Habitat Relations

Linking Alternative Food Sources to Winter Habitat Selection of Herbivores in Overbrowsed Landscapes

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ABSTRACT During winter, ungulates in boreal forests must cope with high energetic costs related to locomotion in deep snow and reduced forage abundance and quality. At high density, ungulates face additional constraints, because heavy browsing reduces availability of woody browse, the main source of forage during winter. Under these severe conditions, large herbivores might forage on alternative food sources likely independent of browsing pressure, such as litterfall or windblown trees. We investigated the influence of alternative food sources on winter habitat selection, by studying female white-tailed deer (*Odocoileus virginianus*) living in 2 landscapes with contrasted browse abundance, recently logged and regenerated landscapes, in a population at high density and on a large island free of predators. We fitted 21 female white-tailed deer with Global Positioning System (GPS) collars and delineated winter home ranges and core areas. We measured snow conditions in different habitat categories and sampled vegetation in the core areas and in the rest of the home ranges to determine how forage abundance, protective cover, and snow conditions influenced habitat selection within the home range. In both landscapes, deer were less likely to use open habitat categories as snow accumulated on the ground. At a finer scale, deer inhabiting the regenerated landscape intensively used areas where balsam fir cover was intermediate with greater balsam fir browse density than in the rest of the home range. In the recently logged landscape, deer were more likely to be found near edges between clear-cuts and balsam fir stands and in areas where windblown balsam fir trees were present; the latter being the most influential variable. Although balsam fir browse was sparse and mainly out of reach in this landscape, deer increased the use of areas where it was present. Our results offer novel insights into the resource selection processes of northern ungulates, as we showed that access to winter forage, such as woody browse and alternative food sources, depends on climatic conditions and stochastic events, such as abundant compacted snow or windthrows. To compensate for these scarce and unpredictable food supplies, deer selected habitat categories, but mostly areas within those habitat categories, where the likelihood of finding browse, litterfall, and windblown trees was greatest. © 2011 The Wildlife Society.

KEY WORDS Anticosti Island, balsam fir, forage, Global Positioning System (GPS), habitat selection, high-density, long-term browsing, *Odocoileus virginianus*, white-tailed deer, winter.

Optimal foraging theory predicts that the distribution of species is strongly influenced by the abundance and the spatial distribution of resources in order to maximize individual fitness (Pyke et al. 1977, Stephens and Krebs 1986). For instance, herbivores select habitats according to forage abundance and availability (Schaefer and Messier 1995, Hansen et al. 2009, van Beest et al. 2010), but other environmental conditions such as predation (Lima and Dill 1990, Verdolin 2006), thermal stress (Parker and Gillingham 1990, Taillon et al. 2006), and locomotion costs (Parker et al. 1984,

Johnson et al. 2002) may also influence their distribution. The multiscale behavioral responses to these environmental conditions result in the disproportionate use of particular habitats or parts of certain habitats (Johnson 1980). This hierarchical process of habitat selection is central to our understanding of how herbivores use the landscape, especially in seasonal environments where foraging benefits and costs vary strongly across temporal and spatial scales.

In temperate and boreal regions, snow accumulation has long been recognized as a key factor shaping winter habitat selection of herbivores because it reduces forage availability (Schwab et al. 1987, Nordengren et al. 2003, Visscher et al. 2006) while also increasing the energy costs of movement (Parker et al. 1984) and vulnerability to predators (Nelson and Mech 1986, Mech et al. 2001). Because snow accumulation decreases with canopy closure (Kirchhoff and Schoen

1987, McNay et al. 1988, Winkler et al. 2005) and forage abundance is greater in open regenerating stands (Weixelman et al. 1998, Morrison et al. 2002), herbivores are expected to make a trade-off between forage and protective cover and thus to select edges between forested and open habitats (Mysterud & Østbye 1999, Dussault et al. 2005).

High population density may impose additional constraints on habitat selection of large herbivores. Selective browsing induces regeneration failure of preferred tree species in many regions worldwide (Alverson et al. 1988, Gill 1992, McInnes et al. 1992, Danell et al. 2003), thereby causing compositional shifts of the dominant and preferred tree species (reviewed by Côté et al. 2004). Under such conditions of food shortage, mortality by starvation during winter may substantially affect population size (Dumont et al. 2000). Alternative food sources such as litterfall or windblown trees could, however, act as ecological subsidies enhancing winter survival (Tremblay et al. 2005, Ward and Marcum 2005), and thereby contribute to maintaining high population densities (Simard et al. 2008, Miyaki and Kaji 2009). As large herbivores aggregate in small areas during winter, populations that have access to forage resources independent of the browsing pressure (Tremblay et al. 2005) and at high density can have greater impacts on tree regeneration (Van Deelen 1999, Weisberg and Bugmann 2003). In the context of deer overabundance, there is a growing need for more information on the relationships between habitat selection patterns of herbivores and the abundance of their forage resources (Gill 2006). Moreover, little is known about the proximate mechanisms behind the maintenance of high population densities and ecological subsidies.

White-tailed deer (*Odocoileus virginianus*) on Anticosti Island are at the northern limit of the species' distribution and must cope with harsh climatic conditions during winter, offering a model species to investigate habitat selection under severe snow conditions. In the absence of predation, the introduced population irrupted to high densities (>20 deer/km²) and chronic browsing resulted in the reduction of preferred deciduous browse (Tremblay et al. 2005). Although balsam fir (*Abies balsamea*) is considered a starvation food for white-tailed deer (Sauvé and Côté 2006), it is their main winter diet on Anticosti (Lefort et al. 2007) and its availability in the understory layer has considerably decreased in the last 25 years (Tremblay et al. 2005). Deer browsing on balsam fir seedlings during summer progressively induces the replacement of balsam fir by white spruce (*Picea glauca*) stands (Potvin et al. 2003). The harsh snow conditions prevailing on Anticosti Island coupled with the low abundance of palatable woody browse and the presence of litterfall and windblown trees as alternative food sources (Tremblay et al. 2005) provide a natural experiment to study winter habitat selection of a large herbivore.

