

# A habitat suitability index model to assess moose habitat selection at multiple spatial scales

Christian Dussault, Réhaume Courtois, and Jean-Pierre Ouellet

**Abstract:** We developed a habitat suitability index (HSI) model for moose (*Alces alces*) in the boreal forest. The model used two components: a suitability index for food ( $SI_{\text{food}}$ ) and another for the interspersed between cover and food ( $SI_{\text{edge}}$ ). We used forest maps as the input data source, and the value of each stand type in terms of cover and food was based on field surveys. To validate the model, the habitat preference of moose equipped with global positioning system telemetry collars was assessed at both landscape and home-range scales. We expected the habitat-preference index to correlate with suitability indices determined using the global model and each of its two components. Habitat suitability was assessed in evaluation plots of 500, 100, and 10 ha. Unexpectedly, the habitat-preference index correlated better with  $SI_{\text{food}}$  and  $SI_{\text{edge}}$  than with the global model. The suitability indices also performed better when assessed in large plots. Selection of 500 ha plots related mostly to  $SI_{\text{edge}}$ , but  $SI_{\text{food}}$  was more important when smaller evaluation plots were used, especially for males. Females preferred plots with intermediate  $SI_{\text{food}}$  values. At the fine scale,  $SI_{\text{edge}}$  was not as attractive to moose as was previously observed, presumably because snow conditions prevailing in our study area were relatively moderate. We recommend utilizing the model with  $SI_{\text{edge}}$  in large plots (ca. 500 ha) and  $SI_{\text{food}}$  in smaller plots. Our model could be adapted and applied to other areas by using empirical data to adjust the relative value of stand types in terms of cover and food.

**Résumé :** Nous avons développé un modèle d'IQH pour l'orignal (*Alces alces*) en forêt boréale. Le modèle utilise deux composantes: un indice de qualité pour la nourriture ( $SI_{\text{food}}$ ) et un pour l'entremêlement entre la nourriture et le couvert ( $SI_{\text{edge}}$ ). Le modèle s'applique sur les cartes forestières et la valeur de chaque type de peuplement en termes de disponibilité de nourriture et de couvert est basée sur des inventaires de végétation. Pour valider le modèle, nous avons évalué la préférence d'habitat d'originaux munis de colliers de télémétrie GPS aux échelles du paysage et du domaine vital. Nous avons prédit que l'indice de préférence serait corrélé avec la qualité de l'habitat estimée par le modèle et ses deux composantes. La qualité de l'habitat dans le site d'étude a été évaluée dans des parcelles de 500, 100 et 10 ha. Contrairement à notre prédiction, la préférence de l'orignal était mieux corrélée à  $SI_{\text{food}}$  et  $SI_{\text{edge}}$  qu'au modèle global. Les indices de qualité d'habitat ont aussi mieux performé lorsque calculés dans de grandes parcelles. La sélection des parcelles de 500 ha était davantage reliée à  $SI_{\text{edge}}$  alors que  $SI_{\text{food}}$  était plus important à fine échelle, particulièrement pour les mâles. Les femelles ont par contre préféré les parcelles avec des valeurs intermédiaires de  $SI_{\text{food}}$ .  $SI_{\text{edge}}$  n'était pas aussi important pour l'orignal que l'ont rapporté d'autres études, possiblement à cause des conditions de neige relativement faciles dans le secteur d'étude. Nous recommandons d'utiliser le modèle en calculant  $SI_{\text{edge}}$  dans de grandes parcelles (environ 500 ha) et  $SI_{\text{food}}$  dans de plus petites parcelles. Le modèle pourrait être adapté et appliqué dans d'autres sites d'étude en utilisant des données empiriques afin d'ajuster la valeur relative des peuplements forestiers en termes de couvert et de nourriture.

## Introduction

Large-scale human activities, such as forest harvesting, hydroelectric development, and road construction, often conflict with protection of wildlife habitats. To mitigate this conflict, new concepts in resource management have been introduced, such as integrated and ecosystem management (Yaffee 1999; Riley et al. 2002). As part of these new ap-

proaches, there is a growing need to develop tools that permit assessment of the impact of habitat modification on wildlife. Habitat suitability index (HSI) models are one of the most popular approaches incorporating wildlife-habitat relationships with other resource-management issues (Schamberger and O'Neil 1986).

The ultimate objective of HSI models is to assess the quality of a species' habitat using relevant habitat attributes.

Received 14 June 2005. Accepted 20 December 2005. Published on the NRC Research Press Web site at <http://cjfr.nrc.ca> on 13 April 2006.

**C. Dussault.**<sup>1</sup> Direction de la recherche sur la faune, ministère des Ressources naturelles et de la Faune du Québec, 4<sup>e</sup> étage, 930, chemin Sainte-Foy, B.P. 92, Québec, QC G1S 2L4, Canada, and Département de biologie, Université du Québec à Rimouski, 300, allée des Ursulines, Rimouski, QC G5L 3A1, Canada.

**R. Courtois.** Direction de la recherche sur la faune, ministère des Ressources naturelles et de la Faune du Québec, 4<sup>e</sup> étage, 930, chemin Sainte-Foy, B.P. 92, Québec, QC G1S 2L4, Canada.

**J.-P. Ouellet.** Département de biologie, Centre d'études nordiques, Université du Québec à Rimouski, 300, allée des Ursulines, Rimouski, QC G5L 3A1, Canada.

<sup>1</sup>Corresponding author (e-mail: [christian.dussault@fapaq.gouv.qc.ca](mailto:christian.dussault@fapaq.gouv.qc.ca)).

Habitat suitability is scored on a scale of 0 (unsuitable) to 1 (optimal) and animals are assumed to occur most frequently in the most suitable habitats. HSI models must be tested for reliability before being used in making management decisions (Schamberger and O'Neil 1986; Roloff and Kernohan 1999; Rothley 2001). The validation phase consists of verifying the correspondence between model predictions and evidence of animal occurrence in the field (Hurley 1986). To check that predictions are robust, generalized, and unbiased, validation must be conducted using a data base that has not been used to build the model (O'Neil et al. 1988; Van Horne and Wiens 1991; Flather and King 1992).

Our objective in this article is to develop and validate a HSI model for moose (*Alces alces*) in the boreal forest. Moose are widely distributed throughout the boreal-forest biome and are a featured species for most wildlife agencies in North America and northern Europe, based on recreational, aesthetic, and economic considerations (Thompson and Stewart 1998; Dettki et al. 2003). In some regions of Scandinavia and North America, elevated moose populations are also a problem because of moose-vehicle collisions or vegetation damage (Groot Bruinderink and Hazebroek 1996; Romin and Bissonnette 1996). We were interested in developing a model that precisely depicts moose habitat selection while being relatively easy to compute. There are at least two published HSI models for moose in North America that can be applied at a spatial scale suitable for forest management. The first model, developed for the Lake Superior region, should be applied in 600 ha units (Allen et al. 1988). It separately evaluates browse abundance, diversity, and quality, as well as the distribution of cover stands in relation to browse resources, in both the dormant and the growing season. It also takes into account aquatic-forage availability, so it requires relatively detailed field data. The second model, developed in Quebec by Courtois (1993), separately evaluates each forest stand in terms of food and cover availability, but does not take into account interspersions between the two resources.

