

HABITAT SELECTION OF A LARGE HERBIVORE AT HIGH DENSITY AND WITHOUT PREDATION: TRADE-OFF BETWEEN FORAGE AND COVER?

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Although herbivores are generally known to trade off forage in open habitat patches and cover in forested habitat patches, it remains unclear if high population density and low predation risk can modulate the trade-off between forage and cover. We studied a population of white-tailed deer (*Odocoileus virginianus*) that was at high density and on a large island free of predators to assess the influence of forage and cover on habitat selection under harsh environmental conditions. We fitted 19 female white-tailed deer with global positioning system collars and delineated summer home ranges and core areas. We sampled vegetation in the core areas and in the rest of the home ranges to determine abundance of forage and forest cover within habitat patches, and assessed habitat selection between open and forested habitat patches. At a coarse scale, white-tailed deer preferred open habitat patches over forested ones, suggesting that they adopted a foraging strategy favoring energy intake. At a fine scale, habitat selection was influenced positively by the percentage of ground cover of forbs and deciduous shrubs, but negatively by conifer density. The biomass of preferred plant species, lateral cover, fir regeneration, and distance to the nearest open-forest edge were not strong predictors of habitat selection by deer. We conclude that fine-scale habitat selection by white-tailed deer at high population density and in the absence of predation is mainly determined by forage abundance. These patterns of habitat selection demonstrate that herbivores can adjust their behavior to other limiting factors when predation risk is relaxed.

Key words: behavioral plasticity, browsing, foraging, limiting factors, *Odocoileus virginianus*

Habitat selection can be viewed as a hierarchical process (Johnson 1980), where animals minimize exposure to factors limiting individual fitness at different spatial and temporal scales (Rettie and Messier 2000). The distribution of resources, foraging costs, and predation risk may vary with scale, thereby influencing patterns of habitat selection (Johnson et al. 2001). Decisions made at coarse scales constrain those made at finer scales (Senft 1987), which may result in a trade-off between minimizing exposure to limiting factors and maximizing energy gain at a fine scale (Dussault et al. 2005; Festa-Bianchet 1988).

In prey species, the most common trade-off occurs between access to foraging sites and exposure to predation risk (Verdolin 2006). Therefore, habitat selection is determined not only by abundance and quality of forage (Bowyer et al.

1998), but also cover (Dussault et al. 2005; Myrsetrud and Østbye 1999). Vertical cover is composed of deciduous and coniferous overstories that reduce exposure to adverse climatic conditions (Ager et al. 2003; Myrsetrud and Østbye 1999), whereas lateral cover decreases predation risk by reducing prey detectability (Tufto et al. 1996). Because shading by cover reduces the abundance of understory plants (Johnson et al. 1995), the most open and productive habitats are generally the most risky. Individuals must therefore trade off risks with benefits while foraging in open and productive habitats (Lima and Dill 1990). Several studies have reported selection by ungulates of feeding sites located at the edge of open and forested habitats that provide protective cover (Tufto et al. 1996; Williamson and Hirth 1985).

Animals may adopt different behaviors in response to changing environmental conditions (Komers 1997). For example, in the absence of predators, we might expect the trade-off between forage and cover to be less important. In support of this hypothesis, large herbivores at low predation risk reduce time spent vigilant (Laundré et al. 2001; Wolff and Van Horn 2003) and use habitats that are normally avoided

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under high predation risk (Mao et al. 2005). On the other hand, ungulates also may maintain antipredator behavior in absence of natural predators (Byers 1997). Roe deer (*Capreolus capreolus*), for example, continue to prefer habitats with high lateral cover in the absence of predators (Tufto et al. 1996).

Population density also may modulate the need to trade off forage and cover (Mysterud and Østbye 1999). At high population density, deer have strong negative impacts on forest vegetation (reviewed in Côté et al. 2004). Decreased abundance of preferred plant species and increased intraspecific competition may lead to changes in foraging behavior and space use of deer (Clutton-Brock et al. 1987). For example, increased competition and low abundance of forage can induce ungulates to spend more time outside protective cover (White et al. 2001). Although it was suggested that high population density and low predation risk can modulate the trade-off between forage and cover (Mysterud and Østbye 1999), little information is available on habitat selection by ungulates concomitantly experiencing these 2 extreme environmental conditions.

The objective of this study was to assess the influence of forage and cover on habitat selection of a large herbivore in the context of high population density and absence of predators. We examined summer habitat selection of white-tailed deer (*Odocoileus virginianus*) females using global positioning system telemetry in a population located at the northern fringe of the species' distribution. The study area lacked predators and the deer population was at high density (>20 deer/km² locally—Potvin and Breton 2005). Under such environmental conditions, we hypothesized that habitat selection by deer within the home range, the 3rd order of selection according to Johnson (1980), should be primarily influenced by abundance of forage among and within habitat patches. At a coarse scale within the home range, we predicted that deer would prefer open habitat patches over forested ones because open habitats are more productive. At a fine scale, we predicted that deer would select specific plant communities within habitat patches where forage abundance is relatively high even though protective cover might be limited.