We used Global Positioning System (GPS) telemetry to investigate how female white-tailed deer modified their winter habitat selection as a function of the abundance of browse and alternative food sources, habitat-specific snow conditions (i.e., accumulation and sinking depth), and protective cover. We first examined habitat selection patterns of female deer inhabiting 2 landscapes with contrasting balsam fir browse abundance: 1) a recently logged landscape characterized by clear-cuts and approximately 70% mature forest stands with reduced browse availability, and 2) a regenerated landscape consisting of mature forest stands with greater browse abundance, simulating Anticosti forests after management to regenerate balsam fir. We hypothesized that deer would select habitats within the home range, the third order of selection according to Johnson (1980), relative to the availability of their food supplies (Vivås and Sæther 1987). At the habitat category scale, we predicted that female deer would select habitat categories where forage was abundant but snow and sinking depths were reduced. In the recently logged landscape, we also predicted that deer would select edges between clear-cuts and balsam fir stands because the odds of a windthrow, and thus the occurrence of windblown trees, increases on open–forest edges (Ruel et al. 2000). Within habitat category, we predicted that deer would select areas where balsam fir browse and alternative food sources, such as windblown trees, were more abundant. In a post hoc analysis, we assessed the abundance of alternative food sources (i.e., windblown balsam fir trees and litterfall) in terms of biomass to compare it to the biomass of available woody browse and examine its effects on deer winter habitat selection.
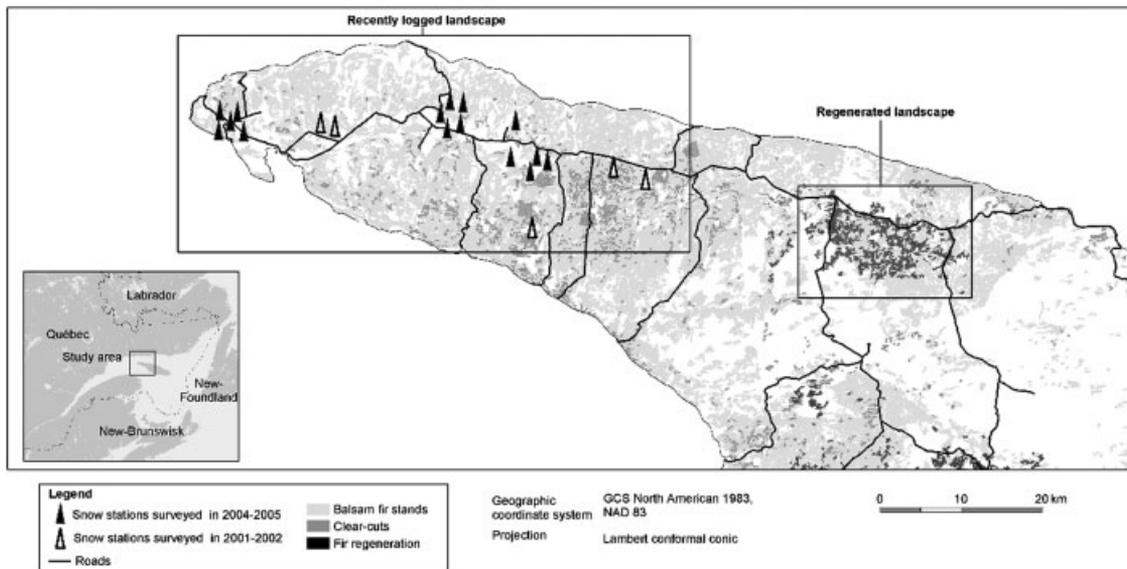
STUDY AREA

Anticosti is a 7,943-km² island located in the Gulf of St. Lawrence, Québec, Canada (49°28′ N, 63°00′ W). The climate on Anticosti Island was maritime and characterized by cool summers and long winters. Mean air temperature on Anticosti was 16° C in July and −11° C in January (Environment Canada 2006). Snow precipitation averaged 328 cm annually and rainfall averaged 61 cm (Environment Canada 1982). Over the last 20 years, average snow sinking depth for deer was 47 ± 3 cm, with sinking depth above 50 cm for about 96 days/year (Simard et al. 2010). The forest of Anticosti Island was dominated by balsam fir, white spruce, and black spruce (*P. mariana*). Large peatlands were also commonly found in depressions.

The recently logged landscape (approx. 1,420 km²) was representative of the western part of the island (Fig. 1) and was dominated by mature balsam fir, white and black spruce stands with low browse abundance and commercial logging since 1995. The regenerated landscape (approx. 97 km²) was located in the center of the island and was logged between 1955 and 1971 (Fig. 1). It was dominated by mature balsam fir stands and 30- to 50-year-old spruce stands, both with a high regeneration of balsam fir, a rare situation on the island.

METHODS

Animal Monitoring

We monitored 21 free-ranging white-tailed deer adult females (aged ≥2 yr) using GPS 2200R and GPS 3000 collars (Lotek Engineering, Newmarket, Ontario, Canada) during winters 2001–2002, 2003–2004, and 2004–2005. Seven deer were followed between 24 January 2002 and

Figure 1. Study area on Anticosti Island, Québec, Canada, showing the 2 landscapes in which we assessed winter habitat selection of white-tailed deer females. The recently logged landscape is characterized by low abundance of balsam fir browse, whereas the regenerated landscape is characterized by balsam fir regeneration, a rare situation on the island.

30 April 2002 in the regenerated landscape, whereas 2 deer were followed between 9 December 2003 and 30 April 2004 and 12 deer between 9 December 2004 and 30 April 2005 in the recently logged landscape. We captured deer with either a net-gun fired from a helicopter, darts with chemical immobilization fired from the ground, Stephenson box traps, or canon-nets baited with balsam fir and commercial cow feed. For chemical immobilization, we used a mixture of Telazol (200 mg/mL; Fort Dodge Animal Health, Fort Dodge, IA) and Xylazine (100 mg/mL; Bimeda-MTC Animal Health, Inc., Cambridge, Ontario, Canada) at doses of 6 mg/kg and 3 mg/kg, respectively and used Yohimbine (2 mg/mL; Lloyd Laboratories, Shenandoah, IA) as an antagonist for Xylazine. We released deer at the capture site. Collars were programmed to record a location every 4 hours during the winter 2001–2002 and every 2 hours during the winters 2003–2004 and 2004–2005. GPS collars were equipped with a time delay drop-off (Lotek Engineering, Newmarket, Ontario, Canada) that allowed us to retrieve collars without re-capturing the animals. We performed field trials with 6 stationary collars distributed in open and forested habitats to determine location success and error. The Animal Care and Use Committee of Université Laval (Québec, Canada) approved all capture methods (protocol number 2005-008) based on the Canadian Council on Animal Care guidelines (Canadian Council on Animal Care 2003).

Snow Conditions

We measured snow accumulation annually every 15 days at 5 different snow stations located in clear-cuts ($n = 2$), balsam fir stands ($n = 2$), and in a spruce stand ($n = 1$) from 10 December to 4 May (Fig. 1). Each station consisted of 10 3-m graduated rulers spaced every 5 m along a transect that started at least 50 m from forest or clear-cut edges. We assessed sinking depth of deer beside each ruler using a penetrometer (Verme 1968), and paired sinking depths with each snow accumulation measurement. In 2004–2005, we installed 15 additional snow stations in balsam fir stands ($n = 3$), spruce stands ($n = 3$), peatlands ($n = 3$), and on edges between clear-cuts and balsam fir stands ($n = 6$; Fig. 1). To evaluate the influence of dominant northeast winds on local snow conditions, we chose edges oriented in that direction. We measured edges with the forest facing east ($n = 3$) and edges with the forest facing west ($n = 3$).

Delineation of Home Ranges and Core Areas

We used the minimum convex polygon (MCP) method (Mohr 1947) with 95% of the locations to delineate winter home ranges. As suggested by Kenward (1987), we visually examined an incremental plot of MCPs relative to the proportion of locations for each animal to determine the percentage of locations to use for core area contours. Using this method, we found that 80% of locations should be used for the determination of core areas, as it corresponded to the largest proportion of locations in the smallest MCP. We thus used 80% clusters with the nearest-neighbor joining method to determine core area contours. In each home range, we defined high-use areas as those delineated by the 80% clusters, and low-use areas as the remnant areas of the home range. We delineated home ranges and core areas using the program RANGES V (Institute of Terrestrial Ecology, Wareham, Dorset, United Kingdom).

Habitat Description

We used 1:20,000 forest cover maps from the Ministère des Ressources naturelles et de la Faune du Québec to determine forage and cover available to deer at the habitat category scale. These maps described tree and shrub strata in terms of species, densities, and height, allowing us to define 8 habitat categories (Table 1). The maps were produced by a photo-interpretation that delineated forest stands and other distinct habitat categories using 1:15,000 aerial photographs taken in

Table 1. Variables included in models of white-tailed deer winter habitat selection on Anticosti Island, Québec, Canada. We investigated habitat selection within the home range at the scale of the habitat categories (A) and within habitat categories (B).

