Linking habitat heterogeneity to space use by large herbivores at multiple scales: From habitat mosaics to forest canopy openings

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ABSTRACT

Although habitat selection and home range size of herbivores in forested landscapes are generally related to the composition and spatial arrangement of open and forested habitat categories, it is unclear how herbivores respond to finer habitat mosaics such as more productive canopy openings within forest stands. We aimed to determine the relationships between habitat selection and home range size of 32 white-tailed deer (*Odocoileus virginianus*) females and spatial heterogeneity in forage and cover at multiple scales. We used GPS telemetry to delineate summer and winter home ranges and to evaluate habitat selection. We used landscape metrics to measure spatial heterogeneity of open and closed habitat categories within each home range and in three circles of radii of 1000, 2000 and 3000 m centered on each home range, and field surveys to quantify spatial patterns in canopy openings within forest stands. Deer responded to forage abundance at multiple scales during summer, as they selected peatlands within the landscape, canopy openings within forest stands, and reduced the size of their home range with increasing forbs and deciduous shrubs cover. Deer also responded to forage abundance during winter as they selected areas with high proportions of food-rich balsam fir stands to establish their home range and had a smaller home range size when the density of food sources increased. However, in areas where the proportion of food-rich balsam fir stands was less available, deer selected heterogeneous habitat mosaics to settle their winter home range. Moreover, deer responded positively to edge density of cut-blocks only during winter and they did not select canopy openings during that season. Winter forage such as windblown fir trees were highly associated to edges between clear-cuts and balsam fir stands making these large openings an important element of deer winter habitat in ecosystem modified by long-term browsing. Our results emphasize the significance of considering multiple and nested mosaics of openings and continuous cover when assessing habitat selection patterns and home range size of herbivores living in forested landscapes, as the influence of spatial heterogeneity in resources varied with the constraints of seasonal environments.

1. Introduction

Spatial heterogeneity is an emergent component of ecological systems (*sensu* Kolasa and Rollo, 1991). Depending on the nature of the pattern of interest, heterogeneity refers to the complexity and variability of any system property in space and time (Li and Reynolds, 1995), and thus is strongly dependent on the observation scale (Gustafson, 1998; Kotliar and Wiens, 1990). How animals respond to spatial heterogeneity in their environment depends on how they perceive multiple scales of patchiness (Kotliar and Wiens, 1990). For instance, positive effects of spatial heterogeneity on the abundance and diversity of animals occur when heterogeneity leads to more ecological niches, whereas negative effects of spatial heterogeneity are found when it is associated with habitat fragmentation (Tews et al., 2004).

In forested landscapes, natural and anthropogenic disturbances such as agriculture and logging, generate spatial heterogeneity by creating openings within the forest matrix (McCarthy, 2001). Given that abundant lateral and vertical cover characterize forest stands but that shading reduces the abundance of understory plants (Johnson et al., 1995), herbivores could perceive recently logged boreal landscapes as mosaics of continuous cover interspersed with small to large scale more productive openings. This spatial heterogeneity in the distribution of forest cover and vegetation in openings may become a key variable influencing habitat selection by herbivores, as they must balance costs and benefits of accessing forage in exposed open areas and shelter against predation and/or harsh climatic conditions in closed forests (Hansson, 1994).

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Several studies focused on trade-offs between forage and cover at broad spatial scales and reported positive associations between heterogeneity of landscapes and occurrence of birds (Radford and Bennett, 2007), rodents (Ritchie et al., 2009) and ungulates (Kie et al., 2002; Walter et al., 2009). Positive responses to edges between open and forested areas of logged or agricultural landscapes have also been documented in birds (Whitcomb et al., 1981), rodents (Desrochers et al., 2003), and ungulates (Walter et al., 2009), mainly in order to reduce predation while maximizing access to forage. At finer scale, forest gaps are likely to be a significant determinant of animal species diversity (Belsky and Canham, 1994) and most studies that have investigated the relationships between canopy openings and species distribution have focused on birds, invertebrates or small mammals (Levey, 1988; Bouget, 2005; Hodson et al., 2010). The only studies linking fine-scale forest gaps and ungulate distribution have either examined visitation frequency and residence time to small openings created by small clear-cuts (Kuijper et al., 2009) or compared browse consumption in windthrow gaps and adjacent undisturbed forest (Moser et al., 2008). To date, no study has investigated the relationships between multiple scales of heterogeneity in forested landscapes and habitat selection of individuals. Given the importance of commercial logging and gap dynamics in boreal forest ecosystems (McCarthy, 2001), there is a growing need to investigate the influence of spatial heterogeneity and patterns of space use by animals.

Our objective was to determine the influence of spatial heterogeneity in forage and cover at several scales on habitat selection and home range size of a large forest herbivore. We used GPS telemetry to investigate summer and winter home ranges and habitat selection patterns of white-tailed deer (Odocoileus virginianus) females in a predator-free population located at the northern limit of the species' distribution in a recently logged boreal landscape. Although high population density coupled with the absence of predation can relax the trade-off between forage and cover (Mysterud and Østbye, 1999), northern latitudes impose additional constraints such as harsh climatic conditions during winter. In this context, we hypothesized that the influence of spatial heterogeneity in forage and cover on habitat selection and home range size of deer would vary between seasons. We expected a lower influence of spatial heterogeneity on home range size during summer than winter, mainly because thermal and locomotion stresses are reduced during summer. We predicted that deer would select open habitat categories rather than a mosaic of open and forested habitat categories to establish their home range during summer because the trade-off between forage and cover is relaxed during summer on Anticosti Island (Massé and Côté, 2009). Because deer must balance access to forage and exposure to thermal and locomotion costs during winter, we predicted that deer would select heterogeneous mosaics of habitat categories with high edge density between food-rich and cover-rich habitat categories. At a finer scale, if forested habitat categories are included in summer home ranges, we predicted that deer would select canopy openings within these forest stands since canopy openings offer a high abundance of forbs as forage (Johnson et al., 1995). We also predicted that deer would select canopy openings within forest stands during winter because forest gaps offer a high abundance of litterfall and windblown trees as forage during winter (Foster and Reiners, 1986).

