



Studying deer habitat on Anticosti Island, Québec: relating animal occurrences and forest map information

Martin Plante^a, Kim Lowell^{a,*}, François Potvin^b,
Barry Boots^c, Marie-Josée Fortin^d

^a Centre de Recherche en Géomatique, Pav. Casault, Université Laval, Québec City, Que., Canada G1K 7P4

^b Société de la Faune et des Parcs du Québec, Québec City, Que., Canada

^c Department of Geography and Environmental Studies, Wilfrid Laurier University, Waterloo, Ont., Canada

^d Department of Zoology, University of Toronto, Toronto, Ont., Canada

Received 6 January 2003; received in revised form 18 August 2003; accepted 2 September 2003

Abstract

Forest maps are widely available and can provide an inexpensive way to analyse ecological phenomena at a landscape level. This paper presents a case study whose objective was to help manage the deer herd and associated habitat on Anticosti Island. The selection by deer of winter habitat was analysed spatially using aerial survey data and a forest map produced by interpretation of aerial photographs. Initially, it was demonstrated that the spatial distribution of deer across the landscape could not be considered random. Grid cells of two different sizes—500 m × 500 m and 1 km × 1 km—were extracted from the forest map, and landscape indices thought to be relevant were calculated for each to characterize the key landscape features on which deer select their winter habitat. To do this, the landscape indices were correlated with the number of deer found in grid cells of a given size. It was found that deer preferred areas on which balsam fir was present, and areas in which there was a relatively high concentration of regeneration/dense forest edge. Correlations were better for the larger grid cell size suggesting that deer on Anticosti Island selected habitat based on an area larger than 500 m × 500 m. However, it is noted that this result is probably also due in part to the modifiable areal unit problem (MAUP) whereby larger window sizes tend to provide better correlations between two variables. The location of the grid cells within the study area also affected the results slightly.

© 2003 Elsevier B.V. All rights reserved.

Keywords: Habitat selection; Landscape indices; Quadrat analysis; White-tailed deer

1. Introduction

At the end of the 1800s, some 220 white-tailed deer (*Odocoileus virginianus*) were released on Anticosti Island in the province of Québec, Canada. Despite a nutritionally poor winter environment, and due to

a lack of natural predators, the present deer population of 120,000 represents 15 deer/km² compared to 2 deer/km² average across the rest of Québec (Potvin and Gingras, 2002). As a result, due to heavy browsing by deer, the commercial forest resource—particularly balsam fir (*Abies balsamea* (L.) Mill.)—has become severely affected on the island. It has become apparent that the forests of Anticosti Island must be managed in a way that controls the impact of the deer on the forest while ensuring their long-term survival. To do

* Corresponding author. Tel.: +1-418-656-2131x7998;

fax: +1-418-656-7411.

E-mail address: Kim.Lowell@scg.ulaval.ca (K. Lowell).

this, the relationship of the deer to their environment at the landscape level must be better understood.

A number of researchers have studied deer in Québec at the individual forest stand level (e.g., Larue et al., 1994; Dumont et al., 1998, 2000). Although it seems reasonable to believe that deer respond to their environment at the landscape level as well as the stand level, few studies have been undertaken to examine the relationship of deer to its environment at the landscape level (Potvin and Gingras, 2002) due in part to the type of data that are normally available.

The most common models are habitat suitability index (HSI) models that estimate the potential of a given species in a given area (Brooks, 1997). HSI models are based on published literature and expert opinion rather than on empirical data of animal populations. For validation of such models, field data are used: telemetry locations (Roloff et al., 2001) or indirect indices of use and abundance such as browse evidence or pellet counts (Morgan et al., 1993; Roloff and Kernohan, 1999; Rothley, 2001). In addition to HSI models, a few statistical models of deer populations based on empirical data have been proposed. Gaudette and Stauffer (1988) used multiple regression analysis based on pellet counts to produce one such model. Pauley et al. (1993) used logistic regression and telemetry data in a probabilistic approach. Such efforts are focused on individual locations whereas examining deer populations at a landscape level requires a population density approach. One of the few density models that has been developed employed density at the township level as estimated by harvest data (Roseberry and Woolf, 1998). While the articles cited make a useful contribution to studying deer populations in relation to habitat, they all are constrained to a single scale.

A central tenet of the present work is that the “best” spatial scale at which to study deer populations is not known a priori. Thus, having methods to examine deer populations at different spatial scales would provide a means to better manage wildlife populations. Certainly in managing the deer population on Anticosti Island there is an interest, and even a necessity, to study the spatial dynamics of the deer population at the landscape level.

As an initial step, one must first examine the spatial distribution of deer and determine if this distribution— independent of any habitat characteristics—can be considered to be random. It could be the case on An-

ticosti Island that, because the deer population is so high, the deer simply occupy the entire island with little thought about habitat selection. If so, then additional study of the relationship of the deer to habitat would be pointless. Given that the locations of deer, or groups of deer, are identified using aerial surveys, point pattern statistics such as Ripley’s *K* (Ripley, 1981) can be used to determine their spatial structure.

Once the spatial distribution of deer is quantified and described, it becomes possible to relate it to the spatial distribution of forest habitat at the landscape level. To study any phenomenon at the landscape level, one must first be able to characterise the landscape in an objective manner. One way that this can be accomplished is through the use of landscape indices (LIs) that characterize landscape features such as habitat composition, configuration, and heterogeneity (e.g., Li and Reynolds, 1994; McGarigal and Marks, 1995; Haines-Young and Chopping, 1996; Gustafson, 1998).

The purpose of this study, therefore, is to examine the characteristics of the spatial distribution of deer and to relate this distribution to habitat characteristics quantified at the landscape level. If strong relationships can be found, such information would be useful to managers of the fauna of Anticosti Island.

2. Study area and data

Anticosti is a 7943 km² island located in the Gulf of St. Lawrence in eastern Québec. It is characterised by topographically gentle terrain, a mean winter temperature of -10°C , and abundant snow. The forest cover is predominantly coniferous (balsam fir and white and black spruce (*Picea glauca* and *Picea mariana*)) although some deciduous trees—particularly trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*)—are present. Because of the high deer population, there is very little understory, and vegetative regeneration is poor.

