moderate (451–500 cm; 28.3%) or high (501–550 cm; 60.3%).

### Habitat description

Vegetation description was based on 1:20 000 forest maps published by the Quebec Ministry of Natural Resources in 1992. These maps were elaborated from 1:15 000 aerial photographs taken in 1990. Minimum mapping unit size was 4 ha for forest stands and 2 ha for non forested areas (water bodies, bogs, etc.). Map

reliability was assessed during summer 1997 by comparing map classification with field measurements (Dussault et al. 2001b). A total of 186 forest stands were surveyed for availability of food, concealment cover and winter cover. Food availability was measured by recording the density of deciduous stems with at least one available twig between 50 and 300 cm above ground level in two  $1 \times 10$  m subplots spaced 20 m apart (Courtois et al. 1998). Concealment cover was assessed by measuring lateral visual obstruction between 0 and 2.5 m in height in 4 cardinal directions for a distance of 15 m with a cover board (Griffith and Youtie 1988). Winter canopy cover was estimated by measuring basal area of conifer trees in 3 subplots located 20 m apart. We used stand cover type and age class, the two variables for which map classification and field measurements corresponded the best, to define 6 habitat types that varied in terms of food availability, concealment cover (from predators) and winter cover for moose (see Table 1 for vegetative categories and acronyms used herein).

#### *Food availability, concealment cover and winter cover at the home-range scale*

Stands with  $\geq 10\,000$  stems  $\text{ha}^{-1}$  of deciduous browse had the highest food abundance in the study area (DT50 and MI10), approximately twice as much as any other stand type. We considered stands with 3 000–5500 stems  $\text{ha}^{-1}$  of browse to offer moderate food availability (MI30 and MI50) whereas other stand types provided low food availability (Table 1). Balsam fir is also consumed by moose during winter when overall food quality is low. However, balsam fir is a low-quality food item that is not preferred by moose and may even negatively affect the energy balance of moose if consumed in large quantities (Crête and Courtois 1997).

Predation risk at the fine scale was assessed using concealment cover. Ungulates living in forested habitats have been reported to be at reduced predation risk in

habitats with increased levels of visual cover that function in concealment (Myserud and Ostbye 1999, Bowyer et al. 1999, White and Berger 2001, Altendorf et al. 2001). No information is available in the literature to determine the amount of lateral cover that could shelter moose from predators and differences in techniques used to measure lateral cover renders comparisons difficult. However, it was possible to compare stand types to determine which provided high, moderate or low concealment cover. To shelter from predators, we expected moose to select stand types with relatively high concealment cover. Stands dominated by mixed and coniferous regeneration (MI10) as well as coniferous stands with trees aged  $\geq 30$  yr old (C30) provided the highest concealment cover during the green season (80–85% cover). These habitats were therefore considered as providing the best protection from predation risk and moose were considered at a relatively lower predation risk in these stand types. Deciduous and mixed stands with shade-intolerant trees aged 30–50 yr old provided moderate concealment during green periods (MI30 and MI50, 65–75% cover). During winter we had no measure of lateral cover but because deciduous trees and shrubs were leafless then, pure coniferous stands (C30) were considered to provide the best shelter against predation risk in that period. Concealment cover at very fine scale could also have been provided by topography or other abiotic features in the environment (Myserud and Ostbye 1999) but the occurrence of such elements did not appear to vary across stand types.

Coniferous trees with diameter at breast height  $\geq 10$  cm have been found to effectively intercept snowfalls (DesMeules 1965, Brassard et al. 1974). Because snow conditions in the study area were relatively severe for moose in North America,  $11 \text{ m}^2 \text{ ha}^{-1}$  was used as a minimal coniferous basal area for providing shelter against deep snow (MI50 and C30; Table 1). This value corresponds to that measured in preferred late winter

Table 1. Characteristics of the 6 stand types found in the study area. Stand types were ground-surveyed to determine food availability, concealment cover and winter cover for moose. Data presented are means  $\pm$  SE.