2. Methods

2.1. Study area

Anticosti is a 7943 km^2 island located in the Gulf of St. Lawrence, Québec, Canada (49°28′ N, 63°00′ W). The climate on Anticosti Island is maritime and characterized by cool summers and long winters. Mean air temperature is 16 °C in July and −11 °C in January. Snow and rain average 406 cm and 630 mm annually, respectively. Forests are dominated by balsam fir (Abies balsamea), white spruce (Picea glauca), black spruce (Picea mariana) and Tamarack Larch (Larix laricina), whereas deciduous tree species such as paper birch (Betula papyrifera), trembling aspen (Populus tremuloides), and balsam poplar (Populus balsamifera) are found irregularly on the island. In 1896–1897, approximately 220 white-tailed deer were introduced on Anticosti Island and their numbers increased rapidly to >100,000 in absence of predators (>20 deer/km^2; Potvin and Breton, 2005). Severe deer browsing on the vegetation has occurred across the island such that deciduous browse species have almost been extirpated (Tremblay et al., 2005) and balsam fir stands are being progressively converted into white spruce stands (Potvin et al., 2003). Although the population is hunted from 1 September to 25 December, most white-tailed deer females do not experience hunters, as the hunting pressure is about 4%, focused on males (Simard et al., 2008), and concentrated near roads (Lebel et al., 2012).

2.2. Animal monitoring

We monitored 32 free-ranging female white-tailed deer using GPS 2200R and GPS 3000 collars (Lotek Engineering, Newmarket, Ontario, Canada) during two summers and two winters. Nineteen deer were monitored during summer between 1 July and 10 November 2001 (n = 8) and 2002 (n = 11), and 13 deer were monitored during winter between 9 December and 30 April 2003–2004 (n = 2) and 2004–2005 (n = 11). Collars were programmed to record a location every 2 h. Mean location error, estimated by stationary collars, was 23 ± 1 m and 11 ± 1 m during summer and winter, respectively (Massé and Côté, 2009; Massé and Côté, 2012). We used the minimum convex polygon method (Mohr, 1947) with 95% of the locations to delineate home ranges using the program RANGESV (Kenward and Hodder, 1996). We chose MCP over kernel estimator because we were interested in using the home range as a measure of use (home range selection, habitat selection at a large scale) and availability (habitat selection at finer scale). Moreover, kernel estimator may produce large biases in home range size when it is calculated with several locations and when animals show high site fidelity (see Hemson et al., 2005), which was precisely our case as we had on average >1000 locations per individual and core areas for individual deer could be as small as 6 ha (Massé and Côté, 2012).

2.3. Forage, cover abundance and heterogeneity

We used digitized 1:20,000 forest maps produced by the interpretation of 1:15,000 aerial photographs from the Ministère des Ressources naturelles et de la Faune du Québec to describe forage and cover at coarse scale. Forest cover maps describe tree and shrub strata in terms of species, densities and height and allowed us to define five habitat categories: clear-cuts resulting from commercial logging since 1995 and windthrows (CUT), large ombrotrophic peatlands dominated by Sphagnum mosses and ericaceous shrubs and large minerotrophic peatlands dominated by sedges, herbs, and brown mosses (PEATLAND), stands with balsam fir > 25% of the basal area (BALSAM_FIR), stands with spruce > 25% of the basal area (SPRUCE), and lakes and rivers (OTHER). We considered clear-cuts and peatlands as food-rich habitat categories for the summer season because they contained more forbs and deciduous shrubs than forested habitat categories, and deer are likely to increase habitat use with increasing abundance of forbs and deciduous shrubs (Massé and Côté, 2009). For the winter season, we considered balsam fir stands as food-rich

habitat category, because deer prefer balsam fir over white spruce (Sauvé and Côté, 2006), and they increased habitat use with increasing total browse of balsam fir between 25 and 325 cm in height, number of windblown fir trees and basal area in balsam fir (see Massé and Côté, 2012 for details).

We used field surveys to quantify forage and cover within habitat categories of summer and winter deer home ranges. Field surveys were conducted in July and August 2002 and 2003 for deer monitored during the summer and in July and August 2004 and 2005 for deer monitored during the winter. We used line intersect point sampling to map canopy openings and continuous conifer cover in balsam fir and spruce stands (Battles et al., 1996). Transects were oriented north–south and were located 50 m apart. The number of transects and their length varied with home range size and shape (mean length: 273 ± 7 m, range: 5–1125 m, n = 876 transects). Every 5 m along each transect, we recorded the dominant tree species >7 m in height (TREE_SPECIES) present in a radius of 10 m (i.e. balsam fir, black spruce, white spruce and larch), and noted if the observer was in a canopy opening or under continuous cover. We recorded canopy openings that were easily distinguishable from the complexity of the forest structure (Brokaw, 1982), and had a diameter > 15 m. Because size of canopy openings may influence plant community characteristics (Runkle, 1985), we visually evaluated the diameter (SIZE) of each opening using three categories: (1) 15–25 m, (2) 26–50 m, and (3) >50 m. We also visually evaluated the origin of the opening using three categories: (1) no disturbance (UND): difference in edaphic conditions created the opening in the forest overstory (Farina, 2006); (2) insect outbreaks (INSECT): spruce budworm (Choristoneura fumiferana) and/or spruce beetle (Dendroctonus rufipennis) outbreaks created the opening; and (3) windthrow (WIND): fallen trees created the opening.