MATERIALS AND METHODS

Study area.—Anticosti is a 7,943-km² island located in the Gulf of St. Lawrence, Québec, Canada (49°28'N, 63°00'W), at the northern fringe of the distribution of white-tailed deer in North America. In 1896–1897, approximately 220 deer were introduced on Anticosti Island where, in absence of predators, the population increased rapidly to $>100,000$ (currently >20 deer/km² locally—Potvin and Breton 2005). High levels of browsing and overuse of woody plants have occurred across the entire island, and at present the shrub layer is almost entirely absent and many of the most palatable species of woody plants are nearly absent (Tremblay et al. 2005). The hunting season lasts from 1 September to 25 December and $<8\%$ of the deer population is harvested annually (Simard et al. 2008). The climate on Anticosti Island is maritime and

characterized by cool summers and mild, long winters. Mean air temperature is 16°C in July and -11°C in January (Environment Canada 2006). Snowfall averages 406 cm annually, and rainfall averages 63 cm (Environment Canada 1982). Anticosti Island is dominated by 2 contrasting habitat patches: coniferous forests and open habitat patches. Forests are dominated by balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*P. mariana*), whereas deciduous tree species, that is, paper birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and balsam poplar (*P. balsamifera*), are irregularly found on the island. Natural disturbances such as windfalls and insect outbreaks have created numerous small openings <2 ha in the canopy throughout the forest. Open habitat patches include large ombrotrophic peatlands (bogs), dominated by *Sphagnum* mosses and ericaceous shrubs; minerotrophic peatlands (fens), dominated by sedges, herbs, and brown mosses; and clear-cuts resulting from commercial logging since 1995.

White-tailed deer monitoring.—We monitored 19 free-ranging adult female white-tailed deer (aged ≥ 2 years) using GPS 2200R and GPS 3000 collars (Lotek Engineering, Newmarket, Ontario, Canada) between July and November 2001 ($n = 8$) and 2002 ($n = 11$). Deer were captured in late June or early July in peatlands within 500 m of a clear-cut with a net-gun fired from a helicopter. Handling time was <5 min and deer were released at the location of capture. Global positioning system collars were programmed to record a location every 2 h, and they were equipped with a time delay drop-off for retrieving collars without recapturing animals. We used field trials with 7 stationary collars distributed in open and forest habitats to determine location success and error. All animal capture and handling protocols adhered to guidelines recommended by the American Society of Mammalogists (Gannon et al. 2007), and also complied with the current laws and regulations in Québec, Canada.

Home range and core-areas delineation.—Global positioning system collars that dropped from the study animals were located for retrieval of deer locations in November 2001 and November 2002. We used the minimum convex polygon method (Mohr 1947), with 95% of the locations to delineate home ranges to assess habitat availability during the snow-free period from 1 July to 10 November 2001 and 2002. We visually examined an incremental plot of minimum convex polygons against proportions of locations to choose the percentage of locations to use to determine core areas (Kenward 1987). We used clusters with the nearest-neighbor joining method and 80% of the locations 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 rest of the home range. Home ranges and core areas were calculated using the program RANGES V (Kenward and Hodder 1996).

Habitat description.—We used 1:20,000 forest maps from the Ministère des Ressources naturelles du Québec to describe habitats available to deer at the coarser scale (habitat patches). These maps comprised a series of variables describing tree and

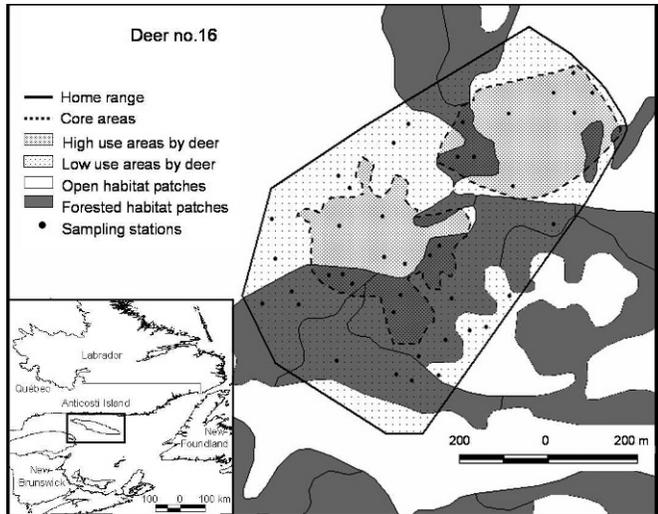


FIG. 1.—Example of the sampling design to characterize plant communities within habitat patches used by white-tailed deer (*Odocoileus virginianus*). Habitat variables were surveyed at 769 sampling stations distributed randomly in the high-use areas and low-use areas of the home ranges of 19 adult female white-tailed deer during the summers of 2002 and 2003 on Anticosti Island, Québec, Canada.

shrub strata in each vegetation association (e.g., tree species, density, and height). Maps were produced by delineating forest stands and other distinct habitat patches from 1:15,000 aerial photographs taken in 1997. Minimum polygon size varied from 2 ha for commercially unproductive areas to 8 ha for forest stands. We grouped all coniferous cover types as suggested by Dussault et al. (2001a).

