Influence of forage biomass and cover on deer space use at a fine scale: A controlled-density experiment

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Abstract: In many areas of North America and Europe, population densities of large herbivores are increasing and strongly affecting species composition and structure of plant communities. Although reduced resources associated with increasing density affect life history traits of large herbivores, their effects on foraging behaviour have received little attention. We experimentally controlled population density in large enclosures to assess how increasing density affected white-tailed deer (Odocoileus virginianus) space use in relation to forage biomass and cover at a fine scale. We quantified space use in 3 blocks, each with 2 enclosures, one containing deer at a density of 7.5 deer·km⁻² (low density) and the other containing deer at a density of 15 deer·km⁻² (high density). We interpolated forage biomass, lateral cover, and canopy cover in space by kriging and divided deer observations (radiolocations) into 3 diel-periods: dawn/dusk, day, and night. Deer space use was positively related to forage biomass and negatively related to lateral cover at both densities, but it was not affected by the diel-period. Deer increased the use of areas with dense canopy cover at low density, but not at high density. Population density thus modified deer resource use by constraining deer at high density to forage where canopy cover is lower but forage biomass higher. Our results provide evidence of density dependence in foraging decisions, as deer space use patterns appeared to be based more strongly on forage biomass than on cover, particularly when population density was high.

Keywords: Anticosti Island, kriging, Odocoileus virginianus, population density, radiotelemetry, white-tailed deer.

Résumé : Dans de nombreuses régions d’Amérique du Nord et d’Europe, l’augmentation des populations de grands herbivores a entraîné des effets sur la structure et la composition des communautés végétales. Bien qu’il ait été démontré que la réduction des ressources alimentaires associée aux hautes densités a un effet sur les composantes biodémographiques des grands herbivores, leur influence sur le comportement d’approvisionnement de ceux-ci reste encore méconnue. Nous avons modifié expérimentalement la densité de population de cerfs de Virginie (Odocoileus virginianus) pour évaluer comment l’augmentation de la densité influence la répartition spatiale des individus en fonction de l’abondance du couvert et de la nourriture. Nous avons quantifié à fine échelle l’utilisation de l’espace par les cerfs dans 3 blocs composés de 2 enclos chacun contenant respectivement 7,5 (faible densité) et 15 cerfs·km⁻² (haute densité). Nous avons interpolé par krigage la biomasse de la nourriture ainsi que le couvert latéral et vertical et nous avons divisé les observations électroniques des cerfs en 3 périodes quotidiennes : aube/crépuscule, jour et nuit. À faible et à haute densité, l’utilisation de l’espace par les cerfs était reliée positivement à la biomasse de la nourriture et négativement au couvert latéral, mais n’était pas affectée par la période quotidienne. Les cerfs ont augmenté l’utilisation des secteurs où le couvert vertical était dense, mais seulement à faible densité. Nos résultats montrent que la densité de population a modifié l’utilisation des ressources, car à haute densité les cerfs étaient contraints de s’alimenter dans les secteurs où le couvert vertical était réduit, mais la biomasse de la nourriture élevée. Le comportement d’approvisionnement des herbivores est dépendant de la densité car les patrons d’utilisation de l’espace à haute densité sont davantage associés à la biomasse de la nourriture qu’au couvert.

Mots-clés : cerf de Virginie, densité de population, île d’Anticosti, krigage, Odocoileus virginianus, radio-télémétrie.


Introduction

In summer, northern ungulates typically devote most of their time to finding and consuming food. Foraging decisions are thus important to their energy and time budget. When food acquisition is the primary determinant of patch selection, use of habitat patches should be positively related to forage availability (MacArthur & Pianka, 1966; McNamara, Houston & Weisser, 1993). There are, however, several other constraints, such as heat or wind exposure (Belovsky, 1997; Dussault et al., 2004), insect harassment (Colman et al., 2003; Skarin et al., 2008), presence of offspring (Grignolio et al., 2007; Hamel & Côté, 2007), and predation risk (Mao et al., 2005), that can affect foraging behaviour in addition to forage characteristics.

Ecologists usually divide cover into 2 components: (1) lateral cover, which consists of concealing understory vegetation or topography, and (2) canopy cover, which corresponds to the projection of the tree crowns to the ground. Lateral cover reduces predation risk and thus time devoted to vigilance (Altendorf et al., 2001) and, in the absence of predators, is considered to play a role in habitat selection related to the “ghosts” of past predators (Byers, 1997; Mysterud & Østbye, 1999). Animals are also more protected from adverse weather conditions (e.g., temperature, wind, or precipitation) in closed habitats than in open habitats (Mysterud & Østbye, 1999).
Open sites generally offer more abundant forage than closed ones in summer (Hanley, 1984; Redburn, Strong & Gates, 2008) but present a higher risk of predation (Tufto, Andersen & Linnell, 1996) and higher thermoregulatory costs due to increased heat load (Parker & Robbins, 1984; Beier & McCullough, 1990). Cervids thus often prefer feeding near edges of forests and open habitats, because edges minimize the trade-off between forage abundance and exposure to predators and/or harsh weather.