We did additional floristic surveys to quantify forage abundance at fine scale. For the summer home ranges, we systematically selected one transect every 150 m to measure forage abundance. Here, we used point intercept sampling and recorded every species of understory plant (e.g. forbs, grasses, and deciduous shrubs) that touched a wooden rod (diameter = 2.5 cm) placed every 5 m along the transects. For the winter home ranges, we recorded the number and location of windblown fir trees that intercepted each transect, because the main food sources during winter on Anticosti are litterfall or windblown fir trees (Tremblay et al., 2005; Massé and Côté, 2012). We recognized previous winter windblown trees because several green twigs remained on the branches (Massé and Côté, 2012). We surveyed a mean of 6488 ± 907 m and 8925 ± 1377 m of linear transects per summer and winter home ranges, respectively. We used Arcview 3.2 (Environmental Systems Research Institute 1999) to georeference all sampling points at 5 m intervals, which corresponded to a mean of 1248 ± 177 and 1621 ± 267 data points per summer and winter home ranges, respectively.

2.4. Data analyses

2.4.1. Habitat selection

We used resource selection functions (RSFs) to evaluate the influence of spatial heterogeneity in forage and cover on habitat selection at the home range scale (Manly et al., 2002). We used a matched case-control design where each observed home range was associated with random home ranges sampled around each location where each deer was captured. This approach was appropriate to compare habitat composition and configuration since landscape metrics may change with the size and shape of the habitat mosaic (McGarigal and Marks, 1995). For each deer, we randomly positioned its own home range using translation and rotation tools within three specific circles with radii of 1000,

2000, and 3000 m centered on the location of each deer captured (Fig. 1). We used a circle radii limit of 3000 m because it encompassed the average distance travelled by a female deer during a daily excursion outside its 95%MCP home range (summer average: 2661 ± 478 m; winter average: 863 ± 150 m). We compared observed to random home ranges within radii of various sizes because we wanted to assess habitat selection at multiple scales (Anderson et al., 2005; Kie et al., 2002). We allowed overlapping random home ranges because female white-tailed deer are non-territorial (Demarais et al., 2000). We used the Patch Analysis extension for Arcview (Elkie et al., 1999) to measure spatial composition (i.e. the proportion of each habitat categories (P_CUT, P_PEATLAND, P_FIR, P_SPRUCE, and P_OTHER) and Shannon's diversity index (SDI) which increases as the number of different habitat patch categories within each home range increases and/or as the proportion of each habitat categories becomes more equitable (McGarigal and Marks, 1995)). We measured spatial configuration of habitat mosaics by quantifying edge density between habitat categories providing forage and cover (m/ha), which were: edges between balsam fir stands and spruce stands and (1) clear-cuts (ED_CUT_FOREST) and (2) peatlands (ED_PEATLAND_FOREST) during summer, and edges between clear-cuts and balsam fir stands (ED_CUT_BALSAM_FIR) during winter. We performed a sensitivity analysis to estimate the number of random home ranges needed to describe the spatial composition and configuration of circles with radii of 1000, 2000, and 3000 m (Potvin et al., 2001). A total of 100, 150 and 150 random home ranges provided stabilized measures of landscape metrics for circles with radii of 1000, 2000, and 3000 m, respectively.

We used conditional logistic regression to evaluate RSFs because we had paired data for each deer (i.e. 1 observed home range vs. 100 or 150 random home ranges, which correspond to a strata). Resource selection was modeled as a function of the characteristics of resources units, and the RSF value, $w(x)$, was proportional to the probability of the unit being used as:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n)$$

where $x_{1..n}$ are explanatory variables and $\beta_{1..n}$ are selection coefficients (Manly et al., 2002). We used Generalized Estimating Equations (GEEs; PHREG with STRATA, SAS Institute Inc. 2002) to evaluate RSFs because they account for the non-independence among observations of a given individual and produce robust standard errors for the parameter estimates (Craiu et al., 2008). We built 26 and 17 candidate RSFs for deer monitored during summer and winter, respectively. RSFs evaluated whether deer selected particular habitat mosaics in their home range based on (1) habitat composition (e.g. proportion of habitat categories (P_CUT, P_PEATLAND, P_FIR, P_SPRUCE, and P_OTHER) and Shannon's diversity index (SDI)), (2) habitat configuration (e.g. edge density between habitat categories providing forage and those providing cover (ED_CUT_FOREST and ED_PEATLAND_FOREST for summer home ranges, and ED_CUT_BALSAM_FIR for winter home ranges)), and (3) a combination of these features at the three scales (i.e. 1000, 2000, and 3000 m; see Tables A.1 and A.2 in Appendix A and B, respectively). We included in candidate models the interaction between the proportion of habitat categories and Shannon's diversity index because we were interested in investigating how home range selection varied with various availability of habitat categories (i.e. functional response in habitat selection (sensu Mysterud and Ims, 1998)). We used the Quasi-likelihood Information Criterion (QIC), which is applicable to GEEs and based on Akaike's Information Criterion (AIC), to select the best RSF model for a given season (Pan, 2001). We considered models with $\Delta QIC_{u \leqslant} 2$ equivalent and used model averaging to calculate parameter estimates and 95% confidence intervals of equivalent models (Burnham and Anderson, 2002). Prior to calculating RSFs, we verified that there were no

Fig. 1. The study area on Anticosti Island, Québec, Canada, illustrating the two scales of analysis used to evaluate habitat selection: the home range scale (A) and within the home range scale (B). Circle radius of 3000 m, observed home ranges (black) and random home ranges (double counter lines in black) are shown in (A). Canopy openings (white dots) and continuous cover (black dots) along linear transects are shown in (B).

collinearity problems between explanatory variables using the multicollinearity diagnostic statistics produced by linear regression analyses (PROC REG, SAS Institute Inc. 2002; Allison, 2003). We removed variables with a tolerance value <0.4 (Allison, 2003). We evaluated the robustness of the best RSF for each season by performing k-fold cross-validation for case-control design by withholding 20% of the strata and using 100 iterations (see Fortin et al., 2009 for details). We applied the same process to a dataset assuming complete random patterns of habitat selection for each season and compared its robustness to those of observed datasets (see Fortin et al., 2009 for details).