We conducted field surveys to describe areas used by deer at a fine scale (within habitat patches). Field surveys were performed in July and August 2002 and 2003 for deer that were monitored during the summers of 2001 ($n = 8$) and 2002 ($n = 11$), respectively. We surveyed the vegetation in each home range using a split-split plot design (Littell et al. 2002) with 2 levels of use by deer (high versus low use), and 2 habitat types (open and forested) based on forest maps. We randomly distributed 40 sampling stations in each home range with 10 sampling stations in every combination of level of use and habitat type (i.e., high use–open, high use–forested, low use–open, and low use–forested). The forested habitat patches included diverse forest stand polygons, whereas the open habitat patches included clear-cuts and peatlands. The number of sampling stations within each habitat patch was proportional to the size of the polygon (Fig. 1). We surveyed a total of 769 sampling stations, and the minimum distance between adjacent stations averaged 56 ± 4 m.

At each sampling station, we measured several habitat variables to assess abundance of forage and cover, as well as interspersions between forage and cover. We assessed abundance of forage by visually estimating percent ground cover (<1%, 1–5%, 10% classes up to 95%, 95–99%, and 100%) of forbs, shrubs, and ericaceous species (species level) as well as sedges and grasses (order level). We estimated ground cover

of forbs, sedges, and grasses in a 1×1 -m plot. We estimated aboveground dry biomass (g/m^2) for the most important forage species to deer in summer and fall on Anticosti Island (balsam fir, bunchberry [*Cornus canadensis*], fireweed [*Epilobium angustifolium*], gold-thread [*Coptis groenlandica*], hairy raspberry [*Rubus pubescens*], hawkweed [*Hieracium*], northern starflower [*Trientalis borealis*], paper birch, raspberry [*R. idaeus*], and wild lily-of-the-valley [*Maianthemum canadense*])—Huot 1982). We harvested the aboveground portion of these preferred plant species in subplots and used linear regressions predicting plant biomass using ground cover and height of each plant species (see Tremblay et al. [2006] for details). We estimated the percentage ground cover of deciduous shrubs <4 m tall, balsam fir regeneration <7 m tall, and ericaceous species in a 1×10 -m plot in the forested habitat patches, and in a 1×5 -m plot in the open habitat patches. We summed the dry biomass of all preferred plants and pooled the percent ground cover of all forbs and of all deciduous shrubs and ericaceous species for the analyses.

We determined the composition of the tree layer by estimating the basal area (m^2/ha) of trees with a prism, by species (Grosenbaugh 1952). We also measured the diameter at breast height (DBH) of all trees selected by the prism and calculated stem density (stems/ha) by species for trees with $\text{DBH} \geq 9$ cm (Grosenbaugh 1952). We summed the stem density of all coniferous species for the analyses. We estimated canopy closure (%) by counting the number of points that were covered by the canopy of trees >7 m tall at 1-m intervals along a 20-m transect oriented east–west and centered on the sampling station (Vales and Bunnell 1988). We estimated lateral cover by measuring lateral visibility (m) along a transect oriented north–south. This was done by noting the distance in meters (up to 25 m) at which a person wearing an orange vest and walking straight forward disappeared from the view of an observer standing in the center of the sampling station (Lesage et al. 2002). Finally, we assessed the interspersions between forage and cover at each sampling station in 2 ways. First, we measured the minimum distance (m) between the center of the sampling station and the nearest open–forest edge using ArcView (version 3.2—Environmental Systems Research Institute 1999). Second, for every sampling station in the forest habitat patches, we recorded if the center of the station was in a canopy opening (≥ 15 m in diameter) or under continuous canopy cover.

Data analyses.—For analysis at the habitat-patch scale, we tested for a functional response in habitat use determined by a variation in relative use with changing availability of 1 of 2 main habitat patches (Myerud and Ims 1998). This approach is applicable to animals with well-defined home ranges encompassing 2 main different habitats and is useful to illustrate situations when individuals experience a trade-off (Myerud and Ims 1998). Anticosti Island is dominated by 2 contrasting habitat patches, which are coniferous forests and open habitats (including both clear-cuts and peatlands). We considered the proportion of coniferous forests and open habitats within the home range as the habitat availability and

the proportion of global positioning system locations in each habitat patch as habitat use. We used a logistic regression to examine the relationship between proportional use against proportional availability of open habitats (Mysterud and Ims 1998). The analysis was performed in SAS (PROC LOGISTIC, version 9.1—SAS Institute Inc. 2002) and model fit was assessed by measuring the area under the receiver operating characteristic curve (Hosmer and Lemeshow 2000).

For analysis within habitat patches, we compared 8 habitat variables measured in the field between high-use and low-use areas. We used logistic regressions to model the probability of intensive use by adult female white-tailed deer. We used conditional logistic regressions (PROC LOGISTIC with STRATA statement—SAS Institute Inc. 2002) because we had paired data for each deer, that is, high-use sampling stations versus low-use sampling stations (Hosmer and Lemeshow 2000). We used an information theoretic approach (Burnham and Anderson 2002) to choose which of the variables measured in the field best predicted intensive use by deer. We tested 20 a priori candidate models and the null model. Candidate models included explanatory variables describing forage, cover, proximity to edges between forage and cover, and a combination of these features. To avoid overparameterization of the models, we did not test for interactions between explanatory variables. We ranked candidate models using the Akaike's information criterion for small sample sizes (AIC_c) and calculated ΔAIC_c , AIC_c weights (ω_i), and evidence ratios between pairs of models (Burnham and Anderson 2002). Models with $\Delta AIC_c \leq 2$ were considered equivalent (Burnham and Anderson 2002). Before the information theoretic analysis, we verified that there was no significant correlation between explanatory variables using the multicollinearity diagnostic statistics produced by linear regression analysis (PROC REG [SAS Institute Inc. 2002]—Allison 1999). We removed any variable with a tolerance value <0.4 (Allison 1999). We assessed the predictive performance of the most-parsimonious model by calculating for each deer the percentage of correct predictions compared to what was observed (e.g., high use versus 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%.