Explanatory variables	Description
A) Habitat category	
Clear-cut	Clear-cuts
Peatland	Minerotrophic and ombrotrophic peatlands
Regeneration	Fir regeneration
Balsam_fir	Stands with balsam fir >25% of the basal area
B_spruce_reg	Stands with black spruce >25% of the basal area and fir regeneration
W_spruce_reg	Stands with white spruce >25% of the basal area and fir regeneration
Spruce	Stands with spruce >25% of the basal area
Other	Lakes and other open habitat categories
Edge	
Edge_cut	Distance to the nearest edge between clear-cuts and balsam fir stands (m)
Edge_reg	Distance to the nearest edge between regenerated and balsam fir stands (m)
Snow	
Snow_depth	Snow depth (cm)
Snow_sinking	Snow sinking depth (cm)
B) Forage	
Fir_browse	Density of twigs of balsam fir between 25 cm and 325 cm (twigs/ha)
Fir_tree	Number of windblown fir trees with at least 1 available twig
Cover	
Fir	Basal area of balsam fir (m²/ha)
Fir_density	Density of stems of balsam fir with a diameter at breast height ≥9 cm (stems/ha)
Concealment	Concealment horizontal cover between 50 cm and 200 cm (%)
Edge	
Edge_cut	Distance to the nearest edge between clear-cuts and balsam fir stands (m)
Edge_reg	Distance to the nearest edge between regenerated and balsam fir stands (m)

1997. Minimum polygon sizes varied from 2 ha for commercially unproductive areas to 8 ha for forest stands.

We conducted field surveys in July and August 2004 ($n = 9$ deer from the winters 2001–2002 and 2003–2004) and 2005 ($n = 12$ from the winter 2004–2005) to describe areas used within habitat categories. At this finer scale, we surveyed the vegetation in each home range and habitat category by randomly distributing 20 sampling stations in the core areas (high-use areas) and 20 sampling stations in the rest of the home range (low-use areas). The number of sampling stations within each habitat category was proportional to its size. We surveyed 536 and 281 sampling stations for deer monitored in the recently logged and the regenerated landscape, respectively. Minimum distance between 2 sampling stations averaged 52 ± 8 m and the overall size of each station was about 314 m².

At each sampling station, we measured 7 habitat variables to assess forage and cover abundance, as well as interspersion between forage and cover (Table 1). We determined the composition of the tree layer by estimating the basal area of trees of each species with a prism (Grosenbaugh 1952). We also measured the diameter at breast height of all trees selected by the prism and calculated stem density by species

(Grosenbaugh 1952). We estimated horizontal vegetation cover using 2 estimates of the visibility of a profile board (2.5 m × 0.3 m divided in 0.5-m sections) positioned at 15 m from the center of the sampling station and oriented north-south (Nudds 1977).

We assessed forage abundance by recording the density of deciduous, balsam fir, and white spruce stems, from either individual tree or layers, with at least 1 twig ≤10 mm in diameter between 25 cm and 325 cm > ground (the height at which deer have access to woody browse in winter) in 1 2 m × 20 m plot per sampling station. For each stem recorded, we visually evaluated browse abundance using 3 categories (low, moderate, high percent cover; see section Estimates of Forage Biomass for details) at 4 different heights (25–75 cm, 76–125 cm, 126–225 cm, and 226–325 cm). For deer monitored during winters 2003–2004 and 2004–2005, we recorded the number of windblown balsam fir trees that intercepted the 2 m × 20 m plot. Previous winter windblown trees were easily recognizable because several green twigs remained on the branches.

We assessed interspersion between forage and cover at each sampling station by measuring the minimum distance between the center of the sampling station and the nearest edge between a clear-cut and a balsam fir stand and the nearest edge between regenerated and balsam fir stands using ArcView (version 3.2, Environmental Systems Research Institute, Inc., Redlands, CA).

Estimates of Forage Biomass

We developed biomass estimates for woody browse abundance by calibrating the percent cover of twigs (any small thin terminal branch of a woody plant) visually estimated using 3 categories (low, moderate, high) and the actual number of twigs ≤10 mm in diameter present (Massé 2011). Low, moderate, and high abundance of balsam fir and white spruce browse corresponded to a mean of 58 ± 7 and 37 ± 6 twigs, 330 ± 28 and 327 ± 28 twigs, and $1,048 \pm 136$ and $1,215 \pm 115$ twigs, respectively (Massé 2011). We used the mean biomass of balsam fir and white spruce twigs (Massé 2011) to convert the 3 categories of browse abundance in biomass estimates. For windblown trees, we cut 29 balsam fir trees and weighed all twigs ≤10 mm in diameter available to develop an allometric relationship based on the volume (V) occupied by the branches to predict the biomass of twigs available. We used the equation:

$$V = \pi/3 \times h \times r^2 \qquad (1)$$

where h is the length of the stem with branches and r is the mean of the length of the 2 longest branches at the base of the stem. The allometric regression corresponding to the biomass of fir twigs available = 18.62 + (0.39 × volume of branches) ($F_{1,27} = 19.98$, $P = 0.0001$, $R^2 = 0.43$), and the cross-validation coefficient ($R^2 = 0.56$, $P = 0.002$) suggested good fit.

Data Analyses

We performed a linear mixed model (LMM; PROC MIXED, SAS Institute, Inc., Cary, NC) to assess the influence of habitat category and period during winter (i.e., a

measure every 15 days) on local snow accumulation and sinking depth using the 150 snow measurements from the winter 2004–2005. We included the snow station as a random factor and the period during winter as a repeated measure. We used least-square means for multiple comparisons and we computed the observed variance of the LMM model following Xu (2003).

For habitat selection within the home range at the habitat category scale, we used resource selection functions (RSFs) to investigate the contribution of snow conditions, forage abundance, protective cover, and the interspersion between forage and cover in explaining winter habitat selection of white-tailed deer. In an RSF, resource selection is modeled as a function of the characteristics of resources units, and the RSF value, $w(x)$, is proportional to the probability of the unit being used as:

$$w(x) = \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \ldots + \beta_n x_n) \qquad (2)$$

where $x_{1\ldots n}$ are explanatory variables and $\beta_{1\ldots n}$ are selection coefficients (Manly et al. 2002). We estimated RSFs using a use–availability design, by contrasting habitat characteristics at observed deer locations with characteristics at random locations distributed within each deer home range. We used the REHOutils extension of ArcView (Courtois 2001) to determine the same number of random locations as the number of GPS locations for each deer during every 15-day period during winter. For a given 15-day period, we assigned to each location the mean snow depth and sinking depth recorded at the nearest snow station. Because we recorded snow conditions in 5 of the 8 habitat categories (Table 1), we assigned snow conditions of a similar habitat in certain situations. For example, snow conditions of "clear-cuts" were assigned to "clear-cuts" and "other" habitat categories, whereas the snow conditions measured in "peatlands" were assigned to "peatlands" and "regeneration" habitat categories. Finally, snow conditions measured in "balsam fir stands" and "spruce stands" were assigned to "balsam fir stands" and "spruce stands" with or without fir regeneration.

We used a generalized estimating equation (GEE; PROC GENMOD, SAS Institute, Inc.) to evaluate RSFs as it accounts for the non-independence among the observations of a given deer, it allows for unequal number of observations of a given animal, and produces robust standard errors for the parameter estimates ($\beta_{1\ldots n}$; Craiu et al. 2008, Koper and Manseau 2009). We built separate RSFs for deer in the recently logged and the regenerated landscapes because we wanted to assess how habitat selection varied with increasing regeneration of balsam fir. We built candidate RSF models with explanatory variables to evaluate how deer selected habitat based on 1) habitat categories, 2) proximity to edges between forage and cover, 3) snow conditions, or 4) a combination of these features (see Appendix A, available online at www.onlinelibrary.wiley.com). We included in models the interaction between snow conditions and habitat categories, because we were interested in investigating how habitat selection varied with snow accumulation or sinking depth. We tested for a quadratic effect of snow depth and sinking depth and the interaction between these 2 variables, because

a low sinking depth may be associated with shallow or deep-crusted snow. Because GEEs are not likelihood-based models, we could not use Akaike's Information Criterion (AIC) for model selection. We selected the most parsimonious RSF model based on Quasi-likelihood Information Criterion (QIC), which is applicable to GEEs and based on AIC (Pan 2001). Prior to calculating RSFs, we verified that there were no collinearity problems between explanatory variables using the multicollinearity diagnostic statistics produced by linear regression analysis (PROC REG, SAS Institute, Inc; Allison 2003). We removed variables with a tolerance value <0.4 (Allison 2003). We evaluated the robustness of the most parsimonious model by performing k-fold cross-validation withholding 20% of the data and using 10 iterations (Boyce et al. 2002).