At a fine scale, we used RSFs and explanatory variables measured in the field to assess the influence of spatial heterogeneity in forage and cover on habitat selection within the home range. Specifically, we tested if deer selected canopy openings within forest stands, and if so we tested if they selected canopy openings with particular characteristics. We used GEEs to estimate RSFs with a use-availability design by contrasting habitat characteristics at observed deer locations with characteristics at random locations distributed in forested habitat within each deer home range with a 1:1 ratio between the number of observed and random locations (Koper and Manseau, 2009). Because habitat characteristics were point data measured along transects, we assigned habitat charac-

teristics of the nearest point to each deer or random location. Mean distance between surveyed points and deer/random locations was 14.8 ± 0.1 m (n = 11,898) and 14.4 ± 0.1 m (n = 17,304) during summer and winter, respectively. Once we had assessed that deer selected for canopy openings, we built 30 candidate RSF models to evaluate how deer selected canopy openings based on (1) the size of the opening (SIZE), (2) the origin of the opening (i.e. UND, INSECT or WIND), (3) the dominant tree species (TREE_SPECIES), or (4) a combination of these features (see Table A.3 in Appendix C). We selected the best RSF models based on QIC, considered models with $\Delta QIC_{u \leqslant} 2$ equivalent and used model averaging if necessary. We used multicollinearity diagnostic statistics to verify that there were no collinearity problems between explanatory variables. We evaluated the predictive success of the best model by performing k-fold cross-validation withholding 20% of the data and using 100 iterations (Boyce et al., 2002).

2.4.2. Home range size

We used a multi-scale approach (Anderson et al., 2005) to investigate the influence of spatial heterogeneity in forage and cover on home range size. We used the same landscape metrics as in the home range selection analysis to measure spatial patterns of habitat categories within each home range and in three circles of

radii 1000, 2000 and 3000 m centered on each home range. We calculated additional explanatory variables based on floristic field surveys. We summed the occurrence of every deciduous shrub and forb species to obtain an estimate of the total abundance of deciduous shrubs (T_ABUN_SHRUBS) and the total abundance of forbs (T_ABUN_FORBS) in each summer home range. We divided these estimates by the total number of sampled points to obtain mean occurrence of deciduous shrubs (M_OCC_SHRUBS) and mean occurrence of forbs (M_OCC FORBS) at a given sampling point per home range. We used field surveys to calculate the density of windblown fir trees (FIR_TREE_D) for each winter home range. We used multiple linear regressions (PROC MIXED, SAS Institute Inc. 2002) to investigate variations in home range size during each season. We built 22 and 19 candidate models for deer monitored during summer and winter, respectively. Models examined the relationships between home range size of individual deer and spatial heterogeneity based on (1) habitat composition, (2) habitat configuration, and (3) a combination of these features measured at four scales (i.e. home range, 1000, 2000, and 3000 m). At the scale of the home range only, we tested additional models including explanatory variables based on field surveys. We used an information-theoretic approach to identify the model best supporting empirical data (Burnham and Anderson, 2002). We ranked candidate models with Akaike's information criterion for small sample size (AIC_c) and calculated ΔAIC_c, and AIC_c weights (ω_i) for each season at the four scales (Burnham and Anderson, 2002). Models with $\Delta AIC_c \leqslant 2$ were considered equivalent (Burnham and Anderson, 2002). We used model averaging to calculate parameter estimates and 95% confidence intervals of equivalent models (Burnham and Anderson, 2002). We verified multicollinearity as described above. Because LMM do not provide R^2 values, we computed the explained variance of each best model following Xu (2003). We log-transformed home range size to meet normality of the residuals and homogeneity of variance.

3. Results

3.1. Habitat selection

Comparisons between deer home ranges and random home ranges within 1000, 2000, and 3000 m radius circles showed that deer were more likely to establish their summer home ranges in areas dominated by peatlands and with high habitat diversity (Table 1A). Although edge density between clear-cuts and forests and between peatlands and forests were included in the best models (Appendix A), their confidence intervals (CI) included 0 (Table 1A). Models that best predicted home range selection during winter had considerable support (Appendix B). Best models

included the interaction between the proportion of balsam fir stands and habitat diversity, indicating that the increasing relative probability of use associated with the augmentation in the proportion of balsam fir stands changed with habitat diversity (Fig. 2, Table 1B). The relative probability of use increased when habitat diversity was high (Table 1).

During summer, deer were 12% less likely to be found under continuous cover than in canopy openings (CI: −0.21 to −0.05). The best model explaining how deer selected canopy openings within forest stands had a relatively high AIC_c weight (0.69) and included the effects of the size of the opening, the origin of the opening and the dominant tree species (Appendix C). For every 10 m increase in the radius of the canopy opening, deer increased their use by about 8% (CI: 0.003–0.013). Deer were 29% more likely to be found in edaphic gaps not originating from natural disturbance (CI: 0.09–0.42) than those resulting from insect outbreaks (CI: −0.04–0.45) and windthrows (CI: −0.29–0.11). Although the 95% CI included 0, the relative probability of use was 42% higher under black spruce cover (CI: −0.06–0.75) than under balsam fir cover (reference slope, i.e. 0), and showed a decreasing trend under white spruce (CI: −0.53–0.34) and larch cover (CI: −0.74–0.61). During winter, however, deer did not respond to spatial heterogeneity in continuous cover and canopy openings (CI: −0.30–0.20).

3.2. Home range size

Home range size did not differ between summer and winter (summer: 42 ± 6 ha and winter: 30 ± 5 ha, $t_{1,31}$ = −0.43 P = 0.67). Variations in home range size during summer were better explained by habitat characteristics within the home range (R^2 = 0.83) than by those measured in radii of 1000, 2000, and 3000 m (R^2 = 0.15, 0.15, and 0.24, respectively). At the scale of the home range, home range size decreased by about 17% as mean occurrence of forbs and deciduous shrubs increased by 0.1% and 0.01%, respectively (Fig. 3). Deer tended to increase their home range size by 28% as edge density between clear-cuts and forested habitats around their home range increased by 10 m/ha, although the 95% CIs included 0 (Table 2A). Deer tended to respond to the proportion of peatlands and habitat diversity within 3000 m, although the 95% CIs included 0 (Table 2A). Proportion of clear-cuts, proportion of forested habitat categories and total abundance of deciduous shrubs and forbs were not included in selected models (Appendix D).