The model we selected was elaborated using the deductive approach and was based on information concerning moose-habitat relationships collected over the past 10 years (Courtois et al. 2002; Dussault 2002; Dussault et al. 2004; Dussault et al. 2005). Our model requires less extensive field data than that developed by Allen et al. (1987) and, in contrast to Courtois's (1993) model, considers interspersions between food and cover to be a critical characteristic of suitable moose habitat.

### Model background

Our HSI model relied on previous observations that suitable moose habitat in the boreal forest is composed of a mosaic of deciduous or mixed regenerating stands intermingled with mature coniferous stands (Courtois 1993; Dussault 2002). The dense shrub layer provides food throughout the year and mature coniferous trees provide shelter from several environmental factors.

Determining the nutritional needs of moose is key to understanding moose habitat selection (Pierce and Peek 1984; Joyal 1987; Crête 1989; Crête and Courtois 1997; Courtois et al. 2002; Dussault et al. 2005). In summer, the moose diet is mostly composed of a large diversity of deciduous tree

and shrub leaves (Renecker and Schwartz 1998). During the period when trees are leafless, moose consume the stems of the same deciduous species and also, in some regions, balsam fir (*Abies balsamea* (L.) Mill.) (Renecker and Schwartz 1998). But balsam fir is only consumed when overall food quality is low and is not preferred by moose (Renecker and Schwartz 1998). Crête (1989) demonstrated that winter moose densities were largely determined by the availability of deciduous browse and that including balsam fir in assessments of habitat carrying capacity yielded inflated estimates. Other coniferous species such as spruces (*Picea* spp.) are not consumed by moose (Kurttila et al. 2002). Moose mostly find their preferred food items in regenerating stands with a dense shrub layer (Courtois 1993; Peek 1998), such as areas that were recently disturbed (e.g., because of insect outbreaks, windthrow, and clear-cutting) and, to a lesser degree, in deciduous or mixed stands (Courtois et al. 2002; Dussault 2002).

The use of vegetation associations that provide high food availability usually implies increased exposure to adverse environmental factors such as predation (Dussault et al. 2005) and extreme weather conditions (Dussault et al. 2004) because of a lack of shelter. Moose are thus forced to make trade-offs between food availability and exposure to such detrimental factors (Dussault 2002). Cover is important to moose on a year-round basis and fulfils different seasonal requirements. During relatively warm periods, moose seek mature stands with coniferous trees to avoid exposure to intense solar radiation (Schwab and Pitt 1991; Dussault et al. 2004). Coniferous trees also provide cover for moose, sheltering them from snow. As winter progresses and snow depth increases, moose reduce their movements and are confined to restricted areas (Courtois and Crête 1988). The energetic cost of locomotion increases exponentially in snow depths above 60 cm (Renecker and Schwartz 1998). During these periods of deep snow, moose are often observed in stands dominated by mature conifers (Coady 1974; Timmermann and McNicol 1988; Courtois et al. 2002).

Finally, mature stands of coniferous trees may protect moose from predators. It has been reported that ungulates living in forested habitats with increased levels of visual obstruction (i.e., lateral cover) are at reduced risk of predation (Mysterud and Ostbye 1999; Altendorf et al. 2001; White and Berger 2001). Lateral cover may negatively affect the vision and locomotion of predators, thereby reducing predation risk. During the growing season, concealment cover is relatively high in most stand types, but during winter, only coniferous trees provide high levels of visual obstruction (Dussault et al. 2005).

Dussault et al. (2005) indicate that not only the availability but also the spatial distribution of food and cover are important to moose. Furthermore, the extent of interspersions between food and cover was found to influence moose habitat selection at both landscape and home-range scales (Courtois and Beaumont 2002; Dussault 2002). In Jacques Cartier Park, Quebec, moose density across the landscape was found to be related more to the degree of interspersions between cover and food stands than to the availability of any one stand type. In addition, distance to protective cover influences the foraging behaviour of moose (Molvar and

Bowyer 1994) when deep snow reduces mobility (Hamilton et al. 1980; Thompson and Vukelich 1981; Mastenbrook and Cumming 1989; Dussault et al. 2005).

## Materials and methods

### Model justification and description

The HSI model we propose should be applicable to the balsam fir – white birch (*Betula papyrifera* Marsh.) bioclimatic domain. Our model evaluates habitat suitability in plots varying in size from 10 to 500 ha and encompassing one or more forest stands instead of assessing each forest stand individually.

We intentionally created a simple HSI model to allow assessment of habitat suitability on a year-round basis. Despite seasonal variations in ecological needs and environmental conditions, moose can meet their individual needs in similar landscapes during summer and winter (Dussault 2002). Even if food quality varies considerably throughout the year, food of the highest quality and density (mostly leaves and twigs of deciduous trees and shrubs) can be found in the same forest stands. Also, forest stands that provide the best shelter against solar radiation (i.e., mature mixed and coniferous stands) also provide the best shelter against snow, as well as relatively good concealment cover (Dussault et al. 2004; Dussault et al. 2005). Our HSI model was therefore intended to identify the most suitable forest mosaics that provide both food and cover at a scale usable by moose on a year-round basis. Like other HSI models, our model should not be used as an indicator of actual moose population densities because major limiting factors such as hunting and predation are not included in the model.

The size and shape of plots for which the HSI model is to be calculated should be determined by the user according to research objectives. These parameters will sometimes be obvious when assessing areas having known limits, such as hunting zones or management units. In this study, we chose to test the model using plot sizes varying from 10 to 500 ha because this corresponds to managers' expectations and requirements. Plots in that size range should allow managers to assess moose habitat at both fine and large scales. We recommend using square or hexagonal plots to avoid long, narrow shapes with little core area. Users should also avoid using plots with borders adjusted to natural landscape features (rivers, forest stands, clearcuts, valleys, etc.). Because such natural borders often separate highly contrasted habitat types, the model would likely be less accurate.

The HSI model requires input data in the form of digitized forest maps such as those published by the Quebec ministry of natural resources (ministère des Ressources naturelles du Québec 2000). These maps were elaborated from 1 : 15 000 aerial photographs. Each forest stand was considered a homogeneous area in terms of cover type (coniferous, deciduous, or mixed), canopy density, height, age-class, and soil type. The minimum mapping-unit size was 4 ha for forest stands and 2 ha for nonforested areas (water bodies, bogs, etc.). The value of each stand type in terms of food and cover availability was determined based on a survey of 186 forest stands in Jacques Cartier Park, where we measured the availability of food, concealment cover, and winter shel-

ter (Dussault et al. 2001b). Food availability was measured by recording the density of deciduous stems between 50 and 300 cm above ground level in two 1 m × 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 the four cardinal directions at a distance of 15 m from a cover board (Griffith and Youtie 1988). Shelter from snow and solar radiation was estimated by measuring the basal area of the coniferous trees in three subplots located 20 m apart. We defined 10 contrasting habitat types that varied in food and cover availability (Table 1) using dominant cover type and age-class, the two map variables most closely related to field measurements (Dussault 2002).