For cervids, a good foraging site is usually characterized by a trade-off between proximity to protective cover and abundance of vegetation (Kotler, Gross & Mitchell, 1994). Deer often use open habitats more during the night than during the day, and since their activity peaks at dawn and dusk (Beier & McCullough, 1990; Ager et al., 2003), the forage and cover trade-off should also depend on diel-periods (Mysterud & Østbye, 1999; Godvik et al., 2009). Clear-cuts provide open habitats that offer abundant food resources to large herbivores, and they are usually interspersed with forest stands that present dense canopy cover but low forage availability (Masters, Lochmiller & Engle, 1993; Stewart, Fulbright & Drawe, 2000). Clearings are commonly used to enhance forage production and thus improve habitat conditions for large herbivores (Masters, Lochmiller & Engle, 1993; Rothley, 2002). Deer select clear-cuts when they produce more abundant food resources than forest stands and if they provide sufficient hiding cover (Lyon & Jensen, 1980).

It has been proposed that population density modulates the trade-off between using habitats offering abundant forage and habitats offering good cover (Mysterud & Østbye, 1999), because population density is generally negatively related to forage availability (Healy, deCalesta & Stout, 1997; Stewart et al., 2006) and increases intraspecific competition (Clutton-Brock, Guinness & Albon, 1982). When food is a limiting factor, deer can modify habitat use to include sufficient feeding habitat, such that availability of resources can change the trade-off between food and cover (Mysterud & Ims, 1998). Rouleau, Crête, and Ouellet (2002) found that white-tailed deer (Odocoileus virginianus) increased the use of agricultural areas at night as density increased, likely because forage was more abundant in open habitats than in closed habitats. An increase in the use of open habitats in summer may indicate the low abundance of forage in areas with adequate cover and the impacts of high deer density on space use (Mysterud & Østbye, 1999). Although of great interest, it is unknown whether increasing density is modifying deer behaviour, especially in relation to trade-offs between selection for forage and selection for cover in the context of landscapes composed of forests and clear-cuts.

We experimentally controlled population density in large enclosures to assess how increasing density affected white-tailed deer space use in relation to forage and cover at a fine scale. We separated radiolocations of monitored individuals into 3 diel-periods (dawn/dusk, day, night) to assess how foraging trade-offs vary with time of day (Godvik et al., 2009). We hypothesized that deer density would be the main determinant of the trade-off between forage abundance and cover. We predicted that deer at high density would use open areas of the enclosures, where forage biomass is more abundant, more frequently than areas where biomass is less abundant, independently of cover characteristics and of diel-periods. Deer at low density, however, were expected to use areas of the enclosures in relation to available cover, because competition for forage would have less influence on deer behaviour at low density.

**Methods**

**Study area**

Anticosti Island (Québec, Canada; 49° 28' N, 63° 00' W) is located at the northeastern fringe of the white-tailed deer range in North America and covers 7943 km². Balsam fir (Abies balsamea), white spruce (Picea glauca), and black spruce (P. mariana) naturally dominate the forests. At the end of the 19th century, 220 deer were introduced on the island. In the absence of predation, the population spread and grew rapidly. Today, deer densities of > 20 deer·km⁻² are found in most areas on the island (Potvin & Breton, 2005). Annually, about 8000 deer are killed by hunters between September and December, and the annual harvest rate is < 5% (Simard et al., 2008). Deer have modified the original forest, greatly reducing the abundance of deciduous woody vegetation and eliminating most of the shrub layer on the island (Potvin, Beaufré & Laprise, 2003; Tremblay et al., 2005). The climate of Anticosti is maritime and characterized by longer and milder winters compared to the white-tailed deer range on the continent. Mean air temperatures are 16 °C in July and –11 °C in January (Environment Canada, 2006). Snow precipitation averages 328 cm annually, while rainfall averages 61 cm (Environment Canada, 1982).