Variations in home range size during winter were better explained by habitat heterogeneity within radii of 1000, 2000, and 3000 m (R^2 = 0.80, 0.72, 0.79, respectively) than within the home range (R^2 = 0.57). At the scale of the home range and 2000 and 3000 m, equivalent models included a negative effect of edge

Table 1
Parameter estimates (β), standard errors (SE) and 95% confidence intervals (95% CI) for best and equivalent models predicting summer (A) and winter (B) home range selection of white-tailed deer females on Anticosti Island, Québec, Canada. 95% CI of parameters in bold exclude 0. Model comparisons are shown in Tables A.1 and A.2 in Appendices 1 and 2, respectively.

Explanatory variables	1000 m			2000 m			3000 m		
	β	SE	95% CI	β	SE	95% CI	β	SE	95% CI
(A) ED_CUT_FOREST*	−0.04	0.03	(−0.10: 0.01)	−0.02	0.02	(−0.05: 0.02)	−0.01	0.01	(−0.04: 0.02)
ED_PEAT_FOREST*	−0.01	0.01	(−0.04: 0.02)	−0.01	0.01	(−0.04: 0.01)	−0.01	0.02	(−0.05: 0.02)
P_PEATLAND*	2	2	(−2: 6)	4	2	**(1: 7)**	5	2	**(2: 8)**
SDI*	**5**	**2**	**(2: 8)**	**4**	**1**	**(2: 6)**	**3**	**1**	**(1: 5)**
SDI × P_PEATLAND*	–	–	–	2	3	(−5: 8)	2	2	(−3: 6)
(B) P_FIR	**29**	**7**	**(15: 43)**	**22**	**5**	**(11: 32)**	**20**	**6**	**(9: 31)**
SDI	**20**	**4**	**(12: 27)**	**15**	**3**	**(9: 21)**	**14**	**3**	**(7: 21)**
SDI × P_FIR	**−15**	**6**	**(−26: −4)**	**−11**	**4**	**(−19: −3)**	**−19**	**4**	**(−17: −2)**

ED_CUT_FOREST = edge density between clear-cuts and balsam fir and spruce stands (m/ha). ED_PEAT_FOREST = edge density between peatlands and balsam fir and spruce stands (m/ha). P_PEATLAND = proportion of peatlands. P_FIR = proportion of balsam fir stands. SDI = Shannon's diversity index.
* Model-averaged estimates with their unconditional standard error and 95% confidence intervals.
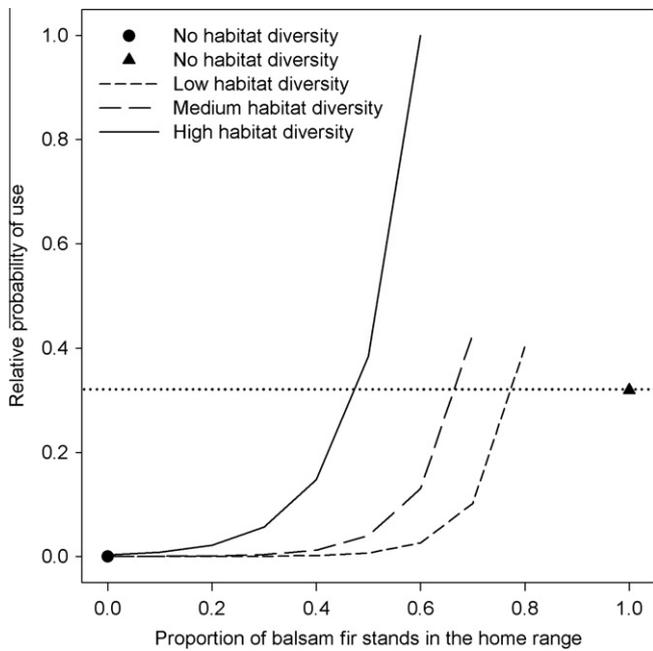
Fig. 2. Resource selection functions at the 3000 m scale showing the relative probability that white-tailed deer females select a mosaic of habitat categories for their home range during winters 2003–2004 and 2004–2005 on Anticosti Island, Québec, Canada. White-tailed deer were more likely to use an area when habitat diversity and availability of balsam fir stands increased (P_fir × SDI interaction, SDI = Shannon's diversity index). Relative probabilities were estimated for 3 classes of habitat diversity (low, medium and high) using 25% (SDI = 0.64), 50% (SDI = 0.83), and 75% (SDI = 1.07) quantiles of Shannon's diversity index, respectively. Relative probabilities were also estimated where habitat diversity was 0 (circle and triangle). The dotted reference line shows the relative probability of selecting a home range including 100% of balsam fir stands. Values are displayed only over the range of proportion of balsam fir stands and habitat diversity observed within observed and random home ranges.

Fig. 3. Relationships between mean occurrence of forbs (A) and mean occurrence of deciduous shrubs (B) and home range size of female white-tailed deer monitored during summers 2001 and 2002 on Anticosti Island, Québec, Canada. Mean occurrence represents the averaged contribution of each sampled point to the total abundance for the whole home range.

density between clear-cuts and balsam fir stands indicating that deer decreased their home range by 16–28% as the edge density within and around their home range increased by 10 m/ha (Table 2B; Fig. 4A; Appendix D). Winter home range size also decreased with increasing density of windblown fir trees and increasing proportion of balsam fir stands within the home range, although the 95% CI of the latter included 0 (Table 2B). Deer responded to habitat composition at a scale larger than their home range, as they decreased home range size with increasing proportion of clear-cuts (at 1000 and 2000 m; Table 2B; Fig. 4B). Home range size increased with habitat diversity within the home range, whereas deer reduced their home range with increasing habitat diversity at larger scales (Table 2B; Fig. 4C).