Our HSI model has only two components: a suitability index for food availability ( $SI_{\text{food}}$ ) (eq. 1) and a suitability index for interspersions between food and cover ( $SI_{\text{edge}}$ ) (eq. 2). The suitability values for each forest stand type in terms of food and cover are based on field data (Dussault et al. 2001b).

$$\begin{aligned}
 [1] \quad SI_{\text{food}} = & (Mi10\% + Dt50\% + Mt50\%) \times 1.0 \\
 & + (Di50\% + Mi30\%) \times 0.5 + (Mi50\%) \\
 & \times 0.4 + (C10\%) \times 0.3 + (CF30\%) \\
 & \times 0.15 + (IMP\%) \times 0.1 + (CS30\%) \times 0.05
 \end{aligned}$$

where Mi10%, Dt50%, Mt50%, Di50%, Mi30%, Mi50%, C10%, CF30%, IMP%, and CS30% are the proportions of each habitat category in the evaluation plot where HSI is calculated. The multiplicative factor associated with the habitat categories is a function of their potential for providing food to moose (deciduous stems/ha), measured through vegetation surveys (Table 1).

To assess the edge component in each evaluation plot, we considered two types of interspersions between cover and food: within and between forest stands. Within-stand edge (eq. 3) was not measured directly in the field. However, vegetation surveys revealed that a mature mixed stand with shade-intolerant trees (Mi50) was the only stand type that supported both a relatively high cover of mature coniferous trees and a relatively high density of deciduous browse. Thus, in these stands, cover was interspersed with food at a very fine scale, and the proportion of evaluation plots covered by this stand type obtained the highest cover–food edge score (i.e., 1.0). Between-stands edges (eq. 4) occurred at the fringe of highly contrasting cover and food habitat types. It was calculated as the distance per unit area (m/ha) along which food-rich stands (Dt50, Mt50, and Mi10) and a stand providing shelter against adverse environmental factors (CF30, CS30, Mi50, and C30) were juxtaposed (McGarigal and Marks 1994). The density of between-stands cover–food edge was calculated in the portion of evaluation plots not occupied by Mi50 stands that already offered within-stand edge. The suitability of evaluation plots in terms of between-stands edge increased linearly with cover–food edge density, but plots with cover–food edge density greater than or equal to the 70th percentile of cover–food edge density among available evaluation plots were considered to provide optimal between-stands edge. This criterion was used because moose density was found to increase linearly with cover–

**Table 1.** Ecological value to moose of 10 different stand types in the boreal forest, based on food and cover availability.

Stand type <sup>a</sup>	Age-class (years) <sup>a</sup>	Browse availability (stems/ha) <sup>b</sup>	Basal area of coniferous trees (m <sup>2</sup> /ha)	Food value <sup>c</sup>	Between-stands edge value <sup>d</sup>
Deciduous with shade-intolerant trees <sup>e</sup> (Di50)	≥30	4 528 ± 1 279	4.9±1.9	0.50	—
Mixed with shade-intolerant deciduous trees (Mi30)	30	5 250 ± 1 221	10.3±1.3	0.50	—
Mixed with shade-intolerant deciduous trees <sup>f</sup> (Mi50)	≥50	3 803 ± 649	13.2±1.4	0.40	Cover
Deciduous with shade-tolerant trees <sup>g</sup> (Dt50)	≥50	13 923 ± 2 257	3.7±1.0	1.00	Food
Mixed with shade-tolerant deciduous trees (Mt50)	≥50	10 432 ± 1 239	7.4±0.9	0.50	Food
Deciduous or mixed in regeneration, recently disturbed stands (insect outbreak, windthrow, etc.; Mi10)	10	10 097 ± 824	2.4±0.6	1.00	Food
Coniferous in regeneration (C10)	10	3 161 ± 1 172	2.6±0.7	0.30	—
Coniferous with balsam fir or white spruce (CF30)	≥30	1 589 ± 295	16.5±0.9	0.15	Cover
Coniferous without balsam fir (e.g., black spruce, tamarack etc.; CS30)	≥30	433 ± 200	19.4±1.8	0.05	Cover
Unproductive areas (bogs, fens, alder stands) (IMP)	—	na	na	0.10	—

**Note:** Browse availability and basal area of coniferous trees were measured in field surveys (Dussault et al. 2001b).

<sup>a</sup>According to forest maps published by the ministère des Ressources naturelles du Québec (2000).

<sup>b</sup>Includes only deciduous tree and shrub species known to be consumed by moose (*Betula* spp., *Populus* spp., *Prunus* spp., *Acer* spp., *Viburnum* spp., beaked hazelnut (*Corylus cornuta* Marsh.), *Sorbus* spp., *Salix* spp.).

<sup>c</sup>Stands with ≥10 000 stems of deciduous browse per hectare supported the highest food availability and were given a food value of 1.0; the food value for other stands was deemed to be proportional to browse availability.

<sup>d</sup>Food: ≥10 000 stems of browse/ha; cover: basal area of coniferous trees ≥13 m<sup>2</sup>/ha.

<sup>e</sup>Mostly white birch, *Populus* spp., and *Prunus* spp.

<sup>f</sup>Stand type Mi50 contained medium availability of both food and cover and so was considered to provide a cover/food edge at a very fine scale (within stand). Food availability in that stand type, however, was much lower than in prime food stands (Mi10, Dt50, and Mt50), which explains why it was considered to provide only cover when between-stands cover/food edge was assessed.

<sup>g</sup>Mostly yellow birch and *Acer* spp.

food edge density before reaching a plateau at the 70th percentile (Dussault 2002).

$$[2] \quad SI_{\text{edge}} = \text{within-stand edge} + \text{between-stands edge}$$

$$[3] \quad \text{Within-stand edge} = (\text{Mi50}\%) \times 1.0$$

$$[4] \quad \text{Between-stands edge} = (1 - \text{Mi50}\%) \times \text{between-stands edge index}$$

$$[5] \quad \text{Between-stands edge index} = \frac{\text{edge density(m/ha) between cover and food stands}}{70\text{th percentile of cover-food edge density across all landscape plots}} (\text{max.} = 1)$$

The two suitability indices,  $SI_{\text{food}}$  and  $SI_{\text{edge}}$ , were then combined in a global suitability index:

$$[6] \quad \text{HSI} = SI_{\text{food}} \times 0.45 + SI_{\text{edge}} \times 0.55$$

As suggested by Kurttila et al. (2002), Dussault (2002), and Courtois et al. (2002), each model component was weighted according to its ability to explain moose habitat selection.  $SI_{\text{edge}}$  (0.55) received a slightly higher weight than  $SI_{\text{food}}$  (0.45) because it explained a higher proportion of between-plots variation in moose density than  $SI_{\text{food}}$  (Dussault 2002). We still consider food to be the key factor in assessing habitat suitability, but for an area to be highly suitable for moose, food resources must be interspersed with sufficient cover. Hereinafter we will refer to eq. 6 when using the global model and eqs. 1 and 2 when using model components  $SI_{\text{food}}$  and  $SI_{\text{edge}}$ , respectively. In our case, habitat composition and edge density were calculated using ArcView GIS 3.2 equipped with the Spatial Analyst extension and Patch Analyst 2.2 (<http://flash.lakeheadu.ca/~rrempel/patch/>), respectively.