We assessed deer habitat selection within habitat categories by comparing habitat variables measured in the field between high- and low-use areas of deer home ranges. We used conditional logistic regressions (PROC LOGISTIC with STRATA statement, SAS Institute, Inc.) to model the probability of intensive use by white-tailed deer females. We built candidate models including exploratory variables based on 1) forage, 2) cover, 3) proximity to edges between forage and cover, and 4) a combination of these features (see Appendix B, available online at www.onlinelibrary.wiley.com). We tested for a quadratic effect of basal area and stem density of balsam fir, because large herbivores are known to select forest stands with intermediate cover during winter (Sabine et al. 2001). We used multicollinearity diagnostic statistics to verify problematic correlations between explanatory variables. We used Akaike's Information Criterion for small sample sizes (AIC_c) to rank the candidate models to evaluate which variables best predicted intensive use of habitat by deer based on AIC_c differences relative to the smallest AIC_c value in the candidate set (ΔAIC_c) and AIC_c weights (ω_i). We considered models with $\Delta AIC_c \leq 2$ equivalent (Burnham and Anderson 2002). We used model averaging to calculate parameter estimates of equivalent models (Burnham and Anderson 2002). We assessed the classification performance of the best model by comparing for each deer the percentage of correct predictions to those observed (e.g., high use vs. low use). We classified a prediction as correct if the outcome was 0 (low use) and the predicted probability of intensive use was below 50%, or if the outcome was 1 (high use) and the predicted probability of intensive use was above 50%.

We compared the abundance of alternative food sources (i.e., windblown balsam fir trees and litterfall) in terms of biomass to the biomass of available woody browse. We used estimates of biomass for litterfall from Tremblay et al. (2005), derived biomass of woody browse from the calibration of visual estimates using 3 categories of abundance, and predicted the biomass of windblown fir trees from the allometric regression we developed (Equation 1). We used LMMs to assess the influence of habitat categories on the biomass of balsam fir and white spruce browse in the recently logged and regenerated landscapes, separately. We considered identity of white-tailed deer females as a random

factor to control for the non-independence of multiple habitat samples collected within each home range (Littell et al. 2002). We log-transformed browse biomasses when they did not meet criteria for normality and homoscedasticity and used least-square means for multiple comparisons. We used Friedman analysis when criteria for normality and homoscedasticity criteria could not be met (Conover 1998). Unless specified, we presented all results as means $\pm$ 1 SE.

RESULTS

We recorded 16,120 telemetry locations of deer during 3 winters from 24 January 2002 to 17 April 2002, 29 November 2003 to 11 April 2004 and 25 November 2004 to 31 March 2005 with a mean of 750 ± 88 locations/deer (range 78–1,523 locations/deer). We discarded 2% of the GPS locations because their dilution of precision (DOP) value was >10, indicating relatively high location error (Dussault et al. 2001). Location success based on field trials using 6 stationary collars was 95% and 90% in forested and open habitats, respectively. Mean location error was 6.3 ± 0.4 m and 12.9 ± 0.7 in open and forested habitats, respectively, and was ≤ 10 m in 62% and ≤ 21 m in 90% of the locations recorded ($n = 1,365$ locations). Winter home range size was 30 ± 5 ha and the mean size of core areas was 6 ± 1 ha ($n = 21$).

Snow Conditions

Snow accumulation was affected by habitat category ($F_{4,8} = 36.5$, $P < 0.0001$) and winter period ($F_{10,20} = 36.7$, $P < 0.0001$), but not by their interaction ($F_{40,80} = 0.8$, $P = 0.8$, $R^2 = 0.7$). The lowest average snow depth across all sampling periods of 2004–2005 was observed in balsam fir stands (i.e., 50 cm), and was 43% lower than in peatlands (Fig. 2A). Average snow depth on east facing edges was 68 cm and was 15% deeper than on west facing edges, which had similar snow accumulation as in spruce stands (Fig. 2A). For snow sinking depth, we found a significant interaction between habitat category and winter period ($F_{40,80} = 2.2$, $P = 0.002$, $R^2 = 0.66$), indicating that snow sinking depth varied differently within each habitat category during the winter (Fig. 2A). Sinking depth ranged between 26 cm and 52 cm and was relatively similar in all habitat categories from December to the end of February. During March and April, however, sinking depth in balsam fir and spruce stands generally greatly exceeded sinking depth in peatlands and in open–forest edges (Fig. 2B).

Habitat Selection Within the Home Range

At the habitat category scale, the best models explaining habitat selection in the recently logged and regenerated landscapes received considerable support (see Appendix A, available online at www.onlinelibrary.wiley.com) and had adequate robustness (recently logged landscape: $r = 0.82 \pm 0.01$, $P = 0.002$; regenerated landscape: $r = 0.74 \pm 0.05$, $P = 0.01$). Deer selected edges between clear-cuts and balsam fir stands in the recently logged landscape (Table 2; Fig. 3A), and tended to select edges between regenerated and balsam fir stands in the regenerated landscape; although the trend was weak (Table 2; Fig. 3D). In both landscapes, the
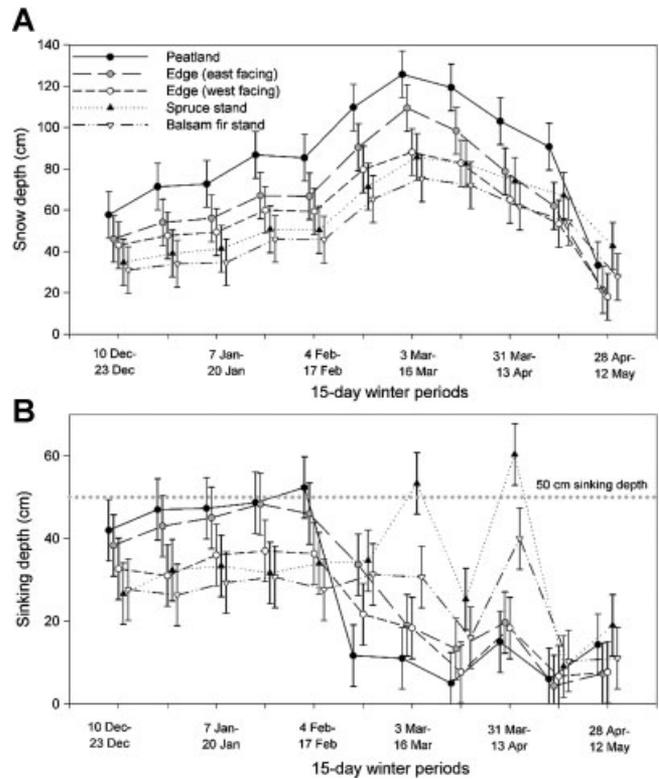
Figure 2. Variations in snow depth (A) and sinking depth (B) in 5 different white-tailed deer habitat categories on Anticosti Island during the winter 2004–2005.

best model included the interaction between snow depth and habitat category, suggesting that the use of a particular habitat varied as snow accumulated. In the recently logged landscape, deer were more likely to use balsam fir stands as snow accumulated (Table 2; Fig. 3C). Deer tended to reduce their use of clear-cuts and spruce stands as snow accumulation increased (Fig. 3B and C). Although deer tended to select peatlands as snow accumulated, the relative probability of using peatlands remained low (Table 2; Fig. 3B). Contrary to the recently logged landscape, deer were less likely to use balsam fir stands and peatlands in the regenerated area as snow accumulated (Table 2; Fig. 3E and F). In this landscape, they tended to increase their use of regenerated stands and spruce stands with fir regeneration (Fig. 3E and G).