**Experimental design**

Our experimental design consisted of 3 sets of enclosures (A, B, C) into which we introduced 24 deer during 2 different years (2002, 2003). Enclosures were located in balsam fir–dominated forests partially cut in the early summer of 2001. Water was easily accessible to deer at many streams or artificial water holes in every enclosure. We erected 1 block (A) in the western part of the island and 2 blocks (B and C) 130 km to the east in the central part of the island. Several residual forest stands of different sizes (0.19–21.6 ha) were left in the enclosures. The proportion of forest was similar in all enclosures and totalled 30 to 40% of the surface. We studied 1 block (A) in 2002 and 3 blocks in 2003. To test the influence of deer density, the blocks were divided into 2 enclosures of different sizes to obtain densities of 7.5 deer·km⁻² (40-ha enclosure with 3 deer, low deer density enclosure or LDE) and 15 deer·km⁻² (20-ha enclosure with 3 deer, high deer density enclosure or HDE). We chose these densities to include white-tailed deer density proposed for sustainable tree regeneration (7 deer·km⁻²; Tilghman, 1989; deCalesta & Stout, 1997) and the estimated density on Anticosti Island at the beginning of the experiment (15.6 deer·km⁻²; B. Rochette, A. Gingras & P. Potvin, Société de la Faune et des Parcs, unpubl. report). The dimensions of the largest
enclosures are similar to the summer home ranges of female white-tailed deer on Anticosti Island (average of 42 ha; Massé & Côté, 2009). We used different animals in 2002 and 2003.

DEER CAPTURES

In late June, we fitted 6 deer in 2002 and 18 deer in 2003 with VHF collars (LMRT series from Lotek, Newmarket, Ontario, Canada) equipped with sto-2a variable pulse activity sensors. We attempted to capture yearling deer to control for age, but this was not always possible. We used different methods to capture deer: dart guns, Stephenson box traps, and cannon nets baited with cattle feed and balsam fir twigs. We released deer in the study enclosures shortly after capture. We removed deer by culling at the end of each summer in November. The Animal Care and Use Committee of Université Laval (Québec, Canada) approved all capture methods (protocol number 2003-014) based on the Canadian Council on Animal Care (1993) guidelines. We verified reproductive status of adult females by direct observation at capture and at the end of the summer. Since only 2 monitored females had a fawn, we did not include reproductive status in the analyses. We tested whether these females could bias the results by removing them from the analyses and verifying if the conclusions were modified.

TELEMETRY

In July and August 2002, we radiotracked 6 deer in block A. In July and August 2003, we radiotracked 16 deer in the 3 blocks. One adult male lost its collar, and 1 yearling male had a malfunctioning one. We located deer with telemetry receivers (SRX-400 version W9, Lotek Engineering, Newmarket, Ontario, Canada and TR-2 scanner/receiver, Telonics, Mesa, Arizona, USA), unidirectional antennas, and compasses. Telemetry stations were positioned with a Garmin GPS (precision of < 5 m) on trails adjacent to the enclosures. To limit disturbance, trails were generally located more than 100 m away from the enclosures. At least 3 azimuths differing by a minimum of 30º were obtained by moving between stations with a vehicle (White & Garrott, 1990). To reduce location error due to changes in animal position, locations had to be determined within 15 min (White & Garrott, 1990). We evenly divided 24-h days into 3 periods of 8 h (0800–1600, 1600–0000, and 0000–0800). These 8-h periods were evenly sampled and rotated between 2 observers and 2 groups of enclosures every 3 d. During sampling periods of 8 h, we located deer about every 2 h. LOAS software (Location Of A Signal, Version 2.07, Ecological Software Solutions, Urnäsch, Switzerland) was used to estimate positions and error polygons. We calculated error polygons with the “Andrews” estimator (White & Garrott, 1990; Lenth, 1981). The average error from plotted to actual locations was determined by using control transmitters set at known locations throughout the enclosures and was estimated at 107 m (SE = 88 m, n = 88 trials). We assigned positions to 3 diel-periods: dawn and dusk (90 min before sunrise to 90 min after sunrise, and 90 min before sunset to 90 min after sunset), day (90 min after sunrise to 90 min before sunset), and night (90 min after sunset to 90 min before sunrise).

FORAGE BIOMASS AND COVER SAMPLING

We conducted field surveys at the end of the growing season (September) every year to describe forage and cover abundance in each enclosure. In order to homogeneously characterize habitat, we sampled vegetation and cover at 5 sampling plots placed randomly in each 2-ha square of a grid superimposed on each enclosure. At each sampling plot, we estimated percent of plant cover in two 1-m² quadrats randomly chosen in a 10- × 10-m quadrat centred at the sample point (Tremblay, Huot & Potvin, 2006). We sampled the same points in block A in September 2002 and 2003, whereas we sampled blocks B and C only in September 2003.

We estimated forage biomass for every major plant component of deer diets and for the most abundant species on Anticosti using regressions between percent of plant cover and biomass of the corresponding dried plants (Bonham, 1989; Tremblay, Huot & Potvin, 2006). We collected plant samples from each sampling point by cutting and drying them until their weight reached a steady value for at least 24 h. We obtained estimates for the following species: *Abies balsamea*, *Betula papyrifera*, *Cirsium spp.*, *Copis groenlandica*, *Cornus canadensis*, *Epilobium angustifolium*, grass spp., *Hieracium sp.*, *Maianthemum canadense*, *Picea glauca*, *Rubus idaeus*, *Rubus pubescens*, and *Trientalis borealis*. For every species or group of species, we estimated the number of samples needed for regressions by plotting regression coefficients between plant cover and biomass of dried plants in relation to the number of samples until coefficients reached an asymptote (Frontier, 1983). To take into account variation in forage biomass, we summed the biomass values of all plant species for each quadrat and used the mean value of the 2 quadrats for each sample point in the analyses.