Stand type <sup>a</sup> (acronym used in text)	n	Food availability <sup>b</sup> (deciduous stems $\text{ha}^{-1}$ )	Concealment cover (%)	Winter cover (conifer basal area, $\text{m}^2 \text{ ha}^{-1}$ )	% of total area
Deciduous and mixed with tolerant hardwoods $\geq 50$ yr old (DT50)	35	$11\,728 \pm 1\,161$	$50.1 \pm 2.9$	$6.0 \pm 0.7$	9.9
Mixed and deciduous with intolerant hardwoods 10 yr old (MI10)	27	$10\,097 \pm 824$	$84.8 \pm 1.5$	$2.4 \pm 0.6$	15.7
Mixed and deciduous with intolerant hardwoods 30 yr old (MI30)	29	$5\,026 \pm 920$	$72.3 \pm 3.3$	$8.6 \pm 1.1$	7.3
Mixed and deciduous with intolerant hardwoods $\geq 50$ yr old (MI50)	38	$3\,803 \pm 649$	$68.7 \pm 3.1$	$13.2 \pm 1.4$	17.6
Coniferous $\geq 30$ yr old (C30)	82	$1\,378 \pm 248$	$79.6 \pm 1.7$	$17.1 \pm 0.8$	37.6
Non regenerated and non forested areas, lakes (OTHER)	0	—	—	—	12.0

<sup>a</sup> Classification based on forest map published by the Quebec Ministry of Natural Resources. <sup>b</sup> Only shrub and tree species known to be consumed by moose (i.e. white and yellow birch, trembling aspen *Populus tremuloides*, pin, choke and black cherry *Prunus* spp., maples, mountain ash, beaked hazelnut and mooseberry but not alders *Alnus* spp. and Ericaceae).

ranges in north-eastern Ontario (Thompson and Vukelich 1981). Unregenerated areas, bogs, alder (*Alnus* spp.) stands and lakes were classified as habitats that provided neither shelter nor food to moose (OTHER).

#### *Interspersion between food and cover*

We expected moose that traded off food availability with protection from predation risk to be attracted to edge between habitats providing abundant food and those sheltering against predation risk (P\_EDGE). Also, moose that traded off food availability with cost of locomotion in deep snow were expected to be attracted by the edge between habitats providing abundant food and those sheltering from snow (S\_EDGE). At the landscape scale, the extent of edge density (P\_EDGE and S\_EDGE) was used as a measure of food and cover interspersion. Edge density was calculated as the number of meters per unit area along which food rich habitats (DT50 and MI10) were juxtaposed to a habitat providing shelter against predation risk (C30) or deep snow (MI50 and C30) ( $\text{m ha}^{-1}$ ; McGarigal and Marks 1994).

The assess moose preference towards P\_EDGE at the home-range scale, availability and use of P\_EDGE were calculated by creating a 100-m buffer zone (50 m on either sides) between habitats providing high food availability (DT50 and MI10) and shelter against predation risk (C30). Similarly, S\_EDGE was defined by creating a 100-m buffer zone between habitats providing high food availability and protection from snow (MI50 and C30).

## **Data analysis**

### *Landscape scale*

Habitat selection at the landscape scale was determined by comparing habitat composition and edge density within moose home ranges to those available within the study area. This approach was adequate because moose in our study area were not migratory and previous studies did not indicate any site fidelity in choice of calving or wintering areas (Chekchak et al. 1998, Laurian et al. 2000). Moose home ranges were delineated with the minimum convex polygon method using all locations during one year (Mohr 1947). Moose movements were the highest during the summer period and summer home range area was > 90% that of the annual home range. As a result, moose that were not monitored during the entire summer period ( $n=4$ ) due to collar failure were not used in the analysis of home range composition. The following parameters were estimated for each moose home range: extent of overlap with wolf territories, amount of overlap with areas receiving low, moderate and high annual snowfalls, proportion of each of the 6 habitat types, P\_EDGE and S\_EDGE. Availability of

P\_EDGE and S\_EDGE and all other habitat types was determined by randomly positioning each moose home range (using rotation and translation) 25 times within the study area (Wilson et al. 1998, Potvin et al. 2001). Random permutations of moose home range were retained if  $\geq 50\%$  of range area overlapped the study area to avoid an underestimation of the study area boundary (Wilson et al. 1998). Arc/View GIS 3.2 (Anon. 1996) and Patch Analyst (Rempel et al. 1999) computer programs were used to calculate the proportion of each habitat type and edge density within home ranges and study area.