Between 11 and 21 January, 1999, FAPAQ (Société de la faune et des parcs du Québec—i.e., the Québec Wildlife and Parks Commission) undertook an inventory of the deer in a northeastern 270 km² portion of Anticosti Island (Potvin and Gingras, 2002) (Fig. 1; the five regions delineated on this figure will be explained in the Results and Discussion). The method employed in the deer inventory is a double count aerial

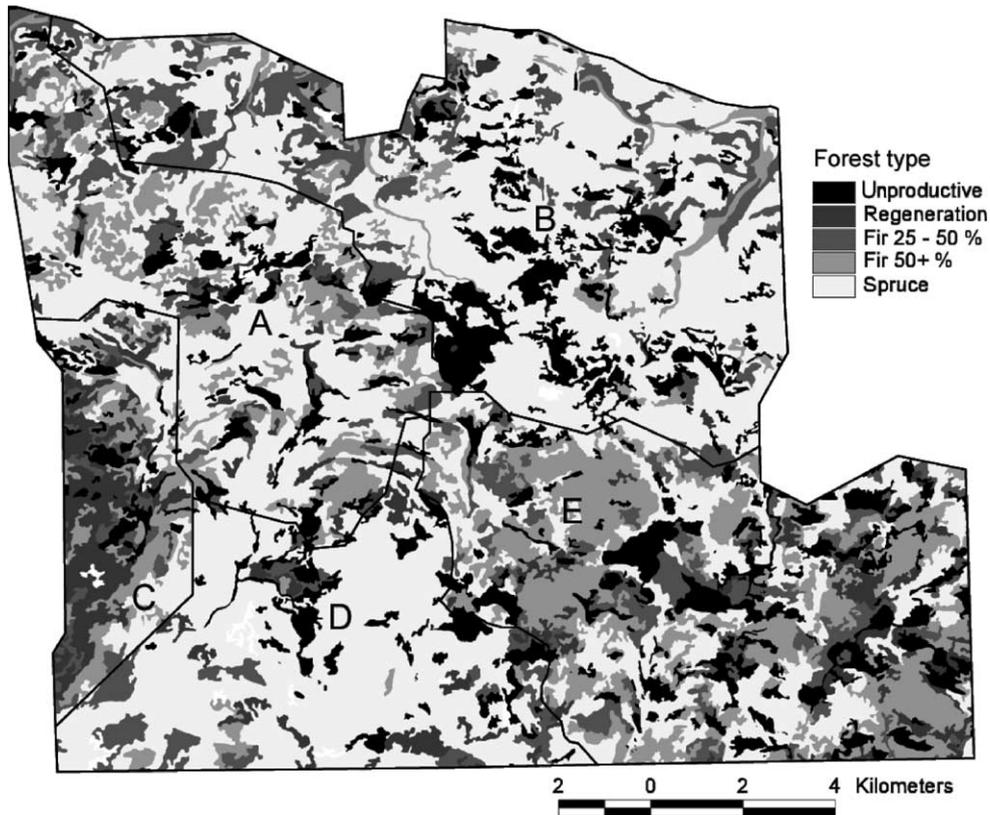


Fig. 1. Forest type map of the study area and stratification into five regions.

inventory (Potvin et al., 1992, 2002). In this method, a helicopter flies a series of flight lines with two observers sitting on the same side, one in front and one in back. In the present study, flight lines were oriented north-south and were spaced 300 m apart. The helicopter flew at an altitude of 60 m and observers closely scrutinised a narrow strip 60 m wide on each flight line. Each observer independently noted the number of deer seen at a given place on the flight line and a third person recorded the position and number of individuals in each group. Although January is an ideal month to survey deer due to their high visibility against the snow, they tend to shelter beneath coniferous trees. Post survey analysis indicated that the observers had rates of observation of 57 and 58% and that this rate was not influenced by the amount of coniferous cover (F. Potvin, unpubl. data). Observers collectively detected 82% of the deer groups which suggests that the location of the detected groups is a representa-

tive sample of the total deer population. For a more detailed description of the deer data, see also Potvin et al. (2003). Fig. 2 provides a map of the number and locations of deer observed.

In addition to the point-based deer data, a conventional 1:20,000 forest map of the area was available in digital format. Such maps are produced by the Québec Ministry of Natural Resources via human interpretation of stereoscopic aerial photographs. Using a well-defined classification system (MNR, 1995), stands of different forest types are identified based on tree species composition, density, height, and age. In addition, areas subjected to disturbances such as windthrow and harvesting are noted, and, depending on the characteristics of the forest type, individual forest stand polygons may be tagged with additional information such as the slope and drainage class. The minimum mapping unit on these maps is generally 8 ha although it can be as small as 2 ha depending on