4. Discussion

We evaluated spatial heterogeneity in forage and cover from habitat mosaics to forest canopy openings to test how heterogeneity influenced habitat selection and home range size of a generalist herbivore. White-tailed deer females responded to forage abundance at multiple scales during summer, as they selected peatlands within the landscape, canopy openings within forest stands, and reduced the size of their home range with increasing forb and deciduous shrub occurrence. Deer also responded to forage abundance during winter as they selected areas with high proportions of balsam fir stands to establish their home range and reduced home range size with increasing density of windblown fir trees. However, deer selected heterogeneous habitat mosaics for their winter home range in areas where the proportion of food-rich
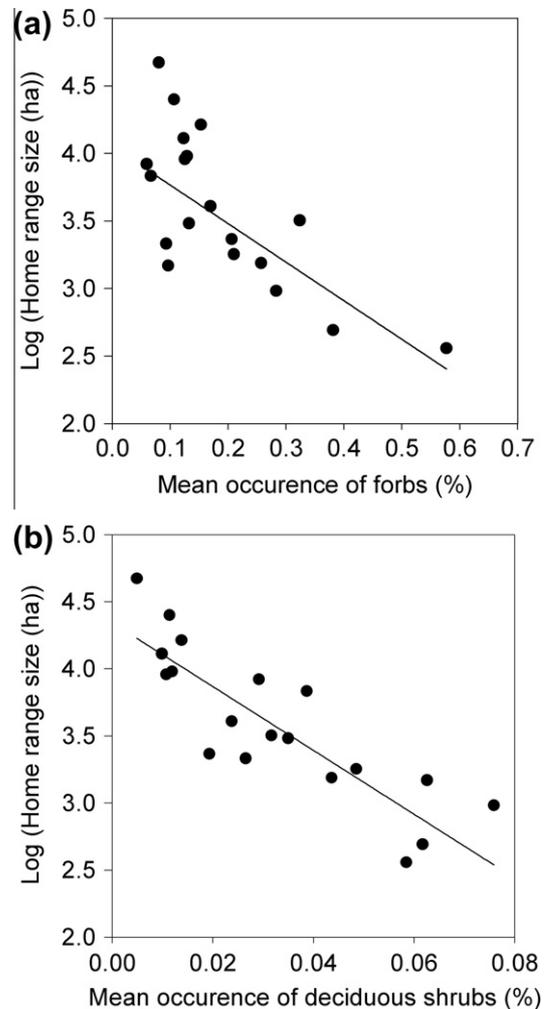
balsam fir stands was reduced. Moreover, deer responded positively to edge density only during winter. Our results provide empirical evidence that deer responded to the nested mosaics of openings and continuous cover within a forested and logged landscape, but the influence of spatial heterogeneity varied with seasonal environmental constraints.

Herbivores in unproductive ecosystems are constrained by forage abundance (Hansen et al., 2009). Anticosti deer live at high density in a landscape that has been modified by long-term browsing and that, therefore, offers limited forage (Tremblay et al., 2005; Simard et al., 2008). During summer, deer were more likely to establish their home range in areas where the proportion of open habitat categories was high and, thus seem to increase access to habitat categories with high forage abundance (Dussault et al., 2005). By adopting this pattern of habitat use, deer may have reduced intra-specific competition for forage (Nilsen et al., 2004). Indeed, female deer harvested in peatland-rich areas had a higher average body condition and started reproducing at an earlier age than those harvested elsewhere on Anticosti Island (Simard, 2010).

Habitat diversity also positively influenced home range selection during summer, indicating that deer needed resources present in different habitat categories (de Beer and van Aarde, 2008), in accordance with the habitat complementary hypothesis (Dunning

Table 2

Parameter estimates (β), standard errors (SE) and 95% confidence intervals (95% CI) for best or equivalent models predicting summer (A) and winter (B) home range size of white-tailed deer females on Anticosti Island, Québec, Canada. 95% CI of parameters in bold exclude 0. Model comparisons are shown in Tables A.4 and A.5 in Appendices 4 and 5, respectively.

Explanatory variables	Home range			1000 m			2000 m			3000 m		
	β	SE	95% CI	β	SE	95% CI	β	SE	95% CI	β	SE	95% CI
(A) ED_CUT_FOREST	–	–	–	0.02[*]	0.01	(<0: 0.05)	0.02[*]	0.01	(<0: 0.05)	0.02[*]	0.01	(<0: 0.05)
ED_PEAT_FOREST							–0.02[*]	0.02	(–0.05: 0.01)	–	–	–
P_PEATLAND	–	–	–	–	–	–	–	–	–	–4[*]	3	(–10: 1)
SDI	–	–	–	–	–	–	–	–	–	0.4[*]	0.3	(–0.2: >0.9)
M_OCC_FORBS	**–1.6**	**0.5**	**(–2.7: –0.5)**	–	–	–	–	–	–	–	–	–
M_OCC_SHRUBS	**–17**	**3**	**(–24: –11)**	–	–	–	–	–	–	–	–	–
(B) ED_CUT_FIR	**–0.018[*]**	**0.006**	**(–0.030: –0.005)**	–	–	–	**–0.03[*]**	**0.01**	**(–0.05: <0)**	**–0.028**	**0.007**	**(–0.043: –0.012)**
P_FIR	–1.1[*]	0.7	(–2.5: 0.2)	–	–	–	–	–	–	–	–	–
P_CUT	–	–	–	**–4.8**	**0.7**	**(–6.4: –3.2)**	**–2.1[*]**	**0.7**	**(–3.4: –0.8)**	–	–	–
SDI	**0.6[*]**	**0.3**	**(>0: 1.2)**	**–2.2**	**0.4**	**(–3.0: –1.3)**	**–1.1[*]**	**0.3**	**(–1.6: –0.5)**	**–1.1**	**0.2**	**(–1.6: –0.6)**
FIR_TREE_D	**–0.4[*]**	**0.2**	**(–0.8: <0)**	–	–	–	–	–	–	–	–	–