### Model validation

The most common standards used to validate HSI models are habitat use, animal density (Schamberger and O'Neil 1986; Allen et al. 1991), home-range size (Allen et al. 1988), survival rate, reproductive success (Van Horne 1983; Allen et al. 1988; Van Horne and Wiens 1991), and physiological condition (Schamberger and O'Neil 1986; Allen et al. 1988). However, the use of density as an indicator of habitat quality is not recommended (Van Horne 1983), and fitness indices such as survival and reproductive success are preferred. Employing such standards for moose, a long-lived species that is adapted to a wide array of environmental conditions, would require tremendous effort and monetary resources. We therefore chose habitat preference as a standard to assess our HSI model for moose.

We expected the habitat-preference index for moose to be positively correlated with the HSI model. We also expected that the habitat preference index would be related to the two model components ( $SI_{\text{food}}$  and  $SI_{\text{edge}}$ ) but the global model would perform better than the two model components considered individually. Since the HSI model and its two com-



ponents rely on habitat parameters found to be important to both males and females across different spatial scales (Dussault et al. 2005; also see the model description), we also expected the habitat-preference indices of males and females to be related to suitability scores at several scales.

### Study area

Model validation was conducted in the Laurentides Wildlife Reserve, a large forested area (7861 km<sup>2</sup>) north of the city of Québec. This area is approximately 40 km north of Jacques Cartier Park, where data used to develop the HSI model were collected. Forest stands in the study area are typical of the boreal forest (Dussault et al. 2001b). Coniferous stands with balsam fir and black spruce (*Picea mariana* (Mill.) BSP) are dominant on high plateaus, whereas areas at lower altitudes and river valleys are covered with mixed and deciduous stands, mostly white birch, trembling aspen (*Populus tremuloides* Michx.), yellow birch (*Betula alleghaniensis* Britt.), and maples (*Acer* spp.). The forest industry has been harvesting the study area for several decades, which has resulted in a heterogeneous mosaic of mature stands intermingled with regenerating stands. A severe eastern spruce budworm (*Choristoneura fumiferana* Clemens, 1865) outbreak occurred approximately 20 years ago and contributed to rejuvenation of the forest.

The mosaic of young and mature stands provides high-quality habitat for moose. Moose density in the reserve is relatively high: 2.2/10 km<sup>2</sup> in the winter of 1994 (8.0/10 km<sup>2</sup> in some sectors; St-Onge et al. 1996). Caribou (*Rangifer tarandus* L., 1758), white-tailed deer (*Odocoileus virginianus virginianus* Zimmerman, 1780), and black bear (*Ursus americanus* Pallas, 1780) are the other large mammals found in the study area. Natural predators of moose are the gray wolf (*Canis lupus* L., 1758) and black bear.

Winters are moderately harsh in terms of snow accumulation. Snow begins to accumulate in early November, reaches a maximum depth of ca. 100 cm around mid-March, and persists until early June under forest cover (ministère de l'Environnement du Québec, unpublished data). Minimum and maximum daily temperatures are -21.7 and -9.0 °C in January and 9.5 and 21.7 °C in July, respectively.

### Telemetry

Global positioning system (GPS) telemetry was used to assess habitat use by moose. Thirty-four individuals were monitored with GPS collars between winter 2002 and winter 2004. Moose were captured between early February and late March and monitored for 1 year ( $n = 23$ ) or 2 years ( $n = 11$ ). Captured moose were adult ( $\geq 2.5$  years old) and 21 were female and 13 were male. Captures followed standard techniques approved by the Animal Welfare Committee of the Société de la Faune et des Parcs du Québec (certificate 97-05), based on Canadian Council on Animal Care (1984) guidelines. Moose were immobilized with carfentanyl and xylazine (Delvaux et al. 1999). Collars were programmed to record a location every 2 or 3 h. We estimated location accuracy to be <35 m 95% of the time (Dussault et al. 2001a).

### HSI-model application

Vector forest maps of the study area (defined here as the minimum convex polygon encompassing locations of all in-

dividuals) were converted to two different raster maps with 5 m  $\times$  5 m cells. In the first map, each cell was categorized into one of the 10 stand types identified in Table 1. In the second map, each cell was categorized as providing "food" or "cover", based on the stand description listed in Table 1, to allow calculation of between-stands cover–food edge density. We applied the HSI model to the study area using three evaluation-plot sizes: 500, 100, and 10 ha. Evaluation plots were square. They were successively overlaid on the two raster maps described above to calculate the proportion of each habitat type as well as within- and between-stands edge, i.e., the parameters required to compute HSI-model components. The 70th percentile of cover–food edge density in the study area (required to calculate  $SI_{edge}$ ) was 30, 45, and 70 m/ha for the 500, 100, and 10 ha plots, respectively. Each evaluation plot was assigned a suitability category using the global HSI model and the two model components,  $SI_{food}$  and  $SI_{edge}$ . Suitability categories were 1 (<0.25), 2 (0.25–0.50), 3 (0.51–0.75), and 4 (>0.75) and were treated as habitat types in standard habitat-selection analyses. Habitat selection was assessed by comparing use and availability of evaluation plots that differed in suitability for each individual at landscape and home-range scales.

### Data analysis

To assess habitat preference at the landscape scale, the proportion of each suitability category was measured within the home range of each animal and compared with its availability within the study area, i.e., Johnson's (1980) second-order selection. We used only the 500 ha plot size to assess habitat selection at the landscape scale, since testing several plot sizes would have been redundant. To assess habitat preference at the home-range scale, use of suitability categories at animal locations was compared with the availability of those categories within individual home ranges, i.e., Johnson's (1980) third-order selection. All three plot sizes (10, 100, and 500 ha) were used at the home-range scale. We used the minimum convex polygon method (Mohr 1947) to delineate annual home ranges. To estimate habitat use at the home-range scale, we considered two contrasting time periods based on variations in food quality and quantity and environmental conditions: (1) summer–fall (1 June to 31 October), when vegetation is mostly green, and (2) winter (1 November to 31 May), when vegetation is leafless and snow renders ground vegetation inaccessible (Dussault 2002).

Telemetry locations were pooled by time period (home-range scale only) for each individual separately to calculate standardized habitat-selection ratios (Manly et al. 1993). Habitat patches and habitat types in the analyses corresponded to evaluation plots and suitability categories (1–5), respectively. 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 will choose one habitat type over all others, assuming equal availability of all habitat types (Manly et al. 1993; McLoughlin et al. 2002). We used these selection ratios in repeated-measures MANOVAs to test the influence of time period (home-range scale) and sex on habitat preference. Animal identification was included as a random factor in the analyses. Standardized habitat-

**Table 2.** Results of MANOVAs testing the effect of sex on moose preference for plots that varied in suitability at the landscape scale.

Effect	HSI			SI <sub>food</sub>			SI <sub>edge</sub>		
	df	F	P	df	F	P	df	F	P
Sex	3,105	8.3	<0.001	3,81	0.4	0.756	3,105	10.8	<0.001

**Note:** Habitat suitability was estimated using the global habitat-suitability index (HSI) model and the food and edge suitability indices in evaluation plots of 500 ha.

**Table 3.** Results of MANOVAs testing the effect of sex and time period on moose preference for plots that varied in suitability at the home-range scale.