There were different plant communities or tree assemblages within forested and open habitat patches. Because we were interested in testing habitat selection within habitat patches while accounting for different plant and tree groups, we defined a posteriori 7 microhabitat categories based on field surveys: balsam fir, black spruce, and white spruce forests; clear-cuts; bogs; fens; and the transition zone between forests and peatlands (lagg ecotone). For each home range, the number of sampling stations within each microhabitat depended on its availability in the high-use and low-use areas of the home range, and thus of its selection by deer. We used the number of high-use sampling stations versus the number of low-use sampling stations within each microhabitat as a

surrogate of deer use. For example, when the number of sampling stations in a microhabitat was similar in high- and low-use areas, we concluded that the use of that microhabitat was proportional to its availability in the home range. If the number of sampling stations in a microhabitat was significantly greater in high-use areas than in low-use areas, we concluded that deer selected this microhabitat. We examined the distribution of high-use and low-use sampling stations among microhabitat categories using goodness-of-fit G -tests.

Once we had selected the best model predicting intensive use by deer, we assessed the effect of the microhabitat on each explanatory variable included in the model using a linear mixed model in a split-split plot design that involved 2 levels of use by deer (high versus low use), 2 habitat types (open and forested), and 7 microhabitat categories nested in a habitat type (forested habitats: balsam fir, black spruce, and white spruce forests; open habitats: fen, bog, lagg ecotone, and clear-cuts [PROC MIXED—SAS Institute Inc. 2002]). We also used a linear mixed model to assess the interspersed between forage and cover within forested habitat patches. This analysis involved 2 levels of use by deer (high use and low use), 3 microhabitats (balsam fir, black spruce, and white spruce), and 2 cover types (canopy opening and continuous cover) nested in a microhabitat. For all linear mixed models, we included "deer identity" nested in "year" as a random factor. All linear mixed models were followed by pairwise comparisons using the LSMEANS statements of SAS Institute Inc. (2002). We ensured that all residuals were normally distributed and applied square-root transformation to variables when necessary (Zar 1999). Unless specified, all results are presented as means $\pm SE$.

RESULTS

We recorded a total of 18,507 locations from 1 July to 10 November 2001 and 2002 with a mean of 974 ± 64 locations per deer (range: 423–1,324 locations). Each location was indexed with a dilution of precision value indicating the quality of the satellite geometry (Trimble Navigation Limited 1996). We discarded 7% of the global positioning system locations because their dilution of precision value was >10 , indicating relatively high location error (Dussault et al. 2001b). Location success based on field trials using 7 stationary collars was 99% in open and 94% in forested habitat patches ($n = 5,806$ locations). Mean location error was 23 ± 1 m, but 54% of locations were accurate to within 10 m, and 90% of the locations were accurate to 32 m. Mean summer home-range size was 42 ± 6 ha (range: 13–107 ha) and the mean size of total core areas was 10 ± 1 ha (range: 4–21 ha; $n = 19$).

Habitat selection at the habitat-patch scale.—The intercept of the regression of the proportion of locations in open habitats versus the proportion of open habitats available was significantly higher than 0 ($\beta_0 = 0.56 \pm 0.10$; 95% confidence interval [95% CI] = [0.35, 0.76]; Wald statistic = 28.2; $P < 0.0001$), suggesting that deer preferred open to forested habitat

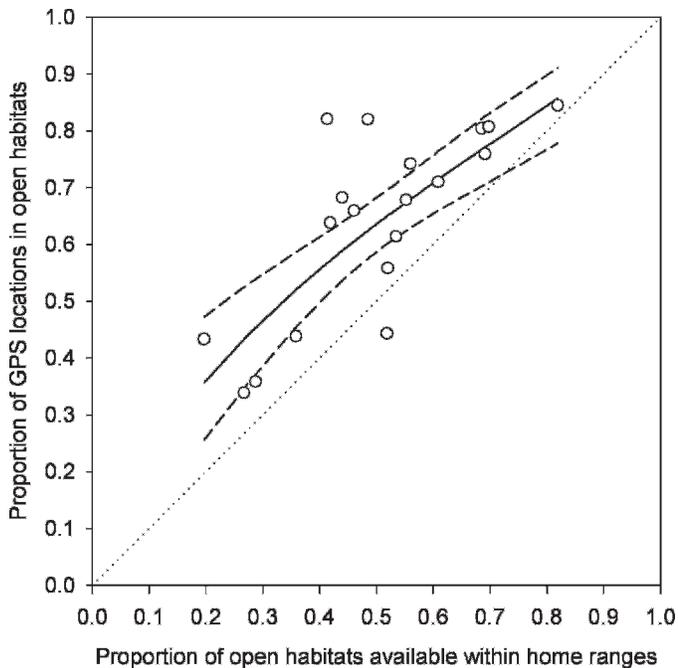


FIG. 2.—Proportional use against proportional availability of open habitat patches within the summer home ranges of 19 female white-tailed deer (*Odocoileus virginianus*) on Anticosti Island, Québec, Canada. The dotted line is the reference slope and indicates the relation when there is no selection. The regression line shows predicted values of the logistic regression equation $\text{logit}(\text{proportion used}) = 0.56 + 0.82[\text{logit}(\text{proportion available})]$ and dashed lines show the 95% confidence interval (CI). Selection for open habitat patches is inferred when the lower 95% CI exceeds the reference slope.