We used a stepwise logistic regression to determine which habitat and edge variables discriminated moose home ranges from random permutations. Whereas probability of use estimates may not be exact with logistic regression, it can be used to assess the relative importance of habitat types (Keating and Cherry 2004). The stepwise approach had the advantage of preventing problems of collinearity among independent variables. A dichotomous variable indicating whether or not the home range belonged to a female accompanied by a calf was forced into the model. Fit of the model was assessed by calculating the area under the Receiver Operating Characteristic (ROC) curve, which can vary between 0.5 (worst fit) and 1 (best fit) (Hosmer and Lemeshow 2000).

### *Home-range scale*

As suggested by Johnson (1980) to study hierarchical habitat selection, habitat use and availability at the home-range scale were measured at telemetry locations and within the home range, respectively. We defined four biologically relevant time periods based on previous observations of moose behaviour in the study area (Chekchak et al. 1998, Dussault and Huot 1999, Laurian et al. 2000): 1) late winter, the period during which snow depth in open areas impeded moose movements ( $\geq 60$  cm), i.e. 10 January in 1996 and 1997 and 4 January in 1998 until 22 April in 1996, 5 May in 1997 and 31 March in 1998; 2) spring, from late winter until 10 June; 3) summer, from 11 June to 9 November; and 4) early winter, from 10 November until late winter. Period 3 was the green period whereas deciduous trees and shrubs were leafless during other periods. Also, there was snow on the ground during periods 1, 2 and 4. Females were categorized as "accompanied by a calf" or "solitary" during each time period based on available data. GPS collars provided sufficient moose locations to perform habitat selection analyses during all annual periods, with 255 locations per individual on average across annual periods (minimum = 31).

Telemetry locations were pooled by individual and period to calculate standardized habitat selection ratios (Manly et al. 1993). Selection ratios constitute the

resource selection function and were used as the basic unit in all subsequent statistical analyses of habitat preference. These indices add up to 1.0 and can be interpreted as the probability that, for any selection event, an animal would choose one habitat type over all others, assuming that all habitats were equally available (Manly et al. 1993, McLoughlin et al. 2002). The selection indices were used to create independent variables by subtracting adjacent pairs of values (Arthur et al. 1996, Rettie and Messier 2000, McLoughlin et al. 2002). We used these synthetic variables in a repeated measure MANOVA using individual moose as sampling unit to test the influence of time period and presence of a calf on habitat selection. Year was included as a random factor in the analysis. Standardized preference indices were log-transformed to improve distribution of the residuals. Lastly, we performed pairwise t-tests for each combination of habitat types to establish a rank order of habitat preference at the home-range scale, with ranks of 1 indicating high preference (Rettie and Messier 2000, Courtois et al. 2002, McLoughlin et al. 2002).

We also used the above method to examine moose selection of P\_EDGE or S\_EDGE. For each time period and moose, the use of edge habitat was calculated as the number of locations that were inside the buffer zone divided by the total number of locations in the two corresponding habitat types including the buffer. Edge availability was calculated by dividing edge buffer area by the total area of the two corresponding habitat types in the home range. For the analyses of edge preference, repeated measure ANOVAs were used with selection ratios as the dependent variable and calf presence and time period as factors. All statistical tests were performed with the SAS program ver. 8.2 (Anon. 1989) with a significant probability level set at 0.05.

# Results

At the landscape scale, 3 variables discriminated the composition of moose home ranges from random permutations (Table 2). The overlap between moose home ranges and wolf territories was much lower than expected (16.1 vs 30.5%). Moose, however, did not preferentially establish their home ranges in areas dominated by habitat types considered to provide protection from predation risk (C30). Rather, moose selected areas where habitats providing high food abundance were interspersed with habitats providing shelter against snow (S\_EDGE = 37.5 vs 28.6 m ha<sup>-1</sup>). Also, moose home ranges contained fewer areas with low snowfall compared to random permutations (3.6 vs 10.6%). No significant interaction existed between the presence of a calf and the variables included in the model. The ROC value of the final model was 0.77.