Within habitat categories, the best model discriminating high- from low-use areas had a very high ω_i for the recently logged landscape (1.0) and achieved 66% correct predictions (see Appendix B, available online at www.onlinelibrary.wiley.com). The best model discriminating high- from low-use areas in the regenerated landscape achieved 64% correct predictions and had a relatively high weight (0.75; see Appendix B, available online at www.onlinelibrary.wiley.com). As we showed previously at the habitat category scale, deer inhabiting the recently logged landscape selected edges between clear-cuts and balsam fir stands (Table 3A; Fig. 4A). In both landscapes, deer intensively used areas where the total browse of balsam fir was greater than in the rest of their home range (Table 3; Fig. 4B and E).

Table 2. Parameter estimates (β) with their standard error (SE) and 95% confidence intervals (CI) for the best model predicting winter habitat selection at the habitat category scale by white-tailed deer females in recently logged and regenerated landscapes of Anticosti Island, Québec, Canada. Explanatory variables are described in Table 1 and model comparisons are shown in Appendix A, available online at www.onlinelibrary.wiley.com. Parameter estimates that are significantly different from 0 are indicated with an asterisk.

Explanatory variables	Recently logged landscape				Regenerated landscape			
	β	SE	95% CI		β	SE	95% CI	
Intercept	1.0*	0.2	0.5	1.4	−1.7*	0.5	−2.7	−0.7
Clear-cut	−0.3	0.4	−1.1	0.5				
Other	−1.1*	0.4	−1.8	−0.3	0.8	0.7	−0.6	2.3
Peatland	−1.3*	0.4	−2.2	−0.5	2.8*	0.7	1.5	4.1
Balsam_fir	−0.7*	0.3	−1.3	−0.2	2.4*	0.5	1.4	3.5
Regeneration					1.4*	0.6	0.3	2.5
B_spruce_reg					1.4*	0.7	0	2.7
W_spruce_reg					1.9*	0.6	0.6	3.2
Spruce	0	0	0	0	0	0	0	0
Edge	−0.0019*	0.0003	−0.0024	−0.0014	−0.0002	0.0001	−0.0004	0
Snow_depth	−0.007*	0.003	−0.013	−0.001	0.022*	0.008	0.006	0.038
Clear-cut × Snow_depth	−0.004	0.005	−0.015	0.006				
Other × Snow_depth	0.013	0.007	−0.001	0.026	−0.04	0.02	−0.08	0
Peatland × Snow_depth	0.009	0.006	−0.002	0.02	−0.08*	0.02	−0.12	−0.05
Balsam_fir × Snow_depth	0.011*	0.004	0.003	0.019	−0.03*	0.009	−0.048	−0.011
Regeneration × Snow depth					−0.01	0.01	−0.03	0.02
B_spruce_reg × Snow_depth					−0.01	0.01	−0.03	0.01
W_spruce_reg × Snow_depth					−0.01	0.01	−0.04	0.01
Spruce × Snow_depth	0	0	0	0	0	0	0	0

An increase of only 100 twigs/ha × 1,000 (i.e., 100,000 twigs/ha) in the regenerated landscape resulted in an increase of 5% in the probability of intensive use by deer, whereas in the recently logged landscape it resulted in an increase of 85%. In the recently logged landscape, the presence of only 1 windblown fir tree increased the probability of intensive use by deer by 1,000%. The presence of ≥3 windblown trees always implied that the area was intensively used

(Fig. 4C). In the regenerated landscape, deer increased the use of the parts of their home range where the basal area of balsam fir increased until a threshold of 20 m²/ha was reached, as revealed by the significance of the term fir² (Table 3B). When the basal area in balsam fir was below or above 26 m²/ha, the probability of intensive use decreased (Fig. 4D). Concealment cover and the distance to the nearest edge between regenerated and balsam fir stands did not
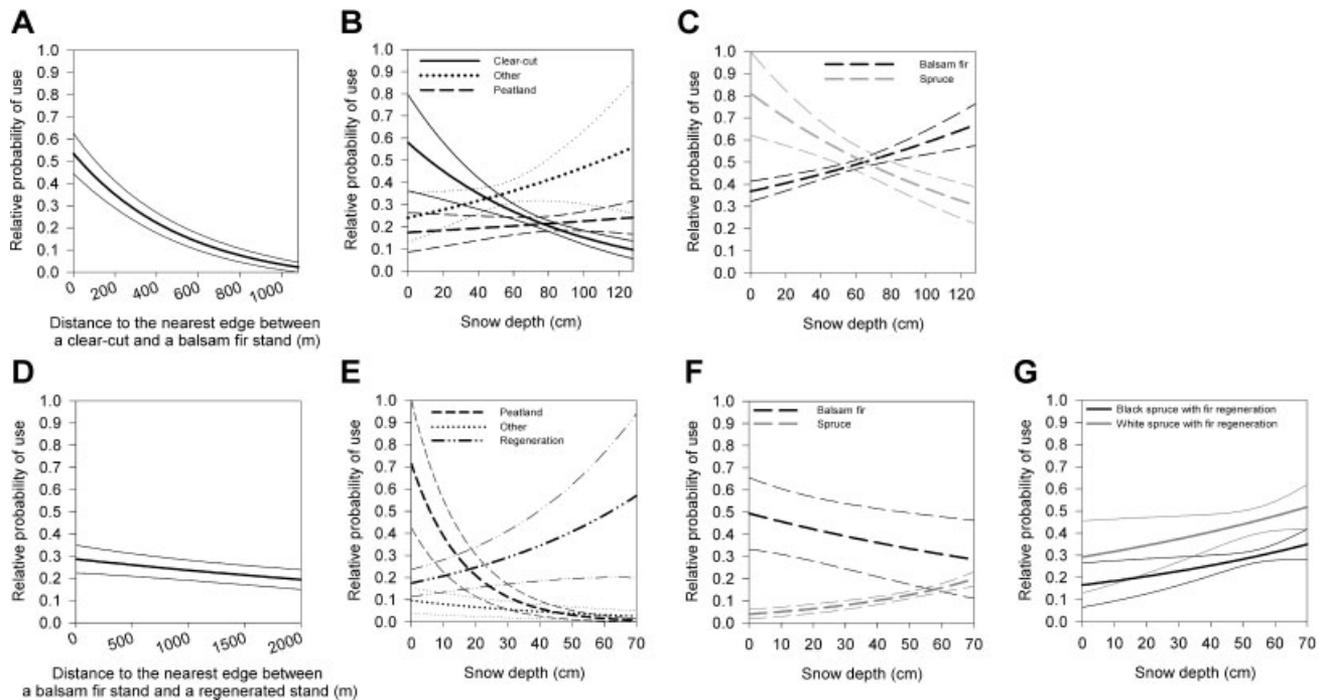
Figure 3. Resource selection functions (±SE) showing the relative probability that white-tailed deer females occupying recently logged (A–C) and regenerated (D–G) landscapes selected edges (A, D) and various habitat categories (B, C, E, F, G) as a function of snow depth during the winters of 2001–2002, 2003–2004, and 2004–2005 on Anticosti Island, Québec, Canada. We estimated relative probabilities for each habitat category while holding the other variables constant at their mean.