patches. Selection for open habitats occurred when the proportion of open habitats available was <70% (Fig. 2). On the other hand, there was a significant decrease in the selection for open habitats as the availability of open areas within home ranges increased (i.e., regression slope was positive but lower than 1; $\beta_1 = 0.82 \pm 0.16$; 95% CI = [0.50, 1.13]; Wald statistic = 25.4; $P < 0.0001$).

Habitat selection within habitat patches.—The best model discriminating high- from low-use areas achieved 58% correct predictions and had 3 times the weight of the next model (Table 1). Although the probability to be the best model was only 0.57 (Table 1), the sums of the weights for each of the explanatory variables were 0.91, 0.90, and 0.83 for coniferous density, forbs, and deciduous shrubs, respectively. Moreover, “deciduous shrubs” was in 7 of the 9 top models, whereas “forbs” was in 8 of the top 9 models and “coniferous density” was in the 4 top models, indicating the relatively high importance of these variables in explaining habitat selection within habitat patches. Deer intensively used areas where percent ground cover of forbs and deciduous shrubs was higher and density of coniferous trees was lower than in the rest of the home range (Table 2). A 10% increase in percent ground cover of forbs and deciduous shrubs resulted in a 12% increase in the probability of high use by deer. An increase in coniferous density of 100 stems/ha resulted in a 4% decrease

in the probability of high use by deer (Table 2). Although lateral cover was included in the 2nd-best model, it had a moderate relative importance (sums of $\omega_i = 0.25$). The biomass of preferred plant species, canopy closure, fir regeneration, and the distance to the nearest open-forest edge also were in 1 or 2 of the 9 top models but the weights of evidence were <0.1 (Table 1).

The distribution of the sampling stations in forested and open habitat patches depended on the microhabitat (forest habitats: $G = 24.8$, $d.f. = 1$, $P < 0.0001$; open habitats: $G = 63.9$, $d.f. = 3$, $P < 0.0001$). In open habitat patches, 79% of the sampling stations in bogs were in low-use areas, whereas 79% of the sampling stations in ecotones were in high-use areas. In forests, 69% of the sampling stations under continuous cover were in low-use areas. Although the proportion of sampling stations was higher in high-use areas than in low-use areas for forest canopy openings (57%), fens (56%), and clear-cuts (56%), their distribution did not differ from 50% (all P -values > 0.05).

Percent ground cover of forbs varied among the 7 microhabitat categories (Table 3a), and deer had access to 19% more forbs in fens and in lagg ecotones than in any other microhabitat (Fig. 3a). Deciduous shrubs were found principally in bogs, fens, and ecotones compared to other microhabitats (Table 3a; Fig. 3b). Ecotones and fens were again the most productive microhabitats, with percent cover of deciduous shrubs about 35% higher in these microhabitats than elsewhere (Fig. 3b). When restricting comparisons to forests, we found that percent ground cover of forbs was 14% higher in canopy openings than under continuous cover (Table 3b; Fig. 4). Percent ground cover of deciduous shrubs did not differ significantly between canopy openings and forest areas with continuous cover (Table 3b).

DISCUSSION

Our results support the hypothesis that habitat selection by white-tailed deer within the home range is primarily influenced by forage abundance among and within habitat patches. These findings suggest that at high density and in the absence of predators, habitat selection by white-tailed deer is driven mainly by forage acquisition rather than a trade-off between forage intake and proximity to protective cover.

Habitat selection at the habitat-patch scale.—Density of white-tailed deer on Anticosti Island is high (>20 deer/km²) and females preferred more-productive open habitats over forested ones, suggesting that they adopted a foraging strategy favoring energy intake when selecting habitat patches. Moreover, by spending more time in the most productive habitats, individual deer may be able to reduce competition for forage. This pattern also was observed in another population of white-tailed deer and in roe deer, where preference for woodlands decreased at high population density (Nilsen et al. 2004; Rouleau et al. 2002).

Our results also revealed that when the availability of open habitats exceeded 70% of the home range, deer were not

TABLE 1.—Logistic regression models explaining summer habitat selection of female white-tailed deer (*Odocoileus virginianus*) within habitat patches on Anticosti Island, Québec, Canada. For each model, differences in Akaike’s information criterion for small sample sizes (AIC_c) are compared to the lowest-scoring model (ΔAIC_c), and AIC_c weights (ω_i) are given.