Effect	HSI			SI <sub>food</sub>			SI <sub>edge</sub>		
	df	F	P	df	F	P	df	F	P
<b>Evaluation plot 500 ha</b>									
Period	3,195	0.5	0.718	3,133	0.7	0.535	3,192	0.8	0.492
Sex	3,195	6.4	<0.001	3,133	2.6	0.056	3,192	6.5	<0.001
Period × sex	4,195	0.7	0.601	4,133	1.4	0.252	4,192	1.2	0.328
<b>Evaluation plot 100 ha</b>									
Period	3,254	1.2	0.316	3,224	0.4	0.786	3,280	0.7	0.585
Sex	3,254	2.4	0.073	3,224	8.5	<0.001	3,280	0.9	0.449
Period × sex	4,254	1.0	0.404	4,224	0.2	0.951	4,280	0.8	0.509
<b>Evaluation plot 10 ha</b>									
Period	3,282	0.4	0.760	3,282	0.6	0.587	3,282	2.3	0.083
Sex	3,282	3.1	0.028	3,282	4.4	0.005	3,282	1.8	0.155
Period × sex	4,282	2.8	0.029	4,282	1.1	0.368	4,282	4.3	0.002

**Note:** Habitat suitability was estimated using the global HSI model and the food and edge suitability indices in evaluation plots of 500, 100, and 10 ha.

preference indices were log-transformed to meet the normality assumption. Lastly, we performed pairwise *t* tests on each combination of habitat types to establish a hierarchical order of habitat preference, with ranks of 1 indicating highest preference (Rettie and Messier 2000; McLoughlin et al. 2002). Separate analyses were conducted for the global HSI model and each of the two model components and were repeated for the three plot sizes and at the two scales.

## Results

Plots falling into suitability categories 3 and 4 were dominant in our study area as determined by the global HSI model (53.3% of the 500 ha plots) and the two model components, SI<sub>food</sub> (30.7%) and SI<sub>edge</sub> (62.6%). Habitat selection was detected for all suitability indices and at the two scales considered.

### Landscape scale

Male and female moose did not establish home ranges randomly in the study area and preferred different types of plots in terms of SI<sub>edge</sub> (Table 2, Fig. 1). At the landscape scale, the habitat-preference index for males increased with the score of the global HSI model, whereas the habitat-preference index for females did not (Fig. 1). This poor performance of the global HSI model for females was apparently due to the fact that unlike males, they did not seek plots with high SI<sub>edge</sub> values. However, the habitat preferences of both males and females were related to SI<sub>food</sub> (Fig. 1).

### Home-range scale

The habitat preference of moose also depended on suit-

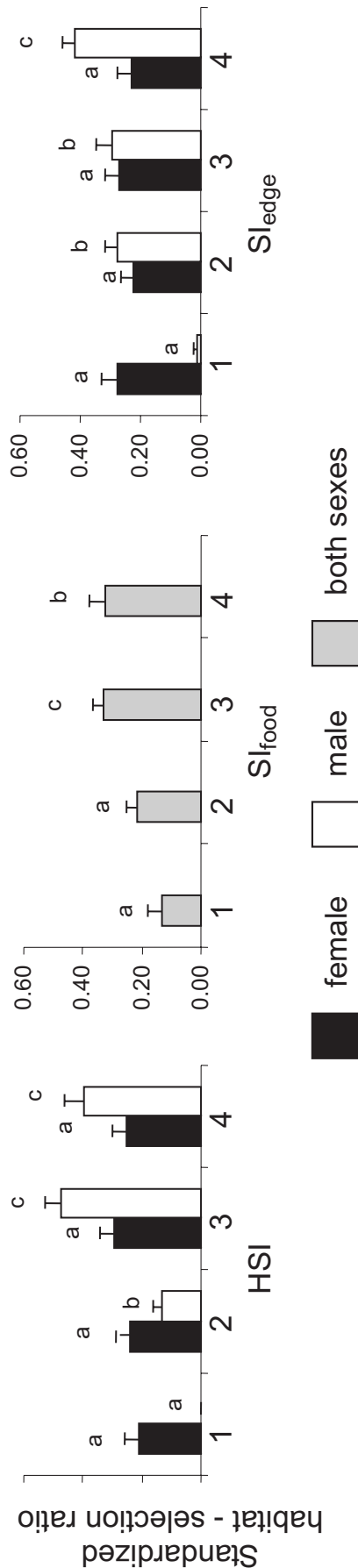
ability indices at the home-range scale, regardless of evaluation-plot size (Table 3, Fig. 2). Overall, the correspondence between habitat-preference index and suitability indices was better when evaluation plots of 500 ha were used. As at the landscape scale, the global HSI model was not the best predictor of moose habitat preference within the home range, and preference varied with sex. The global HSI model successfully identified the 500 ha plots most preferred by males but not those preferred by females. The preference of males for particular 500 ha evaluation plots was mostly related to SI<sub>edge</sub> rather than SI<sub>food</sub> values (Fig. 2), in contrast to the situation using 100 and 10 ha plots, where SI<sub>food</sub> was more important than SI<sub>edge</sub>. Within home ranges, females preferred 500 ha plots with high SI<sub>edge</sub> and intermediate SI<sub>food</sub> values.

Relationships between the suitability indices and habitat-preference index for moose were poor when 10 ha plots were assessed (Fig. 2). For the global HSI model and the model component SI<sub>edge</sub>, the preference of moose for particular suitability categories depended on the interaction between time period and sex (Table 3), but relationships were not positive. The HSI model only allowed plots unsuitable for males to be successfully identified during winter. The males' habitat-preference index was positively related to SI<sub>food</sub>, but females preferred plots with intermediate SI<sub>food</sub> values (Table 3, Fig. 2).

## Discussion

In this article we aim to develop a simple HSI model to depict moose habitat suitability on a year-round basis and we expected this model to be appropriate for both males and females over a wide range of spatial scales. Contrary to our

**Fig. 1.** Standardized habitat-selection ratios (mean  $\pm$  SE) for moose in evaluation plots with different suitability scores (HSI,  $SI_{\text{food}}$ , and  $SI_{\text{edge}}$ ) at the landscape scale. Suitability categories are 1 (<0.25), 2 (0.25–0.50), 3 (0.51–0.75), and 4 (>0.75). Separate values are presented for males and females unless no difference was detected. The same letter above the bars within each sex indicates that values do not differ significantly ( $P < 0.05$ ).