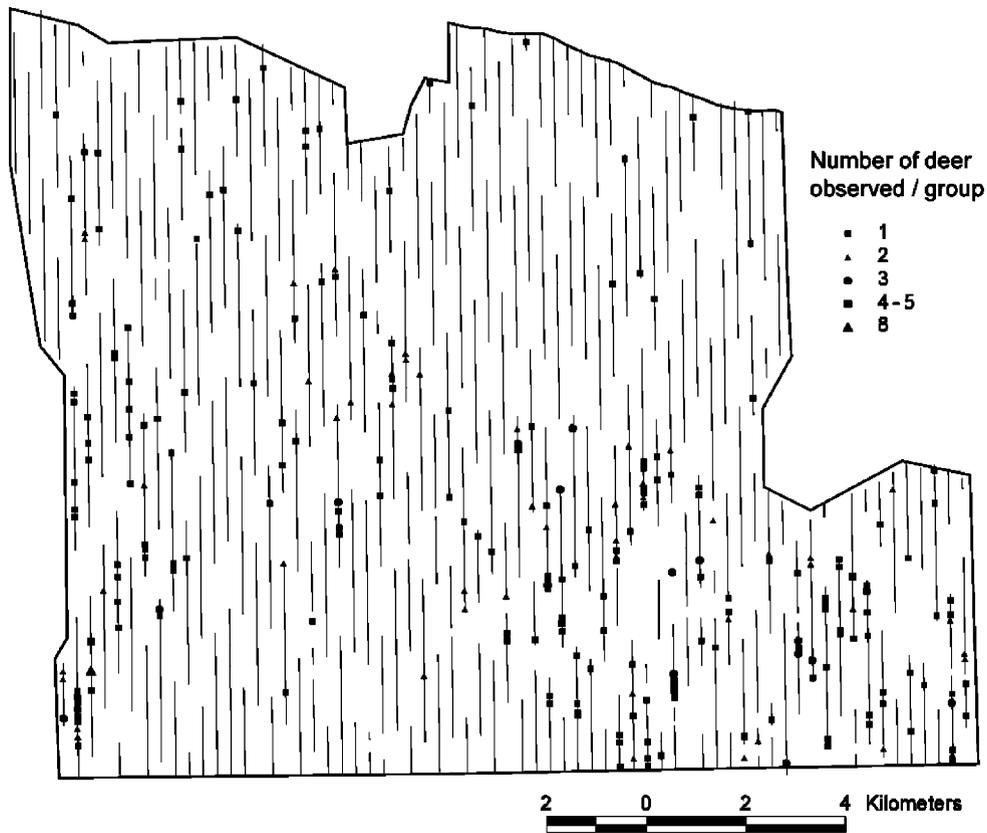


Fig. 2. Number of deer observed and flight lines.

local forest conditions. The map used in this study had been developed in 1997 and updated in 1999. For the purposes of this study, the digitised vector map was converted to raster format composed of pixels that were $10\text{ m} \times 10\text{ m}$ (0.01 ha) in size. Given the number of possible combinations of the vegetative factors that comprise a forest type map, the forest type map had been stratified by FAPAQ into 18 classes thought to be relevant to deer populations based on the primary and secondary tree species, and the age of the overstory individual forest stands (Table 1).

3. Methodology

3.1. Deer distribution

The spatial distribution of deer was studied using K -function analysis—a second order analytical tech-

nique that provides for a description of a point distribution at various scales and can detect spatial dependence among point locations (Bailey and Gatrell, 1995). To estimate K , one calculates the mean number of points that are within a circle of a given radius h of each point; if the point data are spatially clustered, this mean value will be relatively large—particularly for small values of h . To standardize the statistic, one divides the mean value by the mean number of points per unit area (i.e., an area of radius h) (Fotheringham et al., 2000). When simplified, the general form of the equation for K for a distance h is:

$$Khat_h^1 = \frac{A}{n^2} \sum_{w_{ij}} \sum I_h(d_{ij}) \quad \text{for } i \neq j$$

where A is the area of the region studied, n is the total number of points, d_{ij} is the distance between the i th and j th points $I_h(d_{ij})$ is a function that takes the value of 1 (one) when d_{ij} is smaller than the search

Table 1
Eighteen and five map classes used for deer habitat analysis (from Potvin and Gingras, 2002)

General forest type	Percentage of fir	Class name	5-class map description	Group
Non-forest		wat	Water	unp ^a
		unp	Unproductive	unp
Regeneration (<7 m tall)		rct	Recent clearcut	reg
		wnd	Total windthrow	reg
		regfir	Fir regeneration	reg
		regoth	Regeneration of other species	reg
Mature (>7 m tall)	<25	hwmx	Hardwood and mixed	spr
	<25	bsp	Black spruce	spr
	<25	wsp30	White spruce 30 years of age	spr
	<25	wsp50	White spruce 50 years of age	spr
	<25	wsp70	White spruce 70 or more years of age	spr
	<25	wspfir5	White spruce, 5–25% fir	spr
	25–50	bspfir	Black spruce and fir	fir25
	25–50	wspfir25	White spruce and fir	fir25
	25–75	mixfir	Mixed species and fir	fir25
	50–75	firbsp	Fir and black spruce	fir50
	50–75	firwsp	Fir and white spruce	fir50
	>75	fir	Pure fir	fir50

^a unp, unproductive; reg, regeneration; spr, spruce; fir25, fir 25–50% basal area of the stand; fir50, fir >50% basal area of the stand.

radius around the i th observation and 0 (zero) if not, and w_{ij} is a correction factor to account for the border effect of the region under study. It is defined as the conditional probability that a point is observed within the study area given that it is d_{ij} from point i . It is estimated as the proportion of a circle of radius d_{ij} , centred on point i , that lies within the area studied.

If K is estimated for a number of distances, one can examine the spatial dependence of points relative to distance. In addition, the estimate of K can be converted/normalised to a test statistic $Lhat$ that permits the significance of the deviation of an observed value of $Khat$ from its expected value (under an assumption of randomness according to a Poisson distribution) to be tested (Fortin, 1999b); if $Lhat$ is significantly different from zero, then the spatial distribution of points is not random. The general form of $Lhat$ is:

$$Lhat_h = \left(\frac{Khat_h}{\pi} \right)^{0.5} - h$$

$Khat$ (and subsequently $Lhat$) was calculated using the deer point data for progressively larger distances. The only modification to this calculation from what has been described involved a minor treatment of the deer

data. In the present study, each point may represent a group of deer rather than isolated individuals whereas K -function analysis operates on points that represent a single individual. To accommodate this, any point representing more than a single deer was “split” into the appropriate number of points with the resulting points being clustered a small distance around the location of the original point observation.

3.2. Relationship of deer to the forest environment

3.2.1. Treatment of data

In order to compare the point-based deer observations with the polygonal forest type data, it was necessary to convert the deer data to a surfacial—i.e., raster format. This was accomplished by first using spatial interpolation based on the quartic kernel (S-Plus, 2001). In this method, a regular grid of a pre-determined size is established over the study area. Each grid cell is assigned a single value—i.e., the number of deer per kilometer—estimated based on the number of deer around the centre of a grid cell and a distance-decay function. In this study, a 46×46 grid was established meaning that grid cells were $456.6 \text{ m} \times 456.6 \text{ m}$. This grid was then converted to

a grid of 10 m × 10 m pixels simply by subdividing the larger grid cells. For subsequent analysis, these 10 m × 10 m cells were regrouped to estimate the number of deer/km² for a variety of other grids.