Models	AIC _c	ΔAIC _c	ω _i
Forbs + deciduous shrubs + coniferous density	945.30	0.00	0.57
Forbs + deciduous shrubs + coniferous density + lateral cover	947.61	2.31	0.18
Forage biomass + coniferous density	948.90	3.60	0.09
Forbs + coniferous density + lateral cover	949.68	4.38	0.06
Forbs + deciduous shrubs	950.64	5.34	0.04
Forbs + deciduous shrubs + fir regeneration	951.94	6.64	0.02
Forbs + deciduous shrubs + edge	953.29	7.99	0.01
Forbs + deciduous shrubs + canopy closure	953.36	8.06	0.01
Forbs + deciduous shrubs + canopy closure + lateral cover	955.30	10.00	0.00
Forbs + edge	957.99	12.69	0.00
Forbs	958.50	13.20	0.00
Forbs + canopy closure	958.74	13.44	0.00
Forbs + lateral cover	959.94	14.64	0.00
Forbs + canopy closure + lateral cover	960.66	15.36	0.00
Forbs + canopy closure + lateral cover + edge	962.23	16.93	0.00
Forage biomass + canopy closure	965.03	19.73	0.00
Forage biomass + canopy closure + lateral cover	967.66	22.36	0.00
Forage biomass	976.11	30.81	0.00
Forage biomass + lateral cover	978.36	33.06	0.00
Edge	979.83	35.21	0.00
Null model	985.14	39.84	0.00

selecting open or forested habitats. Such a decrease in the preference of open over forested habitats suggests that above a certain threshold, deer do not need to stay in the more-productive open habitats to forage. By analyzing only use versus availability ratios, we would have missed that the preference for open habitats was conditioned on availability. If we seek to fully understand variations in habitat choice across individuals of the same species, we agree with Mysterud and Ims (1998) that habitat selection analysis should not assume that habitat use and availability are directly proportional.

Habitat selection within habitat patches.—The distribution of resources within habitat is generally not homogeneous (Schooley 2006). Small-scale variations in the abundance of forage and cover can influence space use by ungulates if they concentrate their activities in areas where abundance of forage is the highest (Bowyer et al. 1999; Johnson et al. 2001). As predicted, we demonstrated that habitat selection by adult female white-tailed deer at a fine scale was influenced positively by abundance of forage, and more specifically by the percentage of ground cover of forbs and deciduous shrubs. Surprisingly, the biomass of plant species preferred by deer was not included in the best model predicting habitat selection. Deer have modified the forest understory of

Anticosti Island (Potvin et al. 2003; Tremblay et al. 2005) and the abundance of preferred plant species has been strongly reduced (Boucher et al. 2004). Under these difficult conditions of long-term overbrowsing (Simard et al. 2008), deer likely have to forage on every palatable plant species, possibly explaining why biomass of preferred plant species was not helpful in explaining habitat selection at the fine scale. Similarly, white-tailed deer at high density in agricultural landscapes could not compensate for the scarcity of preferred plant forage in the forests by increasing foraging time, and had to feed on cultivated crops (Rouleau et al. 2002). As for the use of cultivated fields in agricultural landscapes, white-tailed deer on Anticosti Island intensively used ecotones and fens and benefited from the relatively high abundance of forbs and deciduous shrubs in these open habitats. This finding was consistent with the results of Pellerin et al. (2006), who showed that deer impacts were low in bogs of Anticosti Island compared to fens. To our knowledge, our study is the 1st to report selection for ecotones and fens by white-tailed deer in summer. However, Clark and Gilbert (1982) suggested that the use of ecotones might increase in areas with high densities of deer because ecotones are characterized by a high diversity of plant species, therefore partly compensating for the scarcity of

TABLE 2.—Parameter estimates (β) for the best model that predicted summer habitat selection within habitat patches by female white-tailed deer (*Odocoileus virginianus*) on Anticosti Island, Québec, Canada.

Explanatory variables	β	SE	95% CI		Odds ratio
Forbs	0.011	0.003	0.005	0.016	1.011
Deciduous shrubs	0.011	0.005	0.001	0.022	1.011
Coniferous density	-0.0004	0.0001	-0.0007	-0.0001	1.000