At each sampling point, we estimated canopy cover by vertically projecting foliage of trees to 20 points distributed every 3 m on the ground in 4 directions from the centre of the sampling unit. Each point was characterized as with cover (value of 1) or not (0), and canopy cover corresponded to the sum of all points with cover (maximal value of 20). We measured lateral cover with a cover board (2.5 × 0.3 m divided into 0.5-m sections) in 2 opposite directions at 15 m from the centre of the sampling plot by attributing board concealment to 4 classes (1: 0–25; 2: 26–50; 3: 51–75; 4: 76–100%; Nudds, 1977). We used the mean value from the first 2 sections of the board (0–1 m) and averaged values from both directions.

ANALYSES

**Spatial analyses of forage biomass and cover**

Using field surveys, we estimated forage biomass and cover at the points sampled in each enclosure. Because we were interested in assessing deer space use in relation to fine-scale variations of vegetation, we used geostatistics to estimate forage biomass and cover for the total surface of each enclosure (Figures 1A to 1C) (Cressie, 1993). We used ordinary kriging (Geostatistical analyst, ArcMap 9.0, Environmental Systems Research Institute, Redlands, California, USA) to estimate changes and trends in forage biomass and cover in the study enclosures. We prepared...
FIGURE 1A. Relative space use of white-tailed deer and abundance of a) forage biomass, b) lateral cover, and c) canopy cover in block A of the controlled-density experiment on Anticosti Island, Québec, Canada in 2003. The left enclosure contained 15 deer·km$^{-2}$, whereas the right enclosure contained 7.5 deer·km$^{-2}$. We used kriging to map vegetation in the enclosures.

FIGURE 1B. Relative space use of white-tailed deer and abundance of a) forage biomass, b) lateral cover, and c) canopy cover in block B of the controlled-density experiment on Anticosti Island, Québec, Canada in 2003. The left enclosure contained 7.5 deer·km$^{-2}$, whereas the right enclosure contained 15 deer·km$^{-2}$. We used kriging to map vegetation in the enclosures.
semivariograms individually for forest stands and cuts of each enclosure because vegetation and cover abundance drastically changed between these 2 habitats (Masters, Lochmiller & Engle, 1993). We determined the best fit of spherical variograms up to a maximum lag distance of 125 m (i.e., half of the minimum enclosure dimension) by generating models in 5-m increments and in all directions (Jurado-Expósito et al., 2004).

We used kriging values to validate the fitted variogram through cross-validation. Validation consisted of the systematic removal of observations, 1 by 1, from the raw data set, which was then estimated by kriging (Isaaks & Srivastava, 1989). Kriging provides an error term for each estimated value, thus giving a measure of reliability for the interpolations. The nugget value divided by the total variance (or sill) gave an estimation of the spatial dependence (Jurado-Expósito et al., 2004; Table I), whereas biases in estimation errors were evaluated using the standardized root mean squared error (Isaaks & Srivastava, 1989; Table I).

**Spatial analysis of radiotelemetry data**

There is inherent error associated with radiotelemetry, and if radiolocations are taken as exact locations, this may introduce a bias to the data (White & Garrott, 1990; Rettie & McLoughlin, 1999). Failure to correctly account for that error can lead to incorrect predictions of wildlife resource use (Montgomery et al., 2010). Rettie and McLoughlin (1999) recommended the use of buffers to account for telemetry error in habitat selection studies. Buffers enabled us to consider the telemetry error of VHF collars and to develop a spatial representation of how deer used the enclosures that can be used to further study resource use at a fine scale. Although this approach does not increase the precision of telemetry locations, it provides conservative results that are less biased because they are based on spatial relationships and not on individual data points distributed through space (Rettie & McLoughlin, 1999).

In our study, the error of locations obtained by telemetry was 107 m on average and thus larger than some forest stands present in the enclosures. We took into account the mean location error by placing a 100-m buffer around each location. We chose to use a 100-m buffer because (1) in 70% of the trials with hidden collars at known locations, collars were located less than 100 m away from the real position and (2) up to 100 m, the probability of obtaining a position closer to the real position was not a function of distance ($F_{1, 9} = 0.11; P = 0.75$). To check whether the buffers were too large, we compared the proportion of randomly drawn points falling in clear-cuts or forests in block A to the mean proportion of these strata in the buffers, and they did not differ (mean proportion of clear-cuts in buffers = 78 ± 3%; mean proportion of random points in clear-cuts = 76 ± 3%; mean ± SE; $F_{1, 8} = 0.26; P = 0.62$), indicating that the size of the buffer was appropriate.