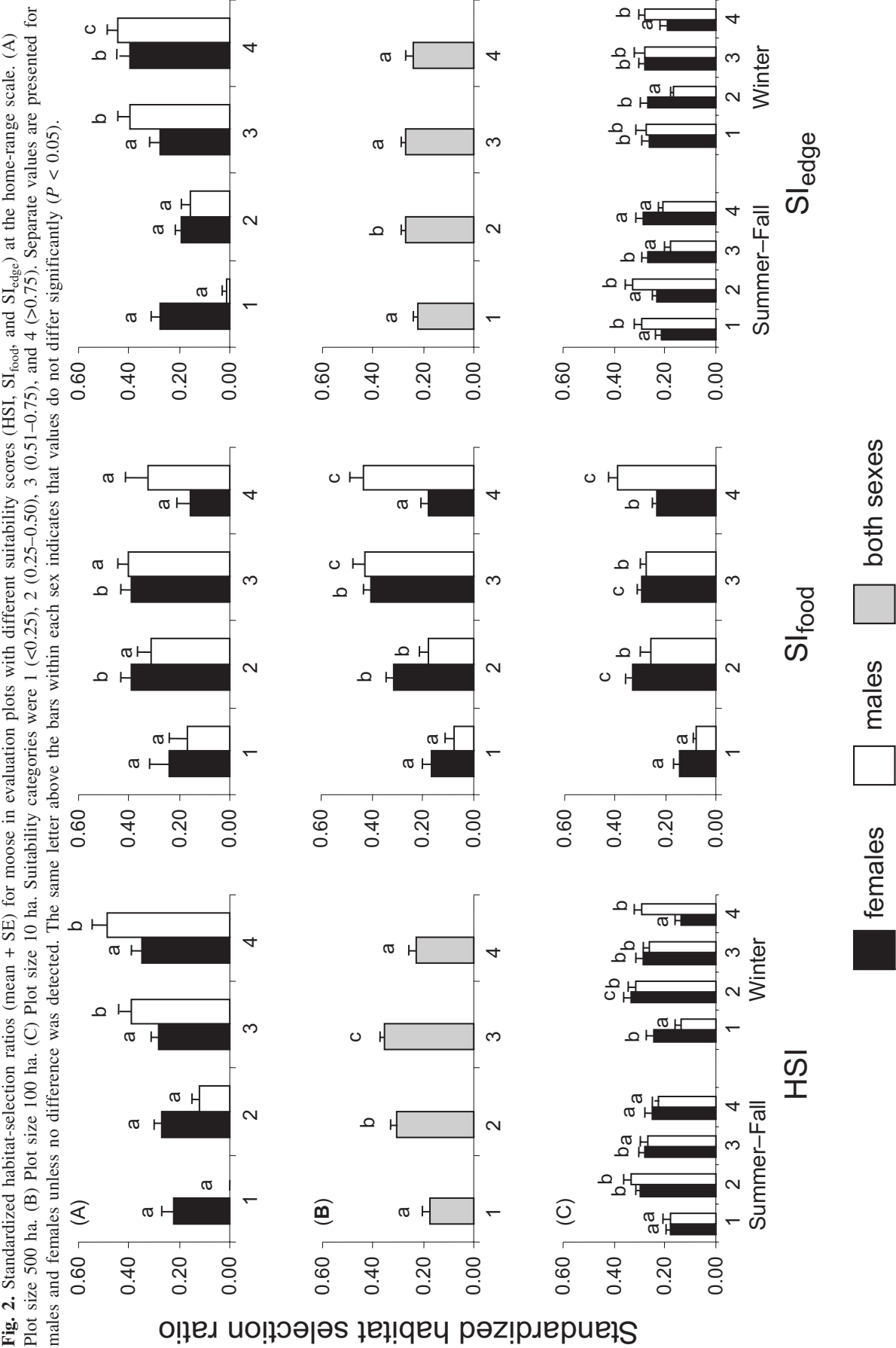
expectations, however, the two model components,  $SI_{\text{food}}$  and  $SI_{\text{edge}}$ , were often more closely correlated with the observed pattern of habitat selection than was the global model, indicating that the global model was not completely appropriate for the study area. Whereas  $SI_{\text{edge}}$  was more important to moose than  $SI_{\text{food}}$  at the largest spatial scale (i.e., 500 ha evaluation plots),  $SI_{\text{food}}$  was clearly more important at finer scales. One important finding was that correspondence between moose habitat-preference index at the home-range scale and all suitability indices was better when assessing the large plots (100 or 500 ha) than the small plots. Also, our suitability indices performed better with males than with females.

Despite these limitations, we think that our suitability indices provide useful tools for managers interested in evaluating habitat suitability for moose. Our model combines most of the advantages of previous HSIs while being relatively easier to calculate. First, it does not necessitate collecting extensive field data, as does model 1 from Allen et al. (1987), which requires measurements of available browse biomass and species composition of the tree layer. Second, it uses a relatively simple method to take into account the proximity of food and cover in assessing habitat suitability, which Courtois's (1993) HSI model does not do. Finally, although a modified version of Allen et al.'s (1987) model 1 was partially validated (Allen et al. 1991), our study provides, to our knowledge, the first complete validation of a moose HSI model. In contrast to our year-long data collection, Allen et al. (1991) conducted only a partial validation during midwinter, and they assessed moose habitat selection using snapshot data, i.e., moose locations obtained during aerial surveys.

Our HSI model successfully identified areas preferred by males to establish their home range because the habitat-preference index for males at the landscape scale was positively related to both  $SI_{\text{food}}$  and  $SI_{\text{edge}}$ . The habitat preference of females, however, was only related to  $SI_{\text{food}}$ . When assessing moose habitat suitability at very large scales (i.e., in areas of ca. 25–50 km<sup>2</sup>, such as hunting zones), therefore, managers should consider using the global HSI model for males but only  $SI_{\text{food}}$  for females.

The fact that suitability indices performed better at the home-range scale when assessing plots  $\geq 100$  ha suggests that suitable patches can be unattractive if they are too small and that a minimal size of adequate habitat is required for the patch to be attractive to moose. Based on this study, we encourage the use of  $SI_{\text{edge}}$  to determine habitat suitability for moose in plots  $\geq 500$  ha. To refine the assessment of habitat suitability at finer scales, we suggest using  $SI_{\text{food}}$  rather than  $SI_{\text{edge}}$ , keeping in mind that suitability for females is highest at intermediate  $SI_{\text{food}}$  values. Furthermore, for the most accurate assessment of habitat suitability, integration of the results obtained at the two scales should be considered. This could easily be done by using the current model and assessing  $SI_{\text{edge}}$  at the large scale (500 ha) and  $SI_{\text{food}}$  at the small scale (<100 ha). The impact of human activities such as forest harvesting could be evaluated by applying suitability indices to landscapes under alternative management scenarios.

The fact that our suitability indices did not precisely identify preferred plots at the smaller spatial scale could discourage their use by managers who are mostly searching for information at a very fine scale, e.g., the forest stand. Our





results, however, indicate that precise assessments of moose habitat suitability are more likely to be obtained at scales larger than the forest stand. The process of habitat selection is very complex and involves making decisions at multiple spatial scales. Although vegetative characteristics are probably the ultimate factor governing habitat selection by moose, there is growing evidence that selection also depends on geographical factors such as topography, roads, and human settlement (Dettki et al. 2003; Nikula et al. 2004). Inclusion of such parameters in our model may be necessary to improve assessment of habitat suitability at very fine scales. We also suggest that developing a HSI model that is simultaneously accurate and simple to use for a highly adaptable species that occupies a wide variety of forest environments (such as moose) may prove to be difficult. Modelling habitat selection by ungulates is complex because ruminants likely alternate their use of feeding and resting sites, which have completely different vegetation characteristics (Rothley 2001). HSI models may underestimate the importance of preferred habitats for resting and ruminating (Rothley 2001).

Our global HSI model did not perform as expected, for two main reasons. First, cover–food edge was not as attractive to moose as was previously observed (Courtois et al. 2002; Dussault 2002; Dussault et al. 2005). In the present study, cover–food edge availability was calculated using the same method as in the above studies, where its usefulness in assessing moose habitat selection was demonstrated. We suspect that edge preference may have been reduced in our study because winter snow conditions prevailing in our study area were much less restrictive to moose than those found in Jacques Cartier Park, where the data used to develop the model were collected (Dussault et al. 2001b; Dussault 2002). Second, the relationship between habitat preference of females and  $SI_{\text{food}}$  was not linear; females preferred plots with intermediate  $SI_{\text{food}}$  values. Evaluation plots with high  $SI_{\text{food}}$  values were open areas such as clearcuts or other recently disturbed habitats that were likely unattractive to females that trade off food acquisition with protection of young.