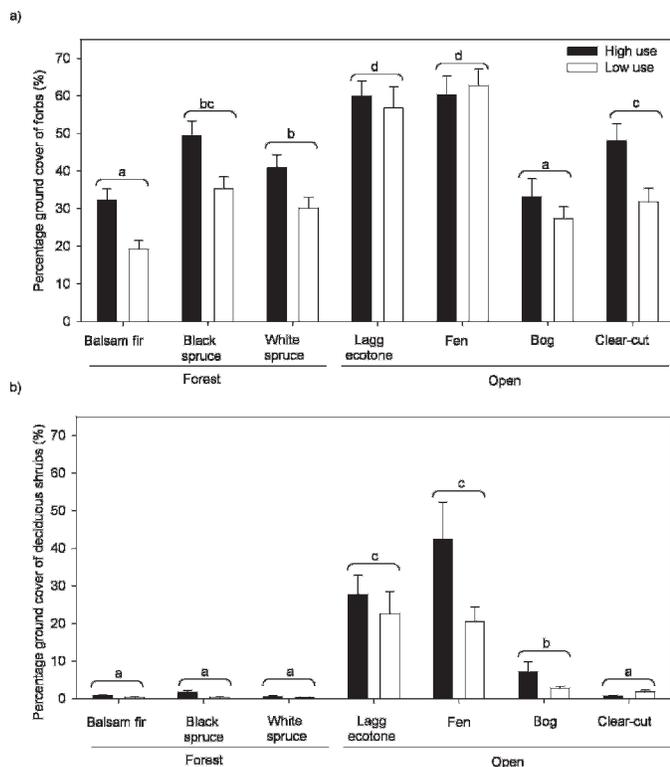


FIG. 3.—Percentage ground cover of a) forbs and b) deciduous shrubs in 7 microhabitat categories in high-use and low-use areas of the home ranges of 19 female white-tailed deer (*Odocoileus virginianus*) during summer on Anticosti Island, Québec, Canada. Least squares means \pm SE of the interaction between use and microhabitats are presented but comparisons were performed between the 7 microhabitat categories. Identical letters indicate that mean percent cover did not differ statistically between microhabitat categories.

preferred forage. Our results also were in accordance with principles from the ideal free distribution theory (Fretwell and Lucas 1969); under conditions of increasing population density and reduced forage quality (Simard et al. 2008), deer increased their use of marginal habitats (ecotones and fens).

In many ungulates, vertical cover influences space use because it offers protection from thermal stress (Mysterud and Østbye 1999). However, in comparison to other cervids such as moose (*Alces alces*) and black-tailed deer (*Odocoileus hemionus*), the thermal cover requirements for white-tailed deer are low during summer (Demarchi and Bunnell 1993). For example, when air temperature is around 30°C, white-tailed deer require a canopy closure of 56–65% to prevent thermal stress (Demarchi and Bunnell 1993), a range similar to what has been measured in canopy openings of the forests of Anticosti Island ($\bar{X} = 55\% \pm 1\%$; $n = 341$). Moreover, maximal air temperature on Anticosti Island was always below 30°C during our study (Environment Canada 2006), suggesting that thermal stress is likely not a limiting factor for habitat selection during summer. During winter, however, high canopy closure offers both thermal and snow cover, and thus could become an important variable positively influencing habitat selection by northern cervids (Sabine et al. 2001).

Trade-off between forage and cover.—Individuals exposed to different limiting factors should select habitat differently (Rettie and Messier 2001) and, thus, the importance of the trade-off between forage and cover may vary (Mysterud and Østbye 1999). When predators are present, the use of edges between open and forested habitats is frequently observed (e.g., in birds [Walther and Gosler 2001], cervids [Lyon and Jensen 1980], and lagomorphs [Banks et al. 1999]) because individuals can maximize energy intake in these habitats while being close to protective cover. However, individuals also may use the center of open habitats away from cover when these habitats offer abundant and preferred forage (e.g., deer [Williamson and Hirth 1985] and rodents [Kotler and Blaustein 1995]). There are no predators on Anticosti Island and hunting pressure for females is <4% (Simard et al. 2008). Under such conditions, we found that the distance to the nearest open–forest edge was not an important variable depicting habitat selection at a fine scale. Moreover, heavy deer browsing on fir seedlings has been previously observed in the center of large clear-cuts on Anticosti Island (Potvin et al. 2003) and elsewhere in North America (Reyes and Vasseur 2003). Similarly, at high population density of moose, browsing activity in clear-cuts was independent of the distance to open–forest edges (Andrén and Angelstam 1993), and elk (*Cervus elaphus*) shifted toward the use of edges only when wolves (*Canis lupus*) were reintroduced in Yellowstone National Park, Wyoming (Hernández and Laundré 2005). Although nonlethal effects of predators may influence behavior of prey (Brown et al. 1999), our results suggest that preference for open–forest edges may be reduced when predation is absent and deer density is high.

Trade-offs between forage and cover occur when benefits and costs are positively correlated (Bowyer et al. 1998). In contrast, individuals are not confronted with a trade-off when the best forage species also provide lateral cover (Pierce et al. 2004). Lateral cover is usually higher in forests than in open habitats and it positively influences space use of cervids, even in predator-free environments (Tufto et al. 1996). Interestingly, lateral cover is relatively low in open habitats as well as in the forests of Anticosti Island because the shrub layer is almost absent (Tremblay et al. 2005). Furthermore, trade-offs between open and forested habitats at a coarse scale may be less important when forage and cover are interspersed at a fine scale (Kremsater and Bunnell 1992), such as in canopy openings of forests (Parker et al. 1999) and ecotones of peatlands. Therefore, our results illustrate the importance of considering microhabitat characteristics when studying habitat selection at a fine scale (Bowyer et al. 1999).

Deer living on Anticosti Island live at the extreme of a continuum of environmental conditions with high population density and the complete absence of predators. Under these conditions, intraspecific competition for forage is likely the most important factor limiting individual fitness. During summer, white-tailed deer on Anticosti Island adopted a habitat-selection pattern favoring forage acquisition (Van der Wal et al. 2000). Our study demonstrates that large herbivores

TABLE 3.—Variations in the percentage of cover of forbs and deciduous shrubs in home ranges of female white-tailed deer (*Odocoileus virginianus*) during summer on Anticosti Island, Québec, Canada. The split-split plot design a) involved 2 levels of use by deer (high versus low use) based on home-range core areas, 2 habitat patches (open and forested), and 7 microhabitat categories nested in a habitat patch (forested habitats: balsam fir, black spruce, and white spruce stands; open habitats: fen, bog, ecotone, and clear-cuts). The split plot design b) involved 2 levels of use by deer (high versus low use) based on home-range core areas, 3 microhabitats (balsam fir, black spruce, and white spruce), and 2 cover types (canopy opening and continuous cover) nested in a microhabitat.