At the home-range scale, habitat preference of moose depended on time period ( $F_{12,268} = 3.74$ ,  $p < 0.001$ ) and presence of a calf ( $F_{4,24} = 3.56$ ,  $p = 0.021$ ), but not on the interaction of these factors ( $F_{12,268} = 1.67$ ,  $p = 0.074$ ). Moose displayed moderate preference for stand types providing the highest food abundance but no protection from predation or snow (DT50); however, this stand type was never preferred to the stand type providing the lowest food availability but the best shelter (C30) (Table 3). The stand type ranking second in terms of food availability and first in terms of protection from predation risk (MI10) was preferred to the stand type providing the best overall shelter (C30) by all moose and during all but the late winter period.

Compared to solitary moose, females with calves had a higher preference for stand types providing protection from predation (MI10 and C30). In contrast, solitary moose showed a higher preference for the stand type providing moderate food abundance, moderate protec-

Table 2. Mean proportion ( $\pm$ SE) of habitat types and edge density (m ha<sup>-1</sup>) within moose home ranges compared to areas of the same size and shape randomly distributed over the study area. A stepwise logistic regression was used to identify variables discriminating moose home ranges ( $n = 26$ ) from random permutations ( $n = 650$ ). See Table 1 for description of stand types.

Variable	Home ranges	Random permutations	DF	$\chi^2$	p
In the model					
Overlap with wolf territories (%)	16.1 $\pm$ 4.1	30.5 $\pm$ 1.4	1	5.70	0.017
S_EDGE density <sup>1</sup> (m ha <sup>-1</sup> )	37.5 $\pm$ 3.1	28.6 $\pm$ 0.6	1	7.59	0.006
Area with low snowfall (%)	3.6 $\pm$ 1.9	10.6 $\pm$ 1.0	1	7.42	0.007
Not in the model					
Area with moderate snowfall (%)	36.3 $\pm$ 7.3	28.0 $\pm$ 1.3			
Area with high snowfall (%)	60.1 $\pm$ 7.9	61.5 $\pm$ 1.7			
C30 (%)	32.9 $\pm$ 3.1	39.6 $\pm$ 0.8			
DT50 (%)	10.0 $\pm$ 2.4	9.8 $\pm$ 0.6			
MI10 (%)	20.5 $\pm$ 2.4	15.6 $\pm$ 0.4			
MI30 (%)	6.0 $\pm$ 0.7	7.6 $\pm$ 0.2			
MI50 (%)	21.6 $\pm$ 1.6	18.3 $\pm$ 0.3			
OTHER (%)	9.0 $\pm$ 1.1	9.1 $\pm$ 0.2			
P_EDGE density <sup>1</sup> (m ha <sup>-1</sup> )	17.7 $\pm$ 1.6	13.4 $\pm$ 0.3			

<sup>1</sup>Edge density between stands offering high food abundance (DT50 and MI10) and stands offering protection against predation (C30) or snow (MI50 and C30).

Table 3. Rank order of preference of habitat types by annual period and for females with calves and solitary moose in the Jacques Cartier Park, Quebec, 1996–1999. > indicates significant difference between habitat types ( $p \leq 0.05$ ). See Table 1 for description of habitat types.

Time period – moose category	Habitat ranking
Spring – all moose	MI10 > MI50 > DT50 = C30 = OTHER = MI30
Summer – all moose	MI10 > MI50 > OTHER = DT50 = MI30 = C30
Early winter – all moose	MI50 > MI10 > DT50 = C30 > MI30 = OTHER
Late winter – all moose	MI50 = DT50 = C30 = MI10 > MI30 = OTHER
All periods – females with calf	MI10 > MI50 = C30 > DT50 > OTHER = MI30
All periods – solitary moose	MI50 > MI10 > DT50 = C30 > MI30 = OTHER

tion from predation and substantial shelter against deep snow (MI50, Table 3).