ED_Cut_Forest = edge density between clear-cuts and balsam fir and spruce stands (m/ha). ED_PEAT_FOREST = edge density between peatlands and balsam fir and spruce stands (m/ha). ED_CUT_FIR = edge density between clear-cuts and balsam fir stands (m/ha). P_CUT = proportion of clear-cuts. P_FIR = proportion of balsam fir stands. P_SPRUCE = proportion of spruce stands. P_FOREST = proportion of balsam fir and spruce stands. SDI = Shannon's diversity index. M_OCC_FORBS = Mean occurrence of forbs at one sampling point within the home range (%). M_OCC_SHRUBS = Mean occurrence of deciduous shrubs at one sampling point within the home range (%). FIR_TREE_D = Density of windblown fir trees (number of winblown fir trees/ha).

[*] Model-averaged estimates with their unconditional standard error and 95% confidence intervals are presented when there were equivalent models (see Tables A.4 and A.5 in Appendices 4 and 5, respectively).

et al., 1992). Although we previously showed that habitat selection was primarily influenced by forage abundance in overbrowsed landscapes during summer (Massé and Côté, 2009), deer could still benefit from a highly heterogeneous home range. For example, red deer (*Cervus elaphus*) in areas where spatial heterogeneity in topography was high had higher body mass than those living in homogenous landscapes; diversity in elevation resulting in spatial variability in plant phenology, and thus, plant nutrient content (Mysterud et al., 2001). Similarly to increasing elevation, plant phenology is delayed with increasing forest cover (Hebblewhite et al., 2008). By selecting home ranges with high habitat diversity, deer on Anticosti Island may have extended access to forage of higher quality during the plant-growing season.

Because forage is less abundant during winter than summer, selection for forage abundance could be stronger at all scales of analysis during winter. Interestingly, we found that deer adopted several tactics of home range selection during winter. Deer either selected areas with food-rich balsam fir stands, or heterogeneous habitat mosaics when the availability of balsam fir stands was intermediate or low. This variation in home range selection with habitat composition suggests a functional response in habitat selection (*sensu* Mysterud and Ims, 1998) at the home range scale. This indicates that deer may compensate for the low availability of balsam fir stands by selecting areas with high diversity of habitat categories. However, selection for heterogeneous habitat mosaics is generally related to greater use of habitat categories with lower resources (Cromsigt et al., 2009), and individuals adopting this tactic might have to compensate behaviorally for lower forage abundance (Sæther and Andersen, 1990).

Spatial heterogeneity in forage and cover within forested habitat categories may also influence habitat selection of white-tailed deer. We expected that deer would respond to fine-grained mosaics of continuous cover and canopy openings and select canopy gaps at a fine scale. As opposed to previous studies on birds (Levey, 1988), invertebrates (Bouget, 2005) and small mammals (Hodson et al., 2010), deer did not select canopy gaps originating from windthrows or insect outbreaks during summer, but rather selected edaphic gaps that tended to be associated with black spruce. Selection for these gaps could be explained by their high forage abundance, as openings in black spruce stands offer more forbs and deciduous shrubs cover than those located in balsam fir stands (Massé and Côté, 2009). These better forage conditions may

explain why female deer harvested in spruce-rich areas had a larger foot length than those harvested elsewhere on Anticosti Island (Simard, 2010).

Deer also responded positively to increasing size of the openings (Kuijper et al., 2009). As forage biomass increases with gap size (Castleberry et al., 2000), the habitat use pattern we observed during summer suggests that deer favored energy acquisition at a fine scale. We expected the same situation to occur during winter, because trees located on the edges of canopy openings are more exposed to wind disturbance and thus are more vulnerable to windthrows (Foster and Reiners, 1986), offering a short-term increase in forage abundance (Gaillard et al., 2003). Although previous work on Anticosti Island demonstrated the strong influence of windblown fir trees on deer habitat selection within the home range (Massé and Côté, 2012), we did not find that deer selected canopy openings during winter. Canopy openings occupy 25 ± 3% (*n* = 13 deer) of the transects in balsam fir stands in winter home ranges, compared to 61 ± 4% (*n* = 19 deer) during summer. This suggests that continuous cover might be of primary importance, especially at northern latitudes during winter, as it intercepts snow (Massé and Côté, 2012) and reduces heat loss (Cook et al., 1998).