To conduct landscape scale analysis, two grid cell sizes were considered—500 m × 500 m and 1 km × 1 km. Hence, for a given analysis, a grid of one of these sizes was established on the study area. For each grid cell, a mean deer density was determined by averaging the density in each of the 10 m × 10 m cells underlying the grid cell. Because the position of each of the 500 m or 1 km grid cells might fall on more than one of the grid cells in the 46 × 46 original interpolation grid, this procedure had the effect of assigning an area-weighted deer density to each of the (500 m or 1 km) grid cells.

These analyses are affected, however, by the size and the placement of the starting location of the grid (Jelinski and Wu, 1996; Fortin, 1999a) which in turn can affect the observed number of deer in each grid cell. Therefore, to evaluate the robustness of results, two grid cell sizes were used: 500 m × 500 m (25 ha) and 1 km × 1 km (100 ha). In addition, after placing the first grid of a given size and analyzing the resulting grid cell data, a new grid of the same size was imposed on the study area, but its origin was moved 200 m south of the original grid origin; the analysis was then reconducted on this second grid. Finally, a third grid of a given size whose origin was 400 m south of the original grid was imposed on the study area and the analysis reconducted on this third grid. (These grid positions are labeled “I”, “II”, and “III” in subsequent discussions of results.) By examining two sizes and three positions of grids, the danger of having subsequent analytical results that are artifacts of grid size and/or placement is reduced, and potential effects of grid placement and size can be observed.

The selected LIs were then also calculated for each grid cell for which the deer density had been estimated. This was repeated for both sizes of grids. In addition, this method of estimating deer density for a given grid cell means that data are sensitive to the placement of the grid. Thus, the three grids of given size but different location employed in the quadrat analysis were also employed herein and results from each analysed individually.

The forest data were analysed using the original 18 classes of the forest map as well as a map containing five classes only. This was done because prior

work suggested that it might be possible to satisfactorily condense the 18 classes into five while retaining a large portion of the forest type information relevant to deer habitat. The five classes employed were defined based on existing knowledge (Potvin and Gingras, 2002) concerning the suitability of certain forest types for deer habitat (Table 1). Hence, in total 12 analyses were conducted for two grid cell sizes, three grid positions, and two maps.

3.2.2. Landscape indices (LIs)

The general framework of the analytical methodology employed herein involved establishing a number of grid cells of a given size and location for which deer density was determined on both the 18-class and 5-class forest maps, and calculating a number of LIs for the grid cell. The grid cell sizes were selected in part because they were believed to be relevant to habitat selection, but also because they provided an adequate sample size for analysis. The LIs selected were intended to reflect existing knowledge about deer habitat selection. For example, it is known that in winter, stands of mature balsam fir are favoured for food whereas spruce stands are rarely used (Lamontagne and Potvin, 1994). Similarly, transition zones between mature forests and areas of regeneration are favoured because they tend to offer cover in the mature forest as well as food in the regeneration. Hence, five LIs addressing various aspects of deer habitat were chosen and calculated for each grid cell selected.

1. *Habitat class area (HCA)*—HCA was calculated for each class. It is expressed as the percentage of a grid cell occupied by a given class and addresses the concentration of each class in a given area/grid cell.
2. *Number of patches (NP)*—NP is the number of different polygons present in a given grid cell. NP provides an indication of the size of the average patch in the grid cell under study without consideration of the type assigned to each patch.
3. *Biggest patch area (BPA)*—BPA is the area of the largest polygon in a grid cell, regardless of which class occupies that polygon. BPA is an indicator of the homogeneity of the forest types present in the grid cell under consideration.
4. *Edge density (ED)*—ED is the length of all or selected boundaries within a grid cell divided by the

total area of the grid cell. It provides a measure of the quantity of ecological edges present. In this study, because we were interested in specific types of boundaries, ED of three types of edges was calculated: regeneration and fir 25–50% density, regeneration and fir >50% density, and regeneration and spruce. These were the types of edges of interest regardless of whether the 18-class map or the 5-class map was being analysed.

5. *Distance to the mean nearest neighbour (DMNN)*—DMNN is the distance from a patch of a given class to a patch of the same class within the grid cell under consideration with the distances for all patches subsequently being averaged. For a given patch, one calculates the distance from it to another patch of the same class within the grid cell under study. Any patch with a class that is unique within the grid cell is excluded from the calculation. The nearest neighbour distances for each patch are averaged over all classes. DMNN provides a measure of the ability of deer to move from an area of a given class to another area of the same class.

3.2.3. Analysis

Each map of deer density (defined by grid cell size and grid origin) was treated similarly. A certain number of grid cells—100 for the 500 m × 500 m grid; 25 for the 1 km × 1 km grid—whose entire area fell within the study area were randomly selected in order to minimize the effects of any spatial autocorrelation that might be present among grid cells. The area of each selected grid cell was super-imposed on the forest map, and the values of the five selected LIs calculated. Note that this produced more than five variables as some of the LIs are class specific. For example, the calculation of edge density produced three variables—one for each of the edges of interest. Pearson's correlation coefficient (r) was then used to measure the strength of the relationship of deer density to each of the LIs. Finally, the value of r was tested for statistical significance using an F test.

After conducting this analysis and examining the results and the forest map, it was decided to partition the study area into five smaller regions that appeared to represent distinct habitat sectors. It was hypothesized that the dynamics of deer habitat selection might be different within each—a supposition that seems reasonable given that the deer density appears (through

visual comparison of Figs. 1 and 2) to be related to the different habitat types. Consequently, the map was divided into five regions (A–E; Fig. 1) and for each the relationship of the deer density to the LIs was determined as before using Pearson's correlation coefficient. In this subsequent analysis, however, to ensure a suitable sample size, instead of choosing grid cells randomly within each region, all grid cells of a given grid whose area fell completely inside the sub-region were employed in the analysis.

4. Results and discussion

To determine if there is a tendency for deer to be non-randomly clustered or dispersed, K -function analysis (and its associated normalisation to the L statistic) was employed over various distances (Fig. 3). Values of $Lhat$ significantly different from zero at a given distance indicate either clustering (positive values of $Lhat$) or dispersion (negative values of $Lhat$) at that distance relative to a random spatial distribution. The high level of statistical significance evident in Fig. 3 makes it clear that significant clustering exists among the location of deer up to a distance of about 10 km, with maximum clustering occurring at 6 km.