Since the buffers were quite large compared to the size of the enclosures (3.1-ha buffers versus 20- and 40-ha enclosures), they overlapped considerably, thus making results dependent on one another (i.e., observed resources in a buffer could be influenced by the results of another

![Figure 1C](image_url) Relative use of white-tailed deer and abundance of a) forage biomass, b) lateral cover, and c) canopy cover in block C of the controlled-density experiment on Anticosti Island, Québec, Canada in 2003. The left enclosure contained 15 deer·km–2, whereas the right enclosure contained 7.5 deer·km–2. We used kriging to map vegetation in the enclosures.
buffer). To take this into account, we randomly placed 1 point in every 150- × 150-m square of a grid placed over each enclosure (ArcView GIS, Version 3.1, Environmental Systems Research Institute, Redlands, California, USA). We used 2.25-ha (150- × 150-m) squares because they were sufficiently large compared to the buffer size and allowed for a reasonable number of sampling points for the regressions (20–30 points). This sampling grid was made of squares slightly larger than those used to select sampling points for forage and cover. This method enabled us to take

Table I. Spatial statistical data of a) forage biomass, b) lateral cover, and c) canopy cover in clear-cuts and residual forests of enclosures containing different densities of white-tailed deer on Anticosti Island, Québec, Canada.

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<th>Range2</th>
<th>C03</th>
<th>C4</th>
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<td>Forest</td>
<td>33</td>
<td>600</td>
<td>12.60</td>
<td>4.37</td>
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<td></td>
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<td>15</td>
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<td>27</td>
<td>500</td>
<td>0.52</td>
<td>0.76</td>
<td>1.26</td>
<td>0.29</td>
</tr>
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<td>660</td>
<td>5.89</td>
<td>28.70</td>
<td>1.10</td>
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<tr>
<td>2003</td>
<td>B</td>
<td>7.5</td>
<td>Cut</td>
<td>53</td>
<td>450</td>
<td>0.22</td>
<td>0.49</td>
<td>0.98</td>
<td>0.31</td>
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<td></td>
<td>Forest</td>
<td>46</td>
<td>500</td>
<td>19.20</td>
<td>7.42</td>
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<td>0.72</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>15</td>
<td>Cut</td>
<td>26</td>
<td>420</td>
<td>0.20</td>
<td>0.14</td>
<td>1.12</td>
<td>0.59</td>
</tr>
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<td></td>
<td>Forest</td>
<td>34</td>
<td>300</td>
<td>11.50</td>
<td>11.80</td>
<td>1.03</td>
<td>0.49</td>
<td></td>
</tr>
<tr>
<td>2003</td>
<td>C</td>
<td>7.5</td>
<td>Cut</td>
<td>61</td>
<td>420</td>
<td>0.31</td>
<td>0.27</td>
<td>1.01</td>
<td>0.54</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Forest</td>
<td>33</td>
<td>350</td>
<td>0.32</td>
<td>0.35</td>
<td>1.09</td>
<td>0.48</td>
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<td></td>
<td>15</td>
<td>Cut</td>
<td>27</td>
<td>420</td>
<td>0.08</td>
<td>0.25</td>
<td>1.08</td>
<td>0.25</td>
</tr>
</tbody>
</table>

1 Number of sample points where biomass, canopy, and lateral cover were measured and used to quantify the semivariogram and cross-validations.
2 Range (m) is the distance over which spatial autocorrelation was detected.
3 The nugget effect (C0) or the inherent data variability below which the minimum lag distance cannot be modelled with the current sampling resolution.
4 The variance (C) associated to the spatial variability in the data.
5 Biases in estimation errors evaluated by the standardized root mean squared error (RMSE) from the cross-validation analysis. The RSME should be close to 1 if the predicted standard errors are valid. If the RSME is greater than 1, the variability is underestimated in the predictions. If the RSME is less than 1, the variability is overestimated.
6 The C-ratio, given by the nugget value divided by the total variance (sill or C0 + C), defines the asymptotic value of semivariance and gives an estimation of the dependence between estimated values of biomass or cover and their position in space. A ratio lower than 0.25 usually represents values that are highly spatially correlated, a ratio between 0.25 and 0.75 usually corresponds to values that are moderately correlated, and a ratio near 1 represents values that are not spatially correlated (Jurado-Expòsito et al., 2004).
7 These models were developed with directional semivariograms (direction of 350º) as they increased the fit of the estimated values.
data from every telemetry location into account and also to assess the dependence of the overlapping buffers.

For each of the 3 diel-periods, we counted the total number of overlapping buffers from deer locations at each random point for each deer. We then divided the total number of overlapping buffers at each random point by the total number of buffers for this deer during each diel-period to estimate “relative use”, a measure of space use that is independent of the number of positions taken on each individual. We used “relative use” in all the following space-use analyses.