Individuals can respond to heterogeneity of forage and cover by adjusting the size of their home range (van Beest et al., 2011). We found that deer did not adjust the size of their home range to cope with seasonal variations in forage abundance and locomotion costs, although they reduced their movements from 64 ± 4 m/h (*n* = 19) in summer to 30 ± 1 m/h (*n* = 15) in winter (Massé and Côté, 2012). Variations in home range size were better explained by forage availability within and among habitat categories for each season (Kie et al., 2002; Anderson et al., 2005; Saïd et al., 2009). We found that deer reduced the size of their home range with increasing occurrence of deciduous shrubs and forbs during summer and with increasing density of windblown balsam fir trees during winter. In agreement with Saïd et al. (2009), total abundance of forbs or shrubs did not explain variations in home range size, suggesting that large herbivores increase the size of their home range in low productive areas (i.e. where the mean occurrence of forbs and deciduous shrubs was low) to obtain the minimum amount of forage required. These results indicate that deer need smaller home ranges to fulfill their energy requirements where forage abundance is high, which supports the habitat productivity-home range size hypothesis (Harestad and Bunnell, 1979).
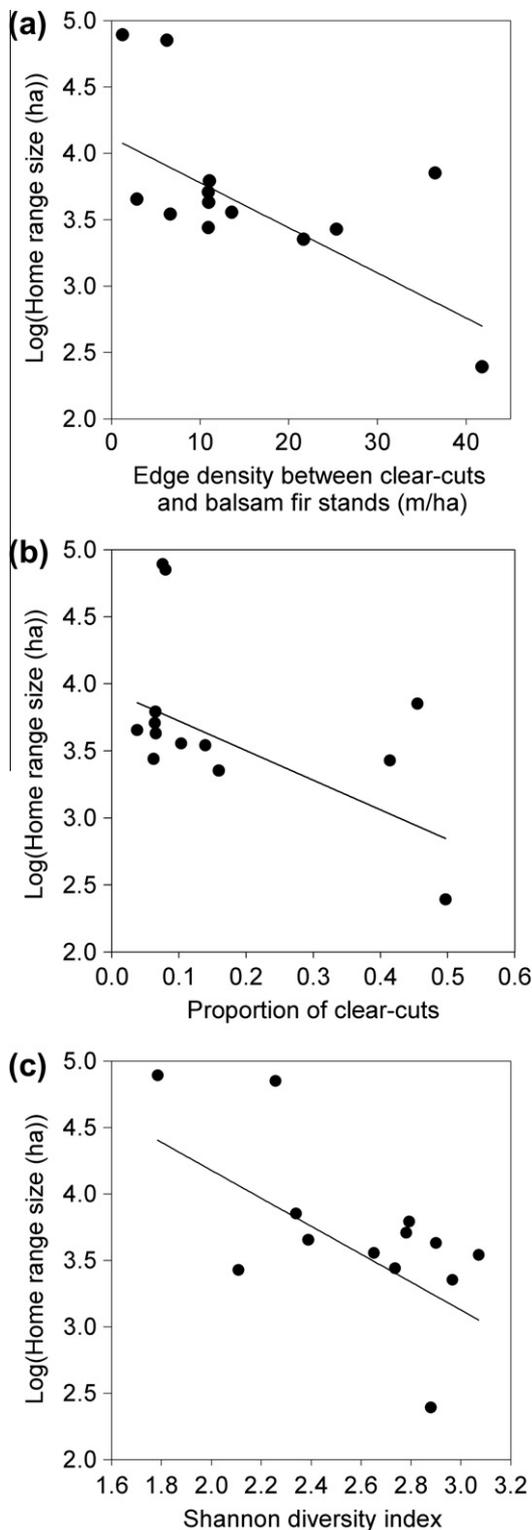
Fig. 4. Relationships between edge density between clear-cuts and balsam fir stands (A), proportion of clear-cuts (B), and Shannon diversity index (C) measured at the 2000 m scale, and home range sizes of female white-tailed deer monitored during winters 2003–2004 and 2004–2005 on Anticosti Island, Québec, Canada.

At larger scale, we found that deer reduced their winter home range in areas where the proportion of clear-cuts increased within 1000 and 2000 m radii of the center of their home range. Although we expected a negative relationship between food-rich balsam fir stands and deer home range size on Anticosti Island, the negative influence of clear-cuts could also be explained by increasing forage.

For example, clear-cuts occupied half of the 1000 and 2000 m radii around the smallest home ranges, and deer living in these areas may have needed smaller areas to meet forage requirements as we found that windblown fir trees, an important source of forage on Anticosti (Massé and Côté, 2012), were highly associated to edges between clear-cuts and balsam fir stands (correlation between the frequency of windblown fir trees and distance to edges: $r = -0.86, P \leqslant 0.0001$). Accordingly, we found that deer reduced the size of their home range in winter with increasing edge density between clear-cuts and balsam fir. Although the strong selection for edges is usually related to the proximity of complementary habitat categories (Dunning et al., 1992), such as those offering food and those offering protective cover, the association to edges on Anticosti was rather related to an increase in forage abundance along edges (Desrochers et al., 2003). Interestingly, Anticosti deer did not respond significantly to edges between complementary habitat categories during summer. These results suggest that the association between edges and herbivores that has been recognized for a long time (Leopold, 1933) may be less important when limiting factors, such as predation risk, are relaxed (Hernández and Laundré, 2005; Massé and Côté, 2009).

Individual characteristics such as sex generally influence home range size in sexually dimorphic large herbivores (Kjellander et al., 2004), because forage requirements are different between sexes. In an ecosystem modified by long-term browsing such as Anticosti Island, we would predict that the strong selection for forage abundance would be greater for males than females as they generally select their habitat based on forage quantity rather than quality (Main et al., 1996; Bowyer, 2004). This, however, remains to be investigated.

5. Conclusions

Spatial heterogeneity of resources might contribute to the maintenance of long-term high densities of large herbivores, because resource heterogeneity may attenuate the effect of density-dependent negative feedbacks (Wang et al., 2006). Because spatial heterogeneity in forage resources may increase selectivity (Senft et al., 1987), it may allow herbivores to cope with temporal changes in resources resulting from varying weather conditions and/or density (Wang et al., 2006). In forested landscapes, logging and natural disturbances generate gaps within the forest matrix, thereby increasing heterogeneity at multiple scales. In our study, deer were living in an ecosystem strongly modified by long-term browsing (Potvin et al., 2003; Tremblay et al., 2005), and individual deer responded positively to habitat heterogeneity when selecting their home range and areas within their home range. Moreover, deer adjusted the size of their winter home range with edge density of cutblocks. As windblown fir trees, an important source of food in over-browsed landscape (Massé and Côté, 2012), were highly associated to edges between clear-cuts and balsam fir stands, these results suggest that logging may be an important element of deer winter habitat in ecosystem modified by long-term browsing. Future research should link variations in habitat composition and configuration at the local scale to habitat selection, life-history traits (Strickland and Demarais, 2008; Hewison et al., 2009), and ultimately population dynamics of herbivores (Fraterrigo et al., 2009).

Appendix A, B, C and D. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2012.07.039.

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