Interestingly, these (and previous) findings are in contradiction to what is known about the winter behavior of deer on Anticosti Island as it has been documented that deer do not congregate in winter, as opposed to deer on mainland Quebec (Zwarts, 1998). This “non-congregation tendency” is also suggested by simply examining the frequency distribution of the number of groups of deer of a given size (Table 2)—76% of deer are found in groups of two or fewer. The reason for this seeming discrepancy

Table 2
Number of groups of deer by the number of deer in the group

Number of deer in group	Number of groups
1	183
2	49
3	18
4	5
5	1
6	0
7	0
8	1

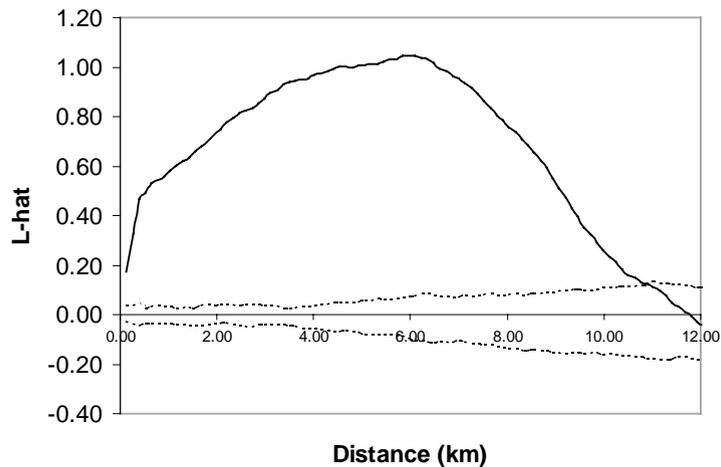


Fig. 3. The L statistic from K -function analysis and statistical significance ($\alpha=0.01$) envelope over various distances (solid line is value of L_{hat} ; dashed lines show 99% confidence interval for a random distribution—i.e., an L_{hat} value outside the dashed lines indicates a non-random spatial distribution.)

is apparent through direct examination of the spatial distribution of the deer (Fig. 2). The deer tend to be clustered in the southeast corner of the study area with an additional band of higher population density located towards the center, and extending to the southwest of the study area. Considering that the study area is approximately 20 km in the east–west direction, from Fig. 2 it is apparent that though deer do not have a tendency to cluster in an area close enough to be considered a single group, over a larger scale there is a tendency for deer to occupy the same area. Thus, the “contradiction” between what is known about deer behaviour and the results of statistics employed herein has to do with spatial scale. If one considers deer on a micro-scale, they do not have a tendency to cluster (or to behave as a pack animal); if one considers their spatial position on a broader scale (i.e., over a larger area), they clearly do have a tendency to prefer being in the same general area. Moreover, in general terms there are two spatial processes that lead to clustering. Interaction (or “real contagion”) occurs when there is a mutual attraction of individuals/deer; “apparent contagion” occurs when there is an environmental inhomogeneity that causes individuals to cluster because of some external factor. On Anticosti Island, it is apparent contagion that produces the clustering observed.

This finding strongly suggests that individual deer make a conscious decision about where they will spend

winter. It thus seems reasonable to believe that they have made this choice relative to the habitat available. The correlation analysis of LIs and deer density over the entire region provides an indication of the types of habitat favoured or avoided by the deer.

For the 5-class map (Table 3) and a grid cell size of 500 m, linear correlations¹ between the number of deer and the values of LIs are generally weak (maximum r of about 0.37 for edge density between regeneration and fir >50% density), and two of the three grid positions (A and B) indicate that deer select for a greater number of patches (NP) in a 500 m area—i.e., r is positive. The third grid position suggests that deer select for areas with a high amount of regeneration/dense fir edge and for areas of dense fir, but select against areas of spruce. Correlations for the 5-class map are generally higher for the 1 km grid cells suggesting that deer habitat selection is made over a larger area than 500 m. The information of the three grid positions considered collectively clearly indicates that in the winter deer select for a more variable area (r for NP is significant and positive; the negative r for biggest patch area (BPA) for grid position III reinforces this finding) and against spruce (r is significant and negative). Results for grid position I also suggest that deer select for dense fir, while results for grid position III

¹ No non-linear correlations were identified either.

Table 3
Landscape Indices for the 5-class map that are significantly correlated with deer density for a given grid cell size and grid position

Grid cell size	<i>n</i>	Grid position	Variable <i>P</i> ^a (<i>r</i> ^b)
500 m	100	I	NP ^{c,*} (0.20)
		II	NP* (0.24)
		III	EDregfir50** (0.37), HCAspr** (−0.22), HCAfir50** (0.25)
1 km	25	I	NP* (0.44), HCAspr** (−0.58), HCAfir50* (0.49)
		II	NP* (0.41), HCAspr* (−0.48)
		III	NP* (0.43), HCAspr** (−0.64), HCAreg** (0.58) BPA* (−0.50), EDregfir50* (0.45)

^a Probability level: **P* ≤ 0.05, ***P* ≤ 0.01.

^b Pearson's correlation coefficient.

^c Abbreviations: LIs: NP, number of patches; ED, edge density; HCA, habitat class area; BPA, biggest patch area; DMNN, distance to the nearest neighbour.

Forest types: As defined in Table 1.

suggest that deer select for regenerated areas and areas containing a high amount of regeneration-dense fir edge. These latter findings are consistent with what is known about deer behaviour (Potvin and Gingras, 2002).

The results of the correlation analysis for the 18-class map (Table 4) reinforce some of the findings for the 5-class map. That the correlations are generally stronger for the 1 km grid cells than for the 500 m grid cells again suggests that deer habitat selection is based on an area larger than 500 m. The results for the 1 km grid cells also suggest that deer select for forest types containing fir and for areas in which there is a relatively large amount of regeneration-dense fir edge. Interestingly, these results do not suggest that

the variability present within a grid cell—either 500 m or 1 km—affects deer habitat selection with NP appearing only for one grid position for the 500 m grid cells, and BPA being significant for only one grid position for 1 km grid cells. The results for the selection by deer of spruce is mixed with the signs of the correlation varying from grid position I and III to II for 50-year-old white spruce; deer preference relative to white spruce is therefore unclear. Results in Table 4 for 1 km grid cells also suggest that in winter deer prefer areas regenerated in tree species other than fir with HCA for “other regeneration” being significant in grid positions II and III. This is somewhat at odds with what is known about winter deer habitat on Anticosti Island.