**Forage biomass and cover abundance in the controlled-browsing experiment**

To compare resource abundance between densities and stratum (residual forest stands or clear-cuts), we used total forage biomass, lateral cover, and vertical cover available at each random point located in each 150- × 150-m square of the grid placed over each enclosure in an analysis of variance with block and year as random factors. As we studied only 1 block for 2 years, year could not be treated as a fixed effect. The factor year was included as a random effect.

**Deer space use**

We examined the influence of resources (i.e., forage biomass, lateral cover, and canopy cover), deer density, and diel-period on the relative space use of deer using linear mixed models with block and year as random factors. For each analysis, we verified the normality of the residuals and the homogeneity of variance by visual examination of the residual plots. We used an alpha (α) level of 0.05.

**Results**

**Spatial analyses of forage biomass and cover**

The relationships between sample location and forage biomass, lateral cover, or canopy cover varied between residual forests and clear-cuts, and between enclosures (Table I). The standardized root mean squared error values ranged from 0.27 to 2.38, but most values were close to 1 (mean = 1.01 ± 0.30; n = 48 models; Table I), indicating that variability was generally not biased towards higher or lower values than those measured. A general feature of the variograms was the relatively close nugget and C values (i.e., the variance explained by the spatial variation in the data; Table I), indicating that spatial autocorrelation could not explain total resource heterogeneity because all variability in values close to each other could not be explained by the model. Additionally, the nugget effect, or variability not explained by the model, was greater than zero in some cases, indicating that observations separated by small distances were variable (Isaaks & Srivastava, 1989; Table I). However, spatial relationships provided a good representation of how forage biomass, lateral cover, and canopy cover (Figures 1A to 1C) varied within clear-cuts and residual forests, and this enabled us to examine how these variables varied with deer density and how they were related to deer space use.

**Table II.** Mean (± SD) forage biomass (g m⁻²), lateral cover¹, and canopy cover² according to white-tailed deer density (deer-km⁻²)³ and stratum (clear-cuts and residual forests) in a controlled-browsing experiment conducted on Anticosti Island, Québec, Canada. We report the results of ANOVAs for each variable.

<table>
<thead>
<tr>
<th></th>
<th>Density</th>
<th>Clear-cut</th>
<th>Residual forest</th>
<th>Source of variation</th>
<th>ANOVAs</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>df</td>
<td>F</td>
</tr>
<tr>
<td>Forage biomass</td>
<td>7.5</td>
<td>81.3 ± 38.6</td>
<td>29.6 ± 12.1</td>
<td>Density</td>
<td>1, 3</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>68.9 ± 20.2</td>
<td>34.1 ± 4.4</td>
<td>Stratum</td>
<td>1, 6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Density × Stratum</td>
<td>1, 6</td>
</tr>
<tr>
<td>Lateral cover</td>
<td>7.5</td>
<td>2.7 ± 0.9</td>
<td>3.0 ± 0.8</td>
<td>Density</td>
<td>1, 3</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>3.1 ± 0.8</td>
<td>3.3 ± 0.4</td>
<td>Stratum</td>
<td>1, 6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Density × Stratum</td>
<td>1, 6</td>
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<tr>
<td>Canopy cover</td>
<td>7.5</td>
<td>1.0 ± 0.4</td>
<td>9.8 ± 3.0</td>
<td>Density</td>
<td>1, 3</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>1.8 ± 3.0</td>
<td>6.8 ± 2.0</td>
<td>Stratum</td>
<td>1, 6</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Density × Stratum</td>
<td>1, 6</td>
</tr>
</tbody>
</table>

1Mean concealment value (attributed to 4 classes: 1: 0-25; 2: 26-50; 3: 51-75; 4: 76-100%) of the first 2 sections of a concealment board (2.5 = 0.3 m divided into 0.5-m sections) in 2 opposite directions.

2Number of points out of 20 where foliage of >4-m trees was present. The 20 points were located every 3 m from the centre of each sampling unit in 4 directions (east, southeast, southwest, and west).

3Deer were kept in 3 sets of enclosures, each of which had 2 densities.
enclosures, but not surprisingly canopy cover was denser in residual forests than in clear-cuts (Table II).

**Deer space use**

Relative space use was positively related to forage biomass and negatively related to lateral cover at both densities (Table III). Indeed, the slope parameter for forage biomass was positive and did not differ between densities (Table III). The negative relationship for lateral cover was weak and similar for both densities (Table III). The influence of canopy cover, however, differed between densities, as it was positively related to relative space use at low density, but not at high density (Table III). Diel-period did not affect the relationships between relative space use and resource availability (Table III). The number of overlapping buffers was correlated during the 3 diel-periods at both densities (LDE: \( r^2 > 0.47; P < 0.01 \); HDE: \( r^2 > 0.46; P < 0.01 \)), indicating that space use patterns were similar during all diel-periods.