Table 3. Parameter estimates (β) with their standard error (SE), 95% confidence intervals (CI) and odds ratio for the best and equivalent models that predicted winter habitat selection within habitat categories by white-tailed deer females in recently logged and regenerated landscapes of Anticosti Island, Québec, Canada. Explanatory variables are described in Table 1 and model comparisons are shown in Appendix B, available online at www.onlinelibrary.wiley.com. Parameter estimates that are significantly different from 0 are indicated with an asterisk.

| Explanatory variables	Recently logged landscape					Regenerated landscape[a]				
	β	SE	95% CI		Odds ratio	β	SE	95% CI		Odds ratio
Edge	−0.0048*	0.0008	−0.0065	−0.0031	0.997					
Fir_browse	0.000008*	0.000002	0.000005	0.000012	1.000	0.0004*	0.0001	0.0002	0.0006	1.000
Fir_tree	2.4*	0.4	1.6	3.1	10.721					
Fir						0.17*	0.07	0.05	0.30	1.185
Fir^2						−0.0034*	0.0015	−0.0063	−0.0005	0.997

[a] Model-averaged parameter estimates (β) with their unconditional standard error (SE).

influence habitat selection at that finer scale (see Appendix B, available online at www.onlinelibrary.wiley.com).

Estimates of Forage Biomass

In the recently logged landscape, balsam fir browse did not differ among habitat categories (all $Ps > 0.05$; Fig. 5A), whereas white spruce browse below 225 cm differed among habitat categories and was highest in clear-cuts (25–75 cm: $F_{4,16} = 4.9$, $P = 0.009$, 76–125 cm: $F_{4,16} = 9.5$, $P = 0.004$, 126–225 cm: $F_{4,16} = 10.2$, $P = 0.003$; Fig. 5B). The vertical distribution of balsam fir contrasted with that of white spruce browse, with 80% of the balsam fir browse found above 225 cm and >70% of the white spruce browse found below 125 cm (Fig. 5A and B). Balsam fir browse did not differ among habitat categories of the regenerated landscape (all $Ps > 0.05$), although the highest biomass tended to be in white spruce stands with fir regeneration (Fig. 5C). White spruce browse between 126 cm and 225 cm in height differed among habitat categories and was highest in regenerated stands ($F_{5,10} = 5.2$, $P = 0.01$; Fig. 5D). Balsam fir browse was 50 times more abundant in the regenerated landscape than in the recently logged
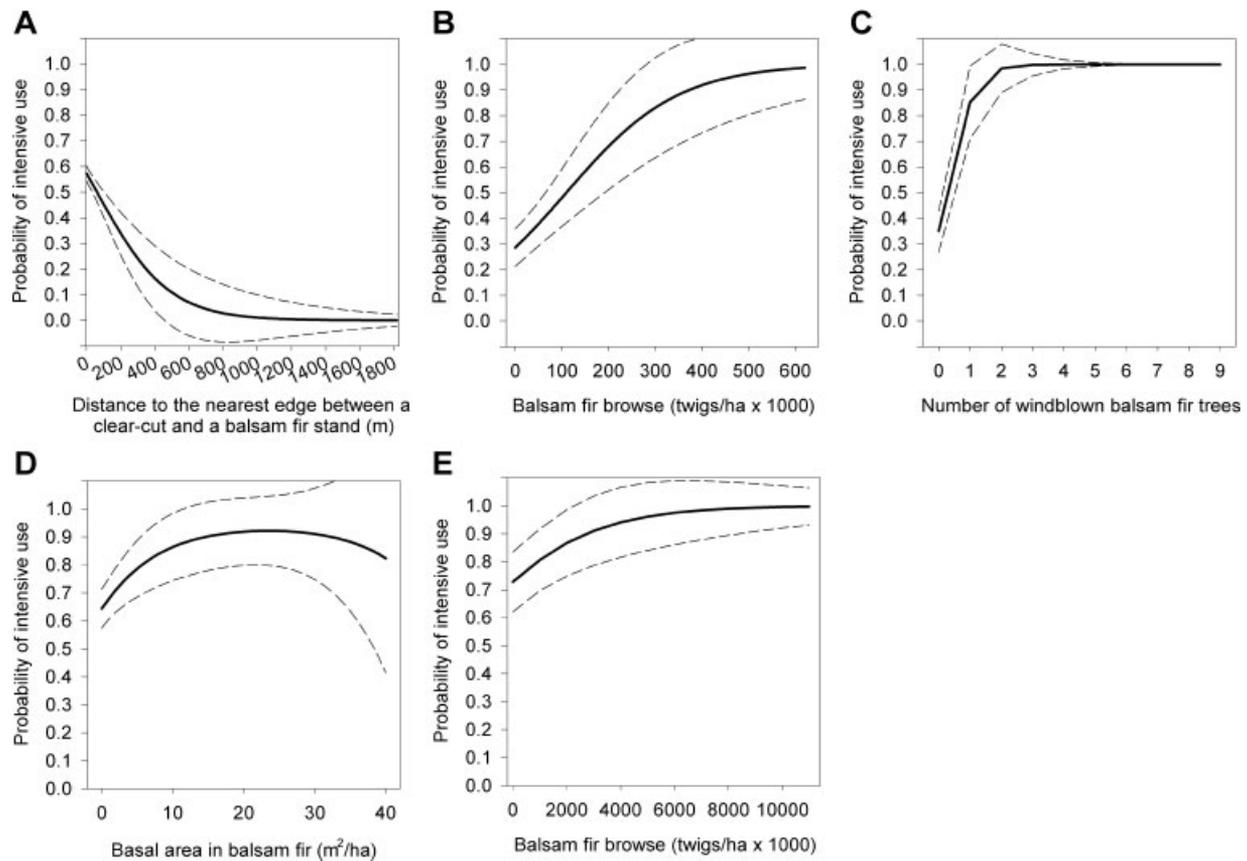
Figure 4. Probability that white-tailed deer females (logistic model predictions ± SE) occupying recently logged (A–C) and regenerated (D–E) landscapes selected edge between a clear-cut and a balsam fir stand (A), balsam fir browse (B, E), balsam fir windblown trees (C), and balsam fir basal area (D) during the winters of 2001–2002, 2003–2004, and 2004–2005 on Anticosti Island, Québec, Canada. We estimated probabilities for each explanatory variable while holding the other variables constant at their mean.
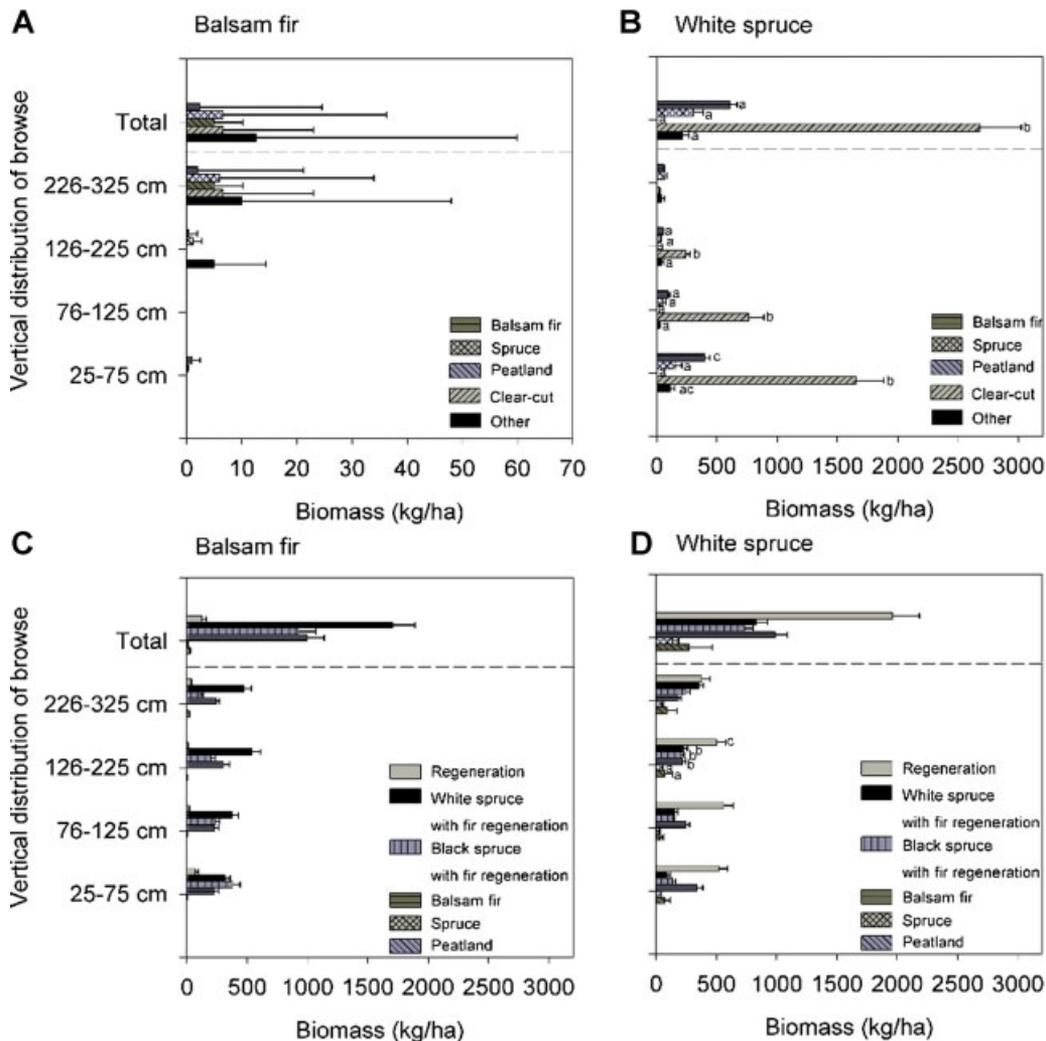
Figure 5. Distribution of the vertical browse biomass (means ± SE) for white-tailed deer by habitat categories in recently logged (A–B) and regenerated (C–D) landscapes of Anticosti Island, Québec, Canada, during the winters of 2001–2002, 2003–2004, and 2004–2005. Bars with different letters are significantly different at α = 0.05.