Table 4
Landscape Indices for the 18-class map that are significantly correlated with deer density for a given grid cell size and grid position

Grid cell size	<i>n</i>	Grid position	Variable <i>P</i> ^a (<i>r</i> ^b)
500 m	100	I	–
		II	NP ^{c,*} (0.21), HCAfirwsp* (0.20)
		III	Edregfir50** (0.37), EDregfir25** (0.38), HCAfirwsp** (0.28)
1 km	25	I	HCAwsp30* (0.49), HCAwsp50** (−0.42), HCAfirbsp* (0.44) HCAfirwsp* (0.45), DMNN* (0.43)
		II	Edregspr* (0.58), HCAwsp50* (0.50), HCAregoth* (0.42)
		III	Edregspr** (0.73), EDregfir25* (0.44), EDregfir50* (0.45) HCAbspfir* (0.47), HCAwsp50* (−0.40), HCAregoth** (0.63) BPA* (−0.44)

^a Probability level: **P* ≤ 0.05, ***P* ≤ 0.01.

^b Pearson's correlation coefficient.

^c Abbreviations: LIs: NP, number of patches; ED, edge density; HCA, habitat class area; BPA, biggest patch area; DMNN, distance to the nearest neighbour.

Forest types: As defined in Table 1.

Table 5

Landscape Indices for the 5-class map that are significantly correlated with deer density for a given grid cell size and grid position for five geographic regions

Grid cell size	<i>n</i>	Grid position	Variable P^a (r^b)
500 m	162	A	HCAfir50 ^{c,**} (0.29)
	264	B	HCAfir25 ^{**} (0.17)
	71	C	EDregfir25 ^{**} (0.39), HCAfir25 [*] (0.29)
	142	D	–
	259	E	EDregfir50 [*] (0.13), DMNN ^{**} (0.19), HCAfir50 [*] (0.16)
1 km	31	A	EDregfir50 [*] (0.37), HCAfir50 [*] (0.37)
	53	B	HCAspr ^{**} (–0.38), HCAfir25 ^{**} (0.56), HCAfir50 [*] (0.28)
		C	–
		D	–
	51	E	EDregfir50 ^{**} (0.40), HCAunp [*] (–0.32), HCAreg [*] (0.34) HCAfir25 [*] (–0.33), HCAfir50 [*] (0.33)

^a Probability level: * $P \leq 0.05$, ** $P \leq 0.01$.

^b Pearson's correlation coefficient.

^c Abbreviations: LIs: NP, number of patches; ED, edge density; HCA, habitat class area; BPA, biggest patch area; DMNN, distance to the nearest neighbour.

Forest types: As defined in Table 1.

In an effort to examine results more locally, the analysis was re-conducted for a single grid position for the study area partitioned into the five geographic regions developed (Fig. 1). These regions can be characterized as follows:

- (A) Dominance of white spruce and white spruce mixed with fir.
- (B) Dominance of white spruce.
- (C) Large areas in regeneration.
- (D) Dominance of black spruce.
- (E) Dominance of balsam fir.

Results for these regions for the 5-class map (Table 5) again reinforce the finding that correlations are generally higher for 1 km grid cells than for 500 m grid cells. For the 1 km grid cells, there is no significant affinity to, or repulsion from, any of the characteristics under consideration for Regions C and D. This is likely due to semi-pure black spruce (Region D) being a poor deer habitat regardless of the spatial characteristics, whereas regeneration (Region C) provides such good habitat that deer need not be selective. Note that this reflects the deer density in each region—Region D contains virtually no deer whereas Region C contains an abundance. For the regions with high amounts of white spruce (A and B), the areas covered by fir are favoured and the regeneration/dense fir edge appears to be important for Region

A; it seems reasonable to believe that this was not similarly important in Region B because the rarity of fir in this region means that such an edge is rare. Finally, Region E is the area that a priori was the region that could be expected to have the highest deer density because of its high concentration of fir. Although this is true, a number of variables are nonetheless important in the selection by deer of winter habitat. Dense areas of fir are favoured at the expense of less dense areas—i.e., negative r on HCA for sparse fir. Unproductive areas appear to be shunned. In addition to favouring dense fir, deer in this region prefer areas in regeneration as well as areas having a high density of regeneration/dense forest edges.

The results for the five regions for 18-class maps (Table 6) again suggest that it is the 1 km rather than the 500 m grid cell at which deer select for winter habitat—i.e., correlations for the 1 km grid cell are higher than those for the 500 m grid cell. These results also reinforce the finding that for Regions A and B, deer select most for areas containing fir. Similarly, in Regions C and D—previously assumed to be uniformly good and poor deer habitat, respectively—there is very little selection by deer of winter habitat relative to landscape characteristics. In Region E, there continues to be a selection of areas containing fir and areas with a high density of regeneration-dense fir boundary.

Table 6

Landscape Indices for the 18-class map that are significantly correlated with deer density for a given grid cell size and grid position for five geographic regions

Grid cell size	<i>n</i>	Grid position	Variable <i>P</i> ^a (<i>r</i> ^b)
500 m	162	A	HCAfirbsp ^c ** (0.21), HCAfirwsp** (0.24)
	264	B	HCAwspfir25** (0.18), HCAwsp50* (−0.13)
	71	C	HCAwspfir25** (0.37), EDregspr* (0.33)
	142	D	–
	259	E	EDregfir25* (0.14), EDregfir50* (0.13)
1 km	31	A	EDregfir50* (0.37), HCAfirwsp* (0.36)
	53	B	HCAunp* (−0.28), HCAwspfir25** (0.57), HCAwsp50* (0.29)
		C	HCAwsp50* (−0.31)
		D	HCAwsp70* (0.61)
	51	E	–
			HCAfirwsp* (0.30)

^a Probability level: **P* ≤ 0.05, ***P* ≤ 0.01.

^b Pearson's correlation coefficient.

^c Abbreviations: LIs: NP, number of patches; ED, edge density; HCA, habitat class area; BPA, biggest patch area; DMNN, distance to the nearest neighbour.

Forest types: As defined in Table 1.