To test whether individual deer could affect the observed results, we checked if including deer identity increased the fit of the model. The models averaging relative space use for deer in an enclosure and the models including deer density explained 10% of the variability. Including deer identity did not increase the fit of the model, despite small sample size. Excluding the 2 reproductive females from the model did not change the conclusions.

**Discussion**

We experimentally controlled population density and mapped spatial heterogeneity in forage biomass and cover to evaluate at a fine scale how space use by large herbivores changed with varying resource levels. Deer space use was positively related to forage biomass and negatively related to lateral cover at both densities. Deer increased the use of areas with dense canopy cover at low density, but not at high density. Our results suggest that space-use patterns by deer are more strongly based on forage biomass than cover in ecosystems where population density is high and predation is reduced.

Sampling of habitat characteristics in cervid habitat-use studies is generally restricted by time and labour, and consequently only a small proportion of the study areas can be described in detail. For these reasons, researchers often estimate mean forage biomass and available cover as a single value for each habitat type (Mysterud & Østbye, 1999) and assume that vegetation and cover are distributed homogeneously over each habitat (Mysterud & Østbye, 1999). In fine-scale habitat studies, however, means cannot account for heterogeneity present in the environment. A better representation of the environment can be achieved by taking surrounding sampling points into account (Turner, Gardner & O’Neill, 1995). For example, as in our study, patches of high-forage biomass may occur in small forest openings or patches of dense canopy, or lateral cover may remain in clear-cuts (Figures 1A to 1C). The high variability in the distribution of forage biomass and cover data reveals the heterogeneity in the distribution of resources and how mean values for clear-cuts and for forest stands could have biased the results. The use of geospatial information system software to account for spatial relationships is of major interest for fine-scale habitat studies (Turner, Gardner & O’Neill, 1995), but still has received little attention. A drawback of such methods in large study areas is that estimated interpolation errors increase as the distance between sampled points increases; nonetheless, for sample points adequately distributed spatially, these methods may provide additional insights into ungulate foraging behaviour and fine-scale habitat use.

An increase in population density generally leads to a decrease in the abundance of plant species preferred by herbivores. We predicted that, as observed in agricultural landscapes (Lesage et al., 2002; Rouleau, Crête & Ouellet, 2002), deer would use open habitats more frequently than closed habitats at high density because more forage biomass was available in open areas than under forest cover and thus competition would likely be lower there than in closed habitats. Deer space use, however, was positively related with forage biomass at both densities during summer. Other studies have also reported that white-tailed deer space use was positively related to plant biomass (Stewart, Fullbright & Drape, 2000; Rothley, 2002; Cimino & Lovari, 2003). Forage biomass did not differ between deer densities during our study, possibly explaining why we found similar relationships between deer space use and forage biomass at both densities. Observations from a companion study suggest that differences in forage biomass between low and high density treatments appeared when the experiment was applied for 1 y longer (Tremblay, Huot & Potvin, 2006). Because plant recovery increased with time elapsed since the onset of the experiment (Tremblay, Huot & Potvin, 2006), strong selection for areas with the highest forage biomass could be a response to cope with reduced forage

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**Table III.** Variation in relative space use of white-tailed deer monitored in a controlled-density experiment conducted on Anticosti Island, Québec, Canada. Relative space use was related to density (7.5 and 15 deer·km\(^{-2}\)), diel-period (dawn and dusk, day, and night), forage biomass, lateral cover, and canopy cover using linear mixed models with block and year as random factors. The slopes are shown for significant effects.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>df</th>
<th>( F )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
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<td>0.10</td>
</tr>
<tr>
<td>Diel-period</td>
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<td>0.85</td>
</tr>
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<td>Biomass ( \times ) density</td>
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<td>4.66</td>
<td>0.03</td>
</tr>
<tr>
<td>Biomass ( \times ) diel-period</td>
<td>2, 446</td>
<td>0.33</td>
<td>0.72</td>
</tr>
<tr>
<td>Biomass ( \times ) density ( \times ) diel-period</td>
<td>2, 446</td>
<td>0.80</td>
<td>0.45</td>
</tr>
<tr>
<td>Lateral cover ( \times ) density</td>
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<td>3.84</td>
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</tr>
<tr>
<td>Lateral cover ( \times ) diel-period</td>
<td>1, 446</td>
<td>0.35</td>
<td>0.55</td>
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<tr>
<td>Lateral cover ( \times ) density ( \times ) diel-period</td>
<td>2, 446</td>
<td>0.49</td>
<td>0.61</td>
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<tr>
<td>Canopy cover</td>
<td>1, 446</td>
<td>2.80</td>
<td>0.06</td>
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<td>Canopy cover ( \times ) density</td>
<td>1, 446</td>
<td>6.73</td>
<td>&lt;0.01</td>
</tr>
</tbody>
</table>