The most obvious changes in selection patterns between time periods concerned stands providing high food availability and protection from predation risk (MI10) which were more preferred in spring and summer compared to winter periods (Table 3). Also, stand types providing protection from snow (C30 and MI50) were relatively more preferred during winter periods, with MI50 even being preferred to all other habitat types in early winter. Preference of moose for OTHER habitats and for stands providing moderate food availability and moderate protection from predation risk (MI30) was low year-round.

Preference for P\_EDGE ( $F_{3,66} = 9.48$ ,  $p < 0.001$ ) and S\_EDGE ( $F_{2,42} = 4.27$ ,  $p = 0.021$ ) within home ranges depended on time period only. Moose preferred to use S\_EDGE during late winter and avoided P\_EDGE in all periods but late winter (no selection).

## Discussion

Moose were selective in their choice of habitat at both the landscape and the home-range scale. Our main hypothesis was that habitat selection should be hierarchical and that landscape-scale selection should aim to reduce predation risk, the most important limiting factor in our study area (Courtois et al. 1994), whereas food availability and deep snow, the other potential limiting factors, should affect habitat selection at the home-range scale only (Rettie and Messier 2000). Globally, our results supported this hypothesis. But contrary to our predictions, moose reacted to several limiting factors at each scale. Clearly, moose distribution across the landscape was the result of a trade-off among the 3 potential limiting factors. Moose avoided areas used by wolf packs. However, by doing so, they concentrated in areas where snow conditions were harsh. To counterbalance this adverse effect of wolf avoidance, moose at the landscape scale utilized areas where habitats providing increased food availability were highly interspersed with those providing shelter against snow.

At the home-range scale, our results also indicated a trade-off but the pattern of habitat selection differed between females with calves and solitary moose. Whereas the behaviour of solitary moose mainly suggested a trade-off between food availability and avoidance of snow, females with calves selected habitats where predation risk was reduced.

We argue that moose, which are morphologically better adapted than wolves to travel in deep snow (Telfer and Kelsall 1984), segregated spatially from wolves by avoiding areas where snowfall was low. Telemetry locations collected on wolves in the study area by Jolicœur (1998) indicated that wolves were located at relatively low altitudes during winter. These observations support earlier reports showing that wolves concentrate hunting activities in areas where snow depth is low (Kunkel and Pletscher 2001) and locate kill sites at lower elevation than random sites (Fuller and Keith 1980, Kunkel and Pletscher 2000). Three wolf packs visited our study area but they used only 30% of the study area despite the high prey density. The Jacques Cartier Park is characterized by deep snow that could have prevented wolves from establishing a permanent territory (Jolicœur 1998). Caribou *Rangifer tarandus* have also been reported to avoid predation risk at the landscape scale both through habitat selection (Rettie and Messier 2000, Mahoney and Virgl 2003) and spatial segregation (Ferguson et al. 1988). But moose behave differently than elk *Cervus canadensis* with regard to snow depth, the latter having been found to move to lower elevations during winter (Boyce et al. 2003).

At the landscape scale, moose were not attracted to habitats providing optimal protection from predation but no food. Moose are the largest cervid and require 3 to 8 kg (dry weight) of daily browse to maintain a positive energy balance (Belovsky and Jordan 1978, Hjeljord et al. 1982). Selecting areas providing protection from predation but low food availability might have incurred a great energetic deficit. Because moose were attracted to areas where habitats providing abundant food were highly interspersed with habitats providing shelter from deep snow (i.e. S\_EDGE), moose at the landscape scale traded off food availability with the cost of locomotion in deep snow. Moose habitat selection was more related to S\_EDGE than to the availability of any

one individual habitat type. Elk and mule deer *Odocoileus hemionus* were also found to select heterogeneous landscapes at relatively large spatial scales (Kie et al. 2002, Boyce et al. 2003).