In looking at the results over all analyses—i.e., Tables 3–6—in relating deer density to habitat characteristics as measured by selected LIs, it is clear that the concentration of certain types (as measured by HCA), and the concentration of certain types of edges (as measured by ED) is of importance. However, the remaining three LIs—NP, BPA, and DMNN—were only rarely correlated with the deer density. Relative to NP (number of patches) and BPA (biggest patch area), this suggests that it is the forest type of a given patch or group of patches within an area that is related to habitat selection rather than the size of individual patches or heterogeneity of the forest types in a given area. The lack of positive results for DMNN may be related to two different factors. First, because deer are highly mobile animals, they are readily capable of moving 1 km (the size of the largest grid cell) within their habitat. Thus, at the grid cell sizes considered, the distance between patches of desirable habitat was unimportant. The second reason involves the nature of the LI and the way that it was employed herein. DMNN involves calculating the distance between two patches of the same class, and averaging these distances over all classes. Therefore, when employed with grid cells of different sizes as was done herein, DMNN is very sensitive to edge effects. This would in turn make it difficult to determine general tendencies of DMNN

relative to deer density, unless grid cells of a relatively large size were employed. Hence, this LI may be of limited utility in this type of analysis.

In this study, better results/correlations were obtained for a larger area. This was attributed to deer on Anticosti Island selecting winter habitat based on an area larger than 500-by-500 m. However, readers should be aware that this may also be related to problems related to the modifiable areal unit problem (MAUP; Qi and Wu, 1996). In working with spatial data, if one does not use the same size of spatial unit in two different analyses—either the window size, or polygons of the same size—results may not be directly comparable. Because of the MAUP, generally as the window size increases, correlations between two variables are expected to improve. In addition, as the number of classes on a map decreases (through the combination of different classes as was done here), the strength of correlations is expected to decrease. In our case, larger windows produced stronger correlations as expected relative to the MAUP, and fewer map classes produced weaker correlations also as was expected relative to the MAUP. Seemingly, it would be ideal to be able to determine the magnitude of the MAUP effect in this study. Although a number of researchers have suggested ways of doing this that in general employ stochastic simulation to generate a number

of different window sizes/aggregation schemes to evaluate the range of correlations (Openshaw, 1984; Jelinski and Wu, 1996), these researchers also note that the magnitude of the MAUP is unique to the phenomenon being studied and cannot be eliminated. Hence, conclusions of any studies that employ areal sample units must be constrained to the spatial units employed (see also Svancara et al., 2002). Relative to this study, this means that, for example, for a five-class map (Table 3), one is able to state that the number of patches (NP) and the habitat class area for spruce (HCA_{spr}) will provide useful estimates of deer density for a given square kilometre. It would be completely inappropriate, however, to employ the same variables for a different grid cell size unless one had re-conducted the analysis for a grid cell of that size.

5. Conclusions

The stated goal of this article was to examine deer populations at the landscape level. In studying wildlife populations, one rarely has data that allow wildlife populations to be studied at this spatial scale. Spatially, one is generally constrained to either point observations taken through telemetry, trapping, or similar techniques (e.g., Pauley et al., 1993) or fixed area estimates based on hunting results (Roseberry and Woolf, 1998). Indeed (Brooks, 1997) noted that reliable density estimates of wildlife populations are rarely available. Analytically, the availability of point or fixed-area wildlife population data limit the analysis that can be conducted. Point data tend to facilitate the study of wildlife populations relative to habitat factors in isolation of their surroundings (Temple and Flaspohler, 1998; Williamson and Hirth, 1985) whereas data for larger areas tend to eliminate the possibility of examining locally important habitat factors. McKelvey and Noon (2001) are among the few researchers who have worked with wildlife data comparable to ours, but their study had different objectives than ours. Thus, this article makes a useful contribution in demonstrating how locally reliable wildlife population density information can be analysed to provide population density estimates at the spatial scale of interest to the model developer.

The work described also makes a useful contribution to the study of winter deer habitat spatially. It

was clearly shown that even in an area of extremely high deer density, deer will not be uniformly nor randomly distributed across their habitat. Of the two grid cell sizes considered in this study—500 m × 500 m and 1 km × 1 km—it appears that the deer on Anticosti Island make a choice of habitat by considering the larger area although this result was probably influenced by the MAUP. No effort was made to determine if this is an “optimal” grid cell size to study winter deer habitat. Moreover, it is not suggested that this grid cell size would be appropriate for studying deer habitat on mainland Quebec or elsewhere. Indeed, Dungan et al. (2002) stressed that studies such as the one described herein must all be conducted at a scale that is appropriate relative to the ecological processes being studied and the associated sampling design and analytical methods. On Anticosti Island, within the area considered by deer, they will favour areas containing high amounts of fir and areas in which there is a high concentration of regeneration/dense forest edge. This occurs regardless of the scale at which the habitat is examined—i.e., over an area containing both good and poor habitat, as well as within an area containing predominantly good habitat only.

Acknowledgements

The authors gratefully acknowledge the contributions made to this work by the *Société de la Faune et des parcs du Québec*, and the funding provide by the National Centres of Excellence network GEOIDE.

References

- Bailey, T., Gatrell, A., 1995. *Interactive Spatial Data Analysis*. Longman, Essex, UK.
- Brooks, R., 1997. Improving habitat suitability index models. *Wildl. Soc. Bull.* 25, 163–167.
- Dumont, A., Huot, J., Ouellet, J.-P., Crête, M., 1998. Caractéristiques des peuplements forestiers recherchés par le cerf de virginie en hiver à la limite nord de son aire de répartition (English: Characteristics of forest stands sought by white-tailed deer in winter at the northern limit of its range). *Can. J. Zool.* 76, 1024–1036 (in French).
- Dumont, A., Lamoureux, J., Crête, M., Ouellet, J.-P., Huot, J., 2000. Population dynamics of northern white-tailed deer during mild winters: evidence of regulation by food competition. *Can. J. Zool.* 78, 764–776.