(7.5 deer·km\(^{-2}\); slope = 0.0037 ± 0.0017, \( t_{446} = 2.15, P = 0.03 \))

(15 deer·km\(^{-2}\); slope = -0.0039 ± 0.0023, \( t_{446} = -1.64, P = 0.10 \))

\( ^{1} \)Relative space use represents the total number of overlapping buffers divided by the total number of positions recorded for a particular deer for each of the 3 diel-periods in each of the 150- × 150-m squares of a grid superimposed on each enclosure.
associated with long-term over-browsing (Boucher et al., 2004; Simard et al., 2008). Such behaviour could be a tactic to increase the rate of energy acquisition when forage is limited (Van der Wal et al., 2000; Hansen et al., 2009). For deer outside enclosures on Anticosti Island at in situ density (> 15 deer·km⁻²), habitat selection within the home range was also found to be primarily influenced by forage abundance among and within habitat patches (Massé & Côté, 2009).

Large herbivores can simultaneously consider other habitat factors, such as cover, in addition to forage biomass and circumstantially adjust their behaviour (Schmitz, 1992; Naugle et al., 1997; Rothley, 2002). Although dense canopy cover provides adequate thermal and radiation cover that enables animals to minimize thermoregulatory costs (Parker & Gillingham, 1990), it was negatively correlated to forage biomass in the enclosures (Table III). Deer at high density increased their use of areas where forage biomass increased and canopy cover decreased, whereas deer in low-density enclosures used habitats with greater canopy cover. Although deer at low density used space in relation to dense canopy cover, this compromise may not have been achieved at high density because increased competition forced deer to stay in open areas where forage was readily available. These results validate the observations of Massé and Côté (2009) showing that free-ranging deer occurring at in situ density > 15 deer·km⁻² decreased their use of areas with dense canopy cover.

Unlike canopy cover, lateral cover negatively influenced deer relative space use at both densities. Lateral cover provides protection from predators, and it may be positively related to forage biomass, but this was not the case in our study as there was no relationship between forage biomass and lateral cover. Since we conducted our study in recently cut balsam fir stands, much of the lateral cover in open areas was not made up of forage but of wood debris left by the machinery after cutting. This might explain why deer more often used the areas where lateral cover was low but forage was readily available. Consistent with this hypothesis, Massé and Côté (2009) found that lateral cover did not explain habitat selection of free-ranging deer during summer on Anticosti Island. Deer on Anticosti Island have been separated from predators for > 100 y, and their antipredator behaviour may have dampened in the absence of a sufficient selective force (Mysterud & Østbye, 1999).

Space use in relation to forage biomass and cover may vary during the 24-h period (Munro et al., 2006; Godvik et al., 2009). For instance, some authors reported that ungulates’ use of open habitats was higher at night than during daytime because herbivores were safer in darkness (Kufeld, Bowden & Schrupp, 1988; Naugle et al., 1997; Godvik et al., 2009). Predation is lacking on Anticosti Island, and deer did not use areas differently according to diel-period. We found that deer used areas with higher forage biomass more often than areas where forage biomass was less abundant in every diel-period. Similarly, predator-free and forage-limited Svalbard reindeer (Rangifer tarandus platyrhynchos) were not crepuscular and likely adopted foraging tactics that maximized energy acquisition (Loë et al., 2007).

Individual characteristics of the deer, such as age and sex, could have had a confounding effect on the relationships between space use and forage biomass and cover. It has indeed been shown that space use in relation to food or cover may differ between sexes (Beier & McCullough, 1990; DePerno, Jenks & Griffin, 2003) and among ages (Mysterud et al., 1999; Saïd et al., 2009). Unfortunately, we did not have enough animals in every block, density, and year to include sex in the models, but since we used mainly juveniles or young adults, the effects of sex were probably limited.

The experimental design we used enabled us to examine questions that could not be answered in a natural context. By using wild-caught deer, outdoor enclosures, and controlling for density in an experimental design where only density differed, we could directly make inferences about the effects of density on deer space use. The use of a controlled-density experiment allowed us to provide evidence of density dependence in foraging decisions. When population density was high, deer space-use patterns appeared to be based more strongly on forage biomass than on cover, whereas it was influenced by both forage biomass and canopy cover when intraspecific competition was relaxed at low density. Our results are in accordance with other findings of deer behaviour on Anticosti Island showing that, at high density, resource use of herbivores was mainly related to forage acquisition rather than to a trade-off between forage intake and protective cover (Massé & Côté, 2009). Thus, it seems that at high density and in the absence of predators, intraspecific competition is likely the most important factor limiting individual fitness. However, the results of the low-density enclosures showed that the trade-off between forage intake and protective cover can return when intraspecific competition is relaxed.

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Literature cited