The HSI model did not assign appropriate values to certain evaluation plots that were used by moose. We argue, however, that our HSI model and suitability indices performed better than our results suggest. Indeed, habitat selection occurred at the landscape and home-range scales, as we have demonstrated. Moose first selected high-quality landscapes to establish home ranges, which likely rendered the detection of small-scale habitat selection more difficult. As shown by Myrsetrud and Ims (1998) and Dussault (2002), it is difficult to measure preference for habitat types that are highly available. Also, the generally suitable vegetative composition of the study area may have caused the relative attractiveness of most suitable evaluation plots to decrease (Aberg et al. 2000). Comparing habitat suitability at moose locations with availability within the study area would certainly have improved the correspondence between model output and moose preference index.

Our study revealed important sex-related differences in the habitat-selection patterns of moose (Miquelle et al. 1992; Nikula et al. 2004). We also have provided evidence that moose habitat selection in our study area was hierarchical (Johnson 1980; Nikula et al. 2004).  $SI_{\text{edge}}$  had a greater in-

fluence than  $SI_{\text{food}}$  on the habitat preference of males at the large scale but the converse was observed at the smaller scale. At the large scale, females preferred to establish home ranges in areas dominated by 500 ha plots with intermediate–high and high  $SI_{\text{food}}$  values, but at the smaller scale, females preferred plots with intermediate–low and intermediate–high  $SI_{\text{food}}$  values. These results indicate that the application of HSI models should be restricted to the range of spatial scales at which the model was developed. Also, a poor relationship between the HSI model and species behaviour does not necessarily indicate that the model is completely useless. It could be that the model was applied at an incorrect scale.

Our HSI model has the major advantage that it uses easily accessible data, which should facilitate communication between wildlife and forestry agencies (Kliskey et al. 1999). Many jurisdictions, such as the Province of Quebec, have forest-inventory programs that contain stand-level information (i.e., tree species composition, density of deciduous shrub species, etc.) that is required to calculate  $SI_{\text{food}}$  and  $SI_{\text{edge}}$ . Because our suitability indices are based on biological requirements, we feel that they have the potential to be exported to other regions of the boreal forest but the relative weight of each model component should be adjusted according to local conditions, such as winter severity. We underline the fact that suitability is a relative measure: a highly suitable habitat on a poor range could be considered to be of intermediate suitability in a prime range. The use of empirical data should be promoted to help refine model applications to take local conditions into account (Dettki et al. 2003; Fankhauser and Enggist 2004). The value of each stand type in terms of food and cover should be reevaluated when exporting HSI models to regions with stand types that differ in availability.

## Acknowledgements

This study was funded by the ministère des Transports du Québec, the ministère des Ressources naturelles et de la Faune du Québec, the Fondation de l'Université du Québec à Rimouski, and the Natural Sciences and Engineering Research Council of Canada. We thank L. Breton, Marius Poulin for his support in both planning and executing the fieldwork, and W.J. King for improving the English.

## References

- Aberg, J., Jansson, G., Swenson, J.E., and Mikusinski, G. 2000. Difficulties in detecting habitat selection by animals in generally suitable areas. *Wildl. Biol.* **6**: 89–99.
- Allen, A.W., Jordan, P.A., and Terrell, J.W. 1987. Habitat suitability index models: moose, Lake Superior region. *US Fish Wildl. Serv. Biol. Rep.* **82**.
- Allen, A.W., Terrell, J.W., and Jordan, P.A. 1988. An overview of a habitat suitability index model for moose: Lake Superior region. *Alces*, **24**: 118–125.
- Allen, A.W., Terrell, J.W., Mangus, W.L., and Lindquist, E.L. 1991. Application and partial validation of a habitat model for moose in the Lake Superior region. *Alces*, **27**: 50–64.
- Atlendorf, K.B., Laundré, J.W., Lopez Gonzalez, C.A., and Brown, J.S. 2001. Assessing effects of predation risk on foraging behavior of mule deer. *J. Mammal.* **82**: 430–439.