- Dungan, J., Perry, J., Dale, M., Legendre, P., Citron-Pousty, S., Fortin, M.-J., Jakomulska, A., Miriti, M., Rosenberg, M., 2002. A balanced view of scale in spatial statistical analysis. *Ecography* 25, 626–640.
- Fortin, M.-J., 1999a. Effects of sampling unit resolution on the estimation of spatial autocorrelation. *Ecoscience* 6, 636–641.
- Fortin, M.-J., 1999b. Spatial statistics in landscape ecology. In: *Landscape Ecological Analysis: Issues and Applications*. Springer, New York, pp. 253–279 (Chapter 12).
- Fotheringham, S., Brunsdon, C., Charlton, M., 2000. *Quantitative Geography: Perspectives on Spatial Data Analysis*, SAGE, London.
- Gaudette, M., Stauffer, D., 1988. Assessing habitat of white-tailed deer in southwestern Virginia. *Wildl. Soc. Bull.* 16, 284–290.
- Gustafson, E., 1998. Quantifying landscape spatial pattern: what is the state of the art? *Ecosystems* 4, 143–156.
- Jelinski, D., Wu, J., 1996. The modifiable areal unit problem and implications for landscape ecology. *Landsc. Ecol.* 11, 129–140.
- Haines-Young, R., Chopping, M., 1996. Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. *Prog. Phys. Geogr.* 20, 418–445.
- Lamontagne, G., Potvin, F., 1994. Plan de gestion du cerf de virginie au Québec 1995–1999. L'espece, son habitat et sa gestion. (English: Management plan for white-tailed deer in Québec 1995–1999. The species, its habitat and management.) Technical report 94-2501-11. Ministère de l'Environnement et de la Faune, Québec.
- Larue, P., Bélanger, L., Huot, J., 1994. La fréquentation des peuplements riverains par le cerf de virginie en hiver: sélection de site ou pure coincidence? (English: Frequent use of riparian forest stands by white-tailed deer: site selection or pure coincidence?). *Ecoscience* 1, 223–230 (in French).
- Li, H., Reynolds, J., 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. *Ecology* 75, 2446–2455.
- McGarigal, K., Marks, B., 1995. FRAGSTATS: Spatial Pattern Analysis Program for Quantifying Landscape Structure. General Technical Report PNW-GTR-351. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon.
- McKelvey, K., Noon, B., 2001. Incorporating uncertainty in animal location and map classification into habitat relationships modeling. In: Hunsaker, C., Goodchild, M., Friedl, M., Case, T. (Eds.), *Spatial Uncertainty in Ecology: Implications for Remote Sensing and GIS Applications*. Springer-Verlag, New York.
- Ministry of Natural Resources of Québec (MNR), 1995. Normes de statification écoforestière: troisième programme de connaissance de la ressource forestière. Gouvernement du Québec, Service des inventaires forestiers, 116 pp.
- Morgan, D., Eng, M., Page, R., McNay, R., 1993. Deer habitat in a visualised programming environment. In: Thompson, I. (Ed.), *Proceedings of the International Union of Game Biologists XXth Congress*, vol. 1. Canadian Forest Service, catalogue no. Fo18-33/1993E, pp. 357–363.
- Openshaw, S., 1984. *The Modifiable Areal Unit Problem*. Norwich: CATMOG 38, 41 pp.
- Pauley, G., Peek, J., Zager, P., 1993. Predicting white-tailed deer habitat use in Northern Idaho. *J. Wildl. Manage.* 57, 904–913.
- Potvin, F., Boots, B., Dempster, A., 2003. Winter habitat selection by deer on Anticosti Island: 1. Comparison among three approaches using deer occurrences from an aerial survey and forest vegetation maps. *Can. J. Zool.* 81, 1662–1670.
- Potvin, F., Breton, L., Rivest, L., Gingras, A., 1992. Application of a double count aerial survey technique for white-tailed deer, *Odocoileus virginianus*, on Anticosti Island, Québec. *Can. Field Naturalist* 106, 435–442.
- Potvin, F., Breton, L., Rivest, L., 2002. Testing double-count aerial survey technique for white-tailed deer, *Odocoileus virginianus*, in Québec. *Can. Field Naturalist* 116, 488–496.
- Potvin, F., Gingras, A., 2002. L'habitat hivernal du cerf sur l'île d'Anticosti défini à partir des inventaires aériens de 1998, 1999 et 2000. (English: The winter habitat of deer on Anticosti Island as defined by aerial inventories in 1998, 1999, and 2000.) Technical Report 8037-02-01, Société Faune et Parcs du Québec, Direction de la recherche sur la faune, Qué., 37 pp. (in French).
- Qi, Y., Wu, J., 1996. Effects of changing spatial resolution on the results of landscape pattern analysis using spatial autocorrelation indices. *Landsc. Ecol.* 11, 39–49.
- Roloff, G., Kernohan, B., 1999. Evaluating reliability of habitat suitability index models. *Wildl. Soc. Bull.* 27, 973–985.
- Roloff, G., Millsaugh, J., Gitzen, R., Brundige, G., 2001. Validation tests of a spatially explicit habitat effectiveness model for rocky mountain elk. *J. Wildl. Manage.* 65, 899–914.
- Roseberry, J., Woolf, A., 1998. Habitat-population density relationships for white-tailed deer in Illinois. *Wildl. Soc. Bull.* 26, 252–258.
- Rothley, K., 2001. Manipulative, multi-standard test of a white-tailed deer habitat suitability model. *J. Wildl. Manage.* 65, 953–963.
- S-Plus, 2001. *S-PLUS 6—Guide to Statistics*. vol. 1. Insightful Corporation, Seattle, Washington.
- Svancara, L., Garton, E., Chang, K.-T., Scott, J.M., Zager, P., Gratson, M., 2002. The inherent aggravation of aggregation: an example with elk aerial survey data. *J. Wildl. Manage.* 66, 776–787.
- Temple, S., Flaspohler, D., 1998. The edge of the cut—implications for wildlife populations. *J. Forestry* 96, 22–26.
- Williamson, S., Hirth, D., 1985. An evaluation of edge use by white-tailed deer. *Wildl. Soc. Bull.* 13, 252–257.
- Zwartz, F., 1998. Guide d'aménagement des ravages de cerfs de Virginie. (English: Management guide for herds of white-tailed deer.) Technical Report 3828-98-03, Direction de la faune et des habitats, Ministère de l'environnement et de la faune, Québec (in French).