Within the home range, moose also traded off food availability with exposure to other potential limiting factors. Patterns of habitat selection varied between time periods but the tendencies were usually the same. Neither predation risk nor food abundance alone determined habitat preference of moose since stands offering the highest food abundance (DT50) and those offering the best concealment cover (C30) were not the most preferred by moose. As expected, the pattern of habitat selection by females with calves and solitary moose differed at the home-range scale. The former associated mostly with stands providing high food availability and protection from predation (MI10 and C30) while solitary moose preferred habitats providing moderate food abundance and shelter against predation and snow (MI50). We interpret this behaviour as a result of females seeking protective cover to protect calves (Patterson et al. 1998, Bleich 1999, Hayes et al. 2000) but females with calves may also have avoided areas used by other moose at the finer scale, as suggested by Miquelle et al. (1992). Because moose generally are tolerant of each other except during short time periods such as calving and rut (Bubenik 1998), it is unlikely that differences in habitat selection were related to the displacement of subordinates to low-quality areas (e.g. Fretwell and Lucas 1970).

Moose, particularly females with calves, preferred habitats providing both food and protection from predation (MI10) to those providing food but no shelter (DT50). During the green periods, the former habitat likely allowed females with calves to feed efficiently while reducing exposure to predation risk (Bowyer et al. 1999). Selecting areas where the likelihood of encountering wolves was low at the landscape scale reduced exposure to predation but did not totally eliminate predation risk. First, complete segregation from wolves was not possible and second, black bears, which likely were more evenly distributed in the study area than wolves, are known to prey on calves during the first few weeks following birth (Van Ballenberghe and Ballard 1998). Also, lactation imposes high energetic demands on female ungulates (Mauget et al. 1999) and using stands that allow a high-energy intake rate may be necessary to avoid leaving the young unattended for long periods of time (White and Berger 2001).

Snow influenced habitat selection of moose at the home-range scale. The preference of moose for habitat types providing shelter against snow but relatively low food availability (C30, MI50) increased during periods with snow on the ground. Moose did not use these sheltering habitats randomly, however; they preferred to use edges between C30 stands and stands

providing abundant food during the deepest snow conditions.

### Linking habitat selection with limiting factors across spatial scales

Moose in our study area avoided wolf predation by selecting areas where snow conditions were not suitable for wolves. But within this partial refuge, moose did not establish home ranges randomly and were also influenced by availability of food and winter cover. Similar to the findings of Schaefer and Messier (1995) on the foraging behaviour of muskoxen *Ovibos moschatus*, the pattern of habitat selection by moose was consistent across the two scales considered and indicated a trade-off between food availability and exposure to predation risk and deep snow. We conclude that moose habitat selection is hierarchical and allows individuals to avoid the effects of important limiting factors, as previously suggested for both caribou (Rettie and Messier 2000) and grizzly bears *U. arctos*; (McLoughlin et al. 2002). But the relationship between hierarchy in selection and hierarchy in limiting factors was not as clear as expected.

For the Rettie and Messier (2000) hypothesis to be applicable, avoidance of the main limiting factor must be possible, which is obviously not always the case. Predators, for example, are often widespread in the environment and spatial refuge may not exist. Similarly, air temperature and other climatic variables may also be relatively homogenous over large areas. In such circumstances, animals should behave so as to avoid the second (or third, etc.) most detrimental limiting factor, if possible. However, when the risk associated with several potential limiting factors varies with scale, we should expect animals to make trade-offs among these. When avoidance of limiting factors is not possible at the larger scale or when distribution of environmental resources does not vary across scales (Boyce et al. 2003), we should expect habitat selection patterns to be comparable across spatial scales.

Results from habitat selection and population dynamics studies should be interpreted together. Habitat selection allows animals to reduce the potential effect of limiting factors. Identifying the limiting factors to which individuals are exposed should allow a better understanding of variations in habitat selection patterns across seasonal and daily periods, as well as variations between populations within species and even among individuals within a population. Furthermore, we argue that although animals can reduce the impact of a limiting factor through habitat selection and thereby reduce potential effects on individual fitness, this limiting factor can still have indirect effects on population dynamics. In this study, avoidance of areas with high wolf density



likely resulted in increased energy expenditure due to travelling in deep snow.

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