- Canadian Council on Animal Care. 1984. Guide to the care and use of experimental animals. Vol. 2. The Canadian Council of Animal Care, Ottawa, Ont.
- Coady, J.W. 1974. Influence of snow on behaviour of moose. *Nat. Can. (Que.)*, **101**: 417–436.
- Courtois, R. 1993. Description d'un indice de qualité d'habitat pour l'orignal (*Alces alces*) au Québec. Direction générale de la ressource faunique, ministère du Loisir, de la Chasse et de la Pêche du Québec, Québec, Que. Doc. tech. 93/1.
- Courtois, R., and Beaumont, A. 2002. A preliminary assessment on the influence of habitat composition and structure on moose density in clear-cuts of north-western Québec. *Alces*, **38**: 167–176.
- Courtois, R., and Crête, M. 1988. Déplacements quotidiens et domaines vitaux des orignaux du sud-ouest du Québec. *Alces*, **24**: 78–89.
- Courtois, R., Ouellet, J.-P., and Gagné, B. 1998. Characteristics of cutovers used by moose (*Alces alces*) in early winter. *Alces*, **34**: 201–211.
- Courtois, R., Dussault, C., and Potvin, F. 2002. Habitat selection by moose (*Alces alces*) in clear-cut landscapes. *Alces*, **38**: 177–192.
- Crête, M. 1989. Approximation of *K* carrying capacity for moose in eastern Quebec. *Can. J. Zool.* **67**: 373–380.
- Crête, M., and Courtois, R. 1997. Limiting factors might obscure population regulation of moose (Cervidae: *Alces alces*) in unproductive boreal forests. *J. Zool. (London)*, **242**: 765–781.
- Delvaux, H., Courtois, R., Breton, L., and Patenaude, R. 1999. Relative efficiency of succinylcholine, xylazine, and carfentanil/xylazine mixtures to immobilize free-ranging moose. *J. Wildl. Dis.* **35**: 38–48.
- Dettki, H., Löfstrand, R., and Edenius, L. 2003. Modeling habitat suitability for moose in coastal northern Sweden: empirical vs. process-oriented approaches. *Ambio*, **32**: 549–556.
- Dussault, C. 2002. Influence des contraintes environnementales sur la sélection de l'habitat de l'orignal (*Alces alces*). Ph.D. thesis, Université Laval, Québec, Que.
- Dussault, C., Courtois, R., Ouellet, J.-P., and Huot, J. 2001a. Influence of satellite geometry and differential correction on GPS location accuracy. *Wildl. Soc. Bull.* **29**: 171–179.
- Dussault, C., Courtois, R., Huot, J., and Ouellet, J.-P. 2001b. The use of forest maps for the description of wildlife habitats: limits and recommendations. *Can. J. For. Res.* **31**: 1227–1234.
- Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L., and Larochelle, J. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. *Ecoscience*, **11**: 321–328.
- Dussault, C., Ouellet, J.-P., Courtois, R., Huot, J., Breton, L., and Jolicœur, H. 2005. Linking moose habitat selection to limiting factors. *Ecography*, **28**: 619–628.
- Fankhauser, R., and Enggist, P. 2004. Simulation of alpine chamois *Rupicapra r. rupicapra* habitat use. *Ecol. Modell.* **175**: 291–302.
- Flather, C.H., and King, R.M. 1992. Evaluating performance of regional wildlife habitat models: implications to resource planning. *J. Environ. Manage.* **34**: 31–46.
- Griffith, B., and Youtie, B.A. 1988. Two devices for estimating foliage density and deer hiding cover. *Wildl. Soc. Bull.* **16**: 206–210.
- Groot Bruinderink, G.W.T.A., and Hazebroek, E. 1996. Ungulate traffic collisions in Europe. *Conserv. Biol.* **4**: 1059–1067.
- Hamilton, G.D., Drysdall, P.D., and Euler, D.L. 1980. Moose winter browsing patterns on clear-cuttings in northern Ontario. *Can. J. Zool.* **58**: 1412–1416.
- Hurley, J.F. 1986. Development, testing, and application of wildlife-habitat models: the manager's viewpoint. In *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Edited by J. Verner, M.L. Morrison, and C.J. Ralph*. University of Wisconsin Press, Madison, Wis. pp. 151–153.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, **61**: 65–71.
- Joyal, R. 1987. Moose habitat investigations in Québec and management implications. *Swed. Wildl. Res. Suppl.* **1**: 139–152.
- Kliskey, A.D., Lofroth, E.C., Thompson, W.A., Brown, S., and Schreier, H. 1999. Simulating and evaluating alternative resource-use strategies using GIS-based habitat suitability indices. *Landsc. Urban Plann.* **45**: 163–175.
- Kurttila, M., Pukkala, T., and Loikkanen, J. 2002. The performance of alternative spatial objective types in forest planning calculations: a case for flying squirrel and moose. *For. Ecol. Manage.* **166**: 245–260.
- Manly, B.F.J., McDonald, L.L., and Thomas, D.L. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London.
- Mastenbrook, B., and Cumming, H. 1989. Use of residual strips of timber by moose within cutovers in northwestern Ontario. *Alces*, **25**: 146–155.
- McGarigal, K., and Marks, B.J. 1994. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. Reference manual. Forest Science Department, Oregon State University, Corvallis, Ore.
- McLoughlin, P.I., Case, R.I., Gau, R.I., Cluff, D., Mulders, R., and Messier, F. 2002. Hierarchical habitat selection by barren-ground grizzly bears in the central Canadian Arctic. *Oecologia*, **132**: 102–108.
- Ministère des Ressources naturelles du Québec. 2000. Normes de cartographie écoforestière — confection et mise à jour. Direction des inventaires forestiers, Forêt Québec, ministère des Ressources naturelles du Québec, Québec, Que.
- Miquelle, D.G., Peek, J.M., and Van Ballenberghe, V. 1992. Sexual segregation in Alaskan moose. *Wildl. Monogr.* **122**. pp. 1–57.
- Mohr, C.O. 1947. Table of equivalent populations of North American small mammals. *Am. Midl. Nat.* **37**: 223–249.
- Molvar, E.M., and Bowyer, R.T. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *J. Mammal.* **75**: 621–630.
- Mysterud, A., and Ims, R.A. 1998. Functional responses in habitat use: availability influences relative use in trade-off situations. *Ecology*, **79**: 1435–1441.
- Mysterud, A., and Ostbye, E. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. *Wildl. Soc. Bull.* **27**: 385–394.
- Nikula, A., Heikkinen, S., and Helle, E. 2004. Habitat selection of adult moose *Alces alces* at two spatial scales in central Finland. *Wildl. Biol.* **10**: 121–135.
- O'Neil, L.J., Roberts, T.H., Wakeley, J.S., and Teaford, J.W. 1988. A procedure to modify habitat suitability index models. *Wildl. Soc. Bull.* **16**: 33–36.
- Peek, J.M. 1998. Habitat relationships. In *Ecology and management of the North American moose. Edited by C.C. Schwartz and L.A. Renecker*. Smithsonian Institution Press, Washington, D.C. pp. 351–376.
- Pierce, D.J., and Peek, J.M. 1984. Moose habitat use and selection patterns in north-central Idaho. *J. Wildl. Manage.* **48**: 1335–1343.
- Renecker, L.A., and Schwartz, C.C. 1998. Food habits and feeding behavior. In *Ecology and management of the North American moose. Edited by C.C. Schwartz and L.A. Renecker*. Smithsonian Institution Press, Washington, D.C. pp. 403–440.

- Rettie, J.W., and Messier, F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. *Ecography*, **23**: 466–478.
- Riley, S.J., Decker, D.J., Carpenter, L.H., Organ, J.F., Siemer, W.F., Mattfeld, G.F., and Parsons, G. 2002. The essence of wildlife management. *Wildl. Soc. Bull.* **30**: 585–593.
- Roloff, G.J., and Kernohan, B.J. 1999. Evaluating reliability of habitat suitability index models. *Wildl. Soc. Bull.* **27**: 973–985.
- Romin, L.A., and Bissonette, J.A. 1996. Deer–vehicle collisions: status of state monitoring activities and mitigation efforts. *Wildl. Soc. Bull.* **24**: 276–283.
- Rothley, K.D. 2001. Manipulative, multi-standard test of a white-tailed deer habitat suitability model. *J. Wildl. Manage.* **65**: 953–963.
- Schamberger, M.L., and O’Neil, L.J. 1986. Concepts and constraints of habitat-model testing. *In* *Wildlife 2000: modeling habitat relationships of terrestrial vertebrates*. Edited by J. Verner, M.L. Morrison, and C.J. Ralph. University of Wisconsin Press, Madison, Wis. pp. 5–10.
- Schwab, F.E., and Pitt, M.D. 1991. Moose selection of canopy cover types related to operative temperature, forage, and snow depth. *Can. J. Zool.* **69**: 3071–3077.
- St-Onge, S., Courtois, R., and Banville, D. 1996. Inventaires aériens de l’orignal dans les réserves fauniques du Québec. Ministère de l’Environnement et de la Faune du Québec, Québec, Que.
- Thompson, I.D., and Stewart, R.W. 1998. Management of moose habitat. *In* *Ecology and management of the North American moose*. Edited by C.C. Schwartz and L.A. Renecker. Smithsonian Institution Press, Washington, D.C. pp. 377–402.
- Thompson, I.D., and Vukelich, M.F. 1981. Use of logged habitats in winter by moose cows with calves in northeastern Ontario. *Can. J. Zool.* **59**: 2103–2114.
- Timmermann, H.R., and McNicol, J.G. 1988. Moose habitat needs. *For. Chron.* **64**: 238–245.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manage.* **47**: 893–901.
- Van Horne, B., and Wiens, J.A. 1991. Forest bird habitat suitability models and the development of general habitat models. *US Fish and Wildl. Serv. Fish Wildl. Res.* **8**.
- White, K.S., and Berger, J. 2001. Antipredator strategies of Alaskan moose: are maternal trade-offs influenced by offspring activity? *Can. J. Zool.* **79**: 2055–2062.
- Yaffee, S.L. 1999. Three faces of ecosystem management. *Conserv. Biol.* **13**: 713–725.