landscape, whereas white spruce browse was similar in both landscapes (Table 4; Fig. 5). In the recently logged landscape, windblown fir trees tended to have a greater biomass than balsam fir browse and litterfall of lichens and fir twigs (Table 4).

DISCUSSION

Our results support the hypothesis that large herbivores may adjust their winter habitat selection in response to variations in the availability of food resources (Vivås and Sæther 1987). Using RSFs that integrated the interaction between snow conditions and habitat categories, we developed a new approach to model how selection for a specific habitat category changed with snow accumulation. Moreover, the hierarchical approach we used allowed us to demonstrate how large herbivores selected habitat categories, but mostly areas within those habitat categories, where the likelihood of finding food resources was highest. Indeed, we showed the strong influence of ecological subsidies, such as windblown trees, on winter habitat selection by deer when woody browse, their main food supply, was scarce. Our results also revealed that

ungulates living in ecosystems affected by long-term browsing may depend on stochastic events, such as abundant compacted snow or windthrows, to have access to food resources.

Habitat Selection Within the Home Range

Snow conditions negatively affect the foraging efficiency of large herbivores by increasing energy expenditure (Parker et al. 1984). Compared to other large herbivores, such as caribou (*Rangifer tarandus*) and moose (*Alces alces*), white-tailed deer have limited morphological adaptations for movements in abundant deep snow (Telfer and Kelsall 1984). The ability of small cervids to cope with severe snow conditions depends instead on how they select their habitat (Telfer and Kelsall 1984). Our results on habitat selection at the habitat category scale revealed that deer on Anticosti responded to spatiotemporal variations in snow accumulation, as shown elsewhere (Fortin et al. 2005). Although snow conditions in 2002 (mean snow depth = 18 cm, n = 15 periods) for the regenerated landscape were below the average for Anticosti (mean snow depth = 39 cm, n = 27 yr × 15 periods,

Table 4. Biomass estimates of the different sources of food available during winter to white-tailed deer on Anticosti Island, Québec, Canada. The abundance of food sources was scaled up to the average home range size (30 ± 5 ha). Values are means (SE).

	Balsam fir browse		Litterfall[a]		Windblown fir trees[b]
	Recently logged landscape	Regenerated landscape	Lichens	Fir twigs	
Estimates (kg/ha)	22 (2)	1,103 (103)	12 (1)	17 (3)	31 (7)
Home range (kg)	660 (125)	33,090 (6,321)	360 (67)	510 (124)	930 (261)

[a] Data from Tremblay et al. (2005).
[b] The mean biomass of balsam fir twigs available in a windblown fir tree (36 ± 3 kg) was multiplied by the mean density of windblown trees per home range (0.9 ± 0.2 tree/ha).

Massé 2011), deer inhabiting both the recently logged and the regenerated landscapes of Anticosti Island responded to an increase in snow depth by decreasing their use of open habitat categories, such as clear-cuts and peatlands. These results could indicate that deer likely adopted habitat selection patterns to reduce movement costs (Fortin 2003), because snow accumulation was greater in open habitat categories than in mature forests (Bunnell et al. 1990, this study), and deer on Anticosti were observed to reduce their movements from 64 ± 4 m/hr ($n = 19$) in summer to 30 ± 1 m/hr ($n = 15$) in winter (Massé 2011). Interestingly, reduction of movement costs alone could not explain habitat selection, since spruce stands offered good snow interception but no food and were not selected by deer in either landscape. Furthermore, models including only snow conditions were not supported and sinking depth was not included in the best models.

Because habitat categories providing the best snow interception usually offer low forage abundance, large herbivores are expected to trade off access to forage and protective cover (Mysterud & Østbye 1999). Large herbivores may, however, have access to forage while minimizing exposition to harsh climatic conditions by selecting edges between habitat categories providing abundant forage and categories providing good cover favoring snow interception (Dussault et al. 2005). Based on previous work on habitat selection at the landscape scale (Plante et al. 2004) and on our results, we confirmed that Anticosti deer minimized locomotion costs while increasing access to forage by selecting edges between clear-cuts and balsam fir stands. However, strong selection for conifer edges may have a cost in systems including predators, because predators move more and encounter more prey along linear features than elsewhere (Bergman et al. 2006). In landscapes where wolfs (Canis lupus) or cougars (Puma concolor) are present, elk (Cervus elaphus) and mule deer (Odocoileus hemioneus) were found to be more vigilant near conifer edges than elsewhere during winter (Altendorf et al. 2001, Halofsky and Ripple 2008).

We evaluated models explaining habitat selection at the habitat category scale with different numbers of deer, years, and months of sampling for the 2 landscapes. To control for these limitations, we used GEE to evaluate RSFs, as it accounts for unequal sample size and non-independent observations (Koper and Manseau 2009). Although GEE provides robust standard errors (Craiu et al. 2008), Koper and Manseau (2009) showed that the use of empirical versus model-based standard errors strongly reduce the statistical

significance of RSF parameters which is also what we observed as the confidence intervals of many parameters in the best RSFs included zero values. Another explanation for the low statistical significance we observed could be related to the ecology of deer and the scale at which they respond to their habitat. Because deer on Anticosti Island select balsam fir stands at a larger scale (Plante et al. 2004), they may not respond to habitat categories within their home range. Weak relationships between deer distribution and habitat categories based on forest inventories could suggest that they respond to spatial heterogeneity in forage and cover at a finer scale (Dumont et al. 1998).