Explanatory variables	Effects	<i>d.f.</i>	<i>F</i>	<i>Pr > F</i>
a) Split-split plot				
Forbs	Use (high versus low)	1, 18	7.16	0.02
	Habitat (open versus forested)	1, 36	11.62	0.002
	Use × habitat	1, 36	1.24	0.3
	Microhabitat(habitat)	5, 74	5.21	0.0004
	Use × microhabitat(habitat)	5, 74	0.39	0.9
Deciduous shrubs	Use (high versus low)	1, 17	6.68	0.02
	Habitat (open versus forested)	1, 20	113.41	<0.0001
	Use × habitat	1, 20	2.56	0.1
	Microhabitat(habitat)	5, 30	14.96	<0.0001
	Use × microhabitat(habitat)	5, 30	1.20	0.3
b) Split plot				
Forbs	Use (high versus low)	1, 18	3.65	0.07
	Microhabitat	2, 40	2.09	0.1
	Use × microhabitat	2, 40	0.41	0.7
	Forest cover type(microhabitat)	3, 40	9.37	<0.0001
	Use × forest cover type(microhabitat)	3, 40	2.22	0.1
Deciduous shrubs	Use (high versus low)	1, 7	4.21	0.08
	Microhabitat	2, 7	1.30	0.3
	Use × microhabitat	2, 7	0.56	0.6
	Forest cover type(microhabitat)	2, 5	1.05	0.4
	Use × forest cover type(microhabitat)	2, 5	2.08	0.2

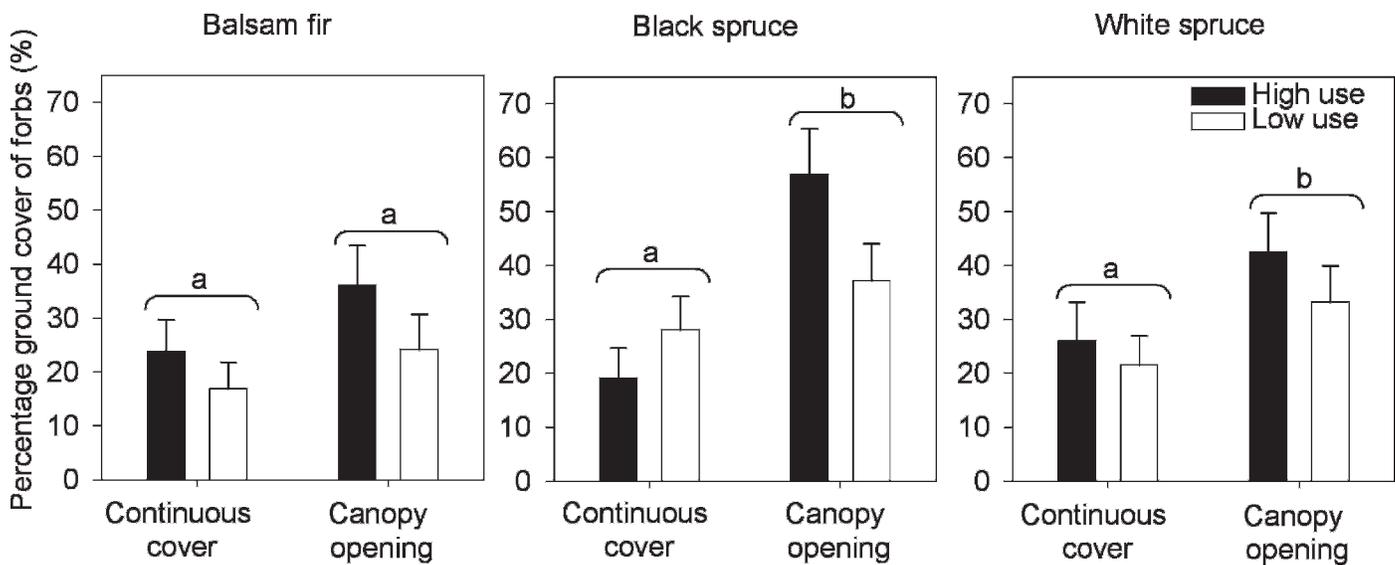


FIG. 4.—Percentage ground cover of forbs in canopy openings and under continuous cover for balsam fir, black spruce, and white spruce microhabitats in high-use and low-use areas of the home ranges of 19 female white-tailed deer (*Odocoileus virginianus*) during summer on Anticosti Island, Québec, Canada. Least squares means ± *SE* of the interaction between use and cover type nested within microhabitat are presented but comparisons were performed between the 2 cover types. Identical letters identify mean percent cover that did not differ statistically between 2 cover types.

are able to adjust their patterns of habitat selection and behavior when common limiting factors such as predation and thermal stress are absent or reduced.

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