Deer inhabiting the recently logged and the regenerated landscapes responded mostly to small-scale variations in forage and cover when selecting areas within habitat categories. Deer in both landscapes were more likely to use intensively areas of their home range where the amount of balsam fir browse was greater than elsewhere. In the regenerated landscape, we found a nonlinear relationship between the probability of intensive use and the basal area in balsam fir, indicating that deer were more likely to use intensively areas of their home range where basal area of balsam fir was intermediate. Northern ungulates have also been reported to select forest stands with intermediate canopy cover; although this was achieved by selecting mixed-wood stands (Sabine et al. 2001, Dussault et al. 2005). Our findings reinforce the influence of fine-scale interspersion of forage and cover, as Anticosti deer reduced foraging costs by selecting for intermediate cover and high forage abundance. Nevertheless, in the near absence of balsam fir regeneration such as in the recently logged landscape, fine-scale habitat selection was mainly determined by the presence of windblown fir trees, a behavior that has mainly been reported for caribou (Terry et al. 2000, Serrouya et al. 2007) and black-tailed deer (O. hemionus columbianus; Parker et al. 1999). Strong selection for edges between clear-cuts and balsam fir stands at fine and larger-scales in the recently logged landscape reinforces the importance of alternative food sources, as the probability of windthrows increases along open–forest edges (Ruel et al. 2000).

The Importance of Alternative Food Sources for Northern Ungulates

Alternative food sources are thought to enhance survival of large herbivores during periods of food limitation (Tremblay et al. 2005, Ward and Marcum 2005). In temperate regions, winter is the primary period of food limitation because the

accessibility of understory vegetation decreases with increasing snow depth (Schwab et al. 1987, Nordengren et al. 2003, Visscher et al. 2006). As a result, many northern ungulates forage on litterfall (black-tailed deer: Parker et al. 1999; caribou: Terry et al. 2000, Serrouya et al. 2007; elk and mule deer: Ward and Marcum 2005; white-tailed deer: Ditchkoff and Servello 1998, Ward and Marcum 2005) and windblown trees (caribou: Terry et al. 2000, Serrouya et al. 2007) during this season. At high population densities, herbivores have strong negative impacts on their food resources (Côté et al. 2004), which in turn may negatively influence their survival and reproduction (McCullough 1999). When the most preferred woody browse species are almost eradicated, ungulates may forage on food sources that are independent of the browsing pressure, such as litterfall of leaves, lichens and twigs (sika deer [*Cervus nippon*]: Takahashi and Kaji 2001; white-tailed deer: Tremblay et al. 2005). Over the long term, however, the abundance of litterfall and windblown trees could decrease with increasing browsing pressure, as overbrowsing induces regeneration failure (Alverson et al. 1988, Gill 1992, McInnes et al. 1992, Danell et al. 2003).

Deer occupying the recently logged landscape of Anticosti had access to 98% less biomass of woody browse than those inhabiting the regenerated landscape, indicating that they had to forage on alternative food sources such as litterfall and windblown trees (Tremblay et al. 2005, Lefort et al. 2007). In the recently logged landscape, we estimated that the biomass of woody browse was comparable to the biomass of litterfall and windblown fir trees, although windblown trees tended to be the greatest. Although we did not quantify it, arboreal lichens on windblown trees may also constitute an important source of food for northern ungulates (Serrouya et al. 2007). Using the regression model developed by Arseneau et al. (1997) for mature balsam fir stands (log(lichen biomass in a single tree) = 2.91 × log(DBH) − 2.07; $R^2 = 0.87$), we can predict that the biomass of arboreal lichens in a balsam fir tree would be around 1.2 kg in stands used by deer during winter on Anticosti Island. The slightly greater biomass of balsam fir twigs and the presence of lichens on windblown trees may explain why their abundance strongly influenced habitat selection at the finer scale in absence of fir regeneration. Lichens could also be beneficial to northern ungulates because they are easily digestible (Robbins 1987). Although we did not test whether the digestibility of balsam fir twigs from windblown trees and litterfall was similar to that of living trees, previous work on Anticosti Island showed that there were no differences in chemical composition (e.g., dietary fibers, total phenols and condensed tannins) between balsam fir twigs collected on live trees between 0.5 m and 3 m from the ground and from twigs harvested on felled trees (D. G. Sauvé and S. D. Côté, Université Laval, personal communication).

Ungulates behaviorally respond to temporal and spatial variations in the distribution of their food supplies (Fryxell et al. 2004). Similarly to the study of Terry et al. (2000) on caribou, we propose that Anticosti deer use their habitat in relation to the spatiotemporal variations in the availability of 3 sources of food which are woody browse, litterfall, and windblown trees. In the absence of fir regeneration, 80% of the balsam fir browse was found between 226 cm and 325 cm in height, and thus became available to deer only in March when there was at least 75 cm of compacted snow on the ground. Litterfall, however, is accessible on the snow surface, but it is frequently covered with snow and then becomes non-available to deer (Ditchkoff and Servello 1998, Tremblay et al. 2005). As opposed to litterfall, windblown trees are greater in size and may be less likely to be covered with snow. Unlike the foreseeable temporal variations in the availability of understory vegetation, litterfall and windblown trees are localized and stochastic events depending on windstorms (Terry et al. 2000). Those food sources are thus sparse and irregularly distributed within habitat categories (Takahashi and Kaji 2001), although their abundance may be relatively stable among years (Tremblay et al. 2005, Ward and Marcum 2005). Northern ungulates exploiting alternative food sources are thus confronted with the difficulty of predicting when and where food would be available (Takahashi and Kaji 2001). The tactic adopted by Anticosti deer was to use more intensively areas of their home range where the likelihood of finding litterfall and windblown trees was greater. These areas corresponded to open–forest edges (Ruel et al. 2000) and areas with standing trees including a high biomass of browse, even if most of it was out of reach (Terry et al. 2000).

MANAGEMENT IMPLICATIONS

Our results demonstrate the high plasticity of deer behavior, as they coped with food shortages by adjusting their habitat selection in response to the abundance and distribution of 3 different sources of forage. Our work is relevant for the management of overabundant populations because the strong association between alternative food sources and deer space use could be a mechanism enhancing winter survival, and thus, maintaining high population densities in overbrowsed landscapes. Consequently, we encourage managers to consider the abundance of litterfall and windblown trees when evaluating carrying capacity of forest stands. In the much larger context of species–habitat relationships, our findings also highlight how the habitat of species is dynamic in space and time. We showed that access to winter forage depended not only on woody browse abundance, but also on stochastic events such as strong winds or compacted snow on the ground. We suggest integrating temporal variations in meteorological conditions when examining plant–herbivore interactions and developing management strategies because meteorological conditions are linked to foraging costs but also benefits (i.e., windthrows and access to browse that were previously out of reach). This could be achieved by modeling snow-burial (White et al. 2009) and windthrow dynamics (Ruel et al. 2000, Ruel et al. 2001). Further research on habitat selection by northern ungulates should investigate how the distribution of woody browse and alternative food sources influence daily movements and search patterns. These relationships should be investigated in ecosystems with and without predation, as

linear features favoring litterfall and windblown trees are also associated with greater risk of predation (Bergman et al. 2006).

ACKNOWLEDGMENTS

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