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Management and Conservation

Influence of Habitat Features and Hunter Behavior on White-Tailed Deer Harvest

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ABSTRACT Sport hunting may help in controlling cervid populations over large areas. As with natural predators, several environmental factors can influence sport harvest. A better understanding of the environmental variables that limit the efficiency of sport hunting could provide guidelines for more efficient wildlife management using hunting. We studied white-tailed deer (*Odocoileus virginianus*) hunting on a high deer density island where hunting was the sole form of predation. Our objective was to study the behavior of sport hunters and determine the habitat characteristics (e.g., abundance of deer forage, visibility of the deer from the hunter's point of view, and accessibility of the territory to hunters) that are associated with a successful harvest. We collected movements and harvest site location data from 477 hunters equipped with handheld Global Positioning System (GPS) units. Harvest sites were visited and characterized, along with a paired random site, to determine the environmental conditions associated with a successful hunt. We also developed a model to predict the daily number of deer seen by hunters considering weather conditions, hunter characteristics (e.g., age, experience), and date of hunting. We used the mean number of deer seen per hunter per day as a relative index of local density in each hunted territory. At both the site and landscape scales, the combination of visibility and access had a positive effect on the distribution of harvested deer. Habitat types with less visual obstruction from vegetation enabled hunters to see more deer in a given day. At the site scale, harvested deer were located in areas with a lower density of access routes compared to areas where hunters travelled throughout the day. Using an innovative approach of studying hunter behavior with GPS technology, digital maps, and questionnaires, we highlighted the factors associated with hunter success. Our study suggests that habitat characteristics could be modified to increase harvest by improving accessibility and visibility near roads. Creating openings in mature and regenerating forest near access roads could make sport hunting a more efficient management tool, but the potential impact of increased forage availability in forest openings should not be overlooked.

KEY WORDS Anticosti Island, Global Positioning System, habitat selection, hunter behavior, hunting, management tool, *Odocoileus virginianus*, white-tailed deer.

In recent decades, several regions including North America and northwestern Europe have experienced a significant increase in cervid populations and their resulting ecological impacts (Côté et al. 2004). Populations of large herbivores have benefited from the reduction or disappearance of large predators (Crête et al. 2001), increased availability of suitable habitats, reduced hunting pressure, more conservative hunting regulations, and milder winter conditions (Côté et al. 2004). High herbivore densities directly affect plant communities, and indirectly other animal species through trophic cascades (Ripple and Beschta 2003). The management of high-density herbivore populations has thus become a challenge.

To control deer populations, wildlife managers have manipulated fertility both chemically (Bradford and Hobbs 2008) and through immunocontraception (Turner et al. 1992), introduced predators (Bangs and Fritts 1996), and also used culling (Doerr et al. 2001, Gogan et al. 2001), relocation (O'Bryan and McCullough 1985), and commercial hunting (Nugent and Choquenot 2004). These methods, however, can be expensive, logistically difficult to implement (Turner et al. 1992, McCullough et al. 1997), and are not

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always socially acceptable. Sport hunting, on the other hand, is recognized as a viable alternative for managing deer populations. In addition to generating high economic returns (Brown et al. 2000, Doerr et al. 2001), it is generally considered a socially acceptable management tool (Stedman et al. 2004).

The efficiency of sport hunting, however, is limited as it may be difficult or even impossible to control deer populations in the absence of natural predators (Brown et al. 2000), particularly over large areas and if the desired reduction in deer density is high (Nugent and Choquenot 2004). Population reduction programs should also consider immigration from nearby areas and target the appropriate segments of the population (Forsyth 1999). Gogan et al. (2001) reported a successful example of exotic axis deer (*Axis axis*) and fallow deer (*Dama dama*) control in a >100-km^2 peninsula in California through a combination of sport hunting and culling. A better understanding of the factors promoting successful harvest could improve the effectiveness of hunting in controlling deer populations locally.

An interesting parallel exists between natural predators and hunters, allowing us to identify factors likely to influence hunter success (Nugent and Choquenot 2004). For natural predators, the probability of a successful attack depends on habitat features affecting prey vulnerability similarly to hunting (Kunkel and Pletscher 2000, Thogmartin and Schaeffer 2000). Variables like forest canopy and understory vegetation can influence detection probability and mobility of the prey, ultimately affecting capture success (Bergman et al. 2006, Kauffman et al. 2007). Predators may also select preferred feeding habitat types of their prey (Lima 2002) and use access roads to facilitate movements (James and Stuart-Smith 2000). Individual characteristics of the predator (e.g., age, physical condition), weather conditions, and prey density may also influence predator success (Mech and Peterson 2003).

Anticosti (Québec, Canada) is a predator-free island supporting an overabundant white-tailed deer (*Odocoileus virginianus*) population (>20 deer/km^2) that has damaged local vegetation (Tremblay et al. 2005, Côté et al. 2008). Sport hunting, the single management tool used, has little impact on the population because the harvest rate is only about 1 deer/km^2 or <5% of the population (Simard et al. 2010). However, sport hunting could potentially be used to reduce deer densities locally in places where immigration is limited (Forsyth 1999, McDonald et al. 2007).

Very little is known about hunters' behavior compared to prey (Van Deelen and Etter 2003). Our overall objective was to study the behavior of sport hunters to determine the environmental conditions that are associated with the successful harvest of game. We hypothesized that the ability of a hunter to harvest a deer should be, as with natural predators, influenced by the selected hunting areas, hunter behavior, and environmental conditions prevailing during their hunt. More specifically, we examined the relationship between habitat characteristics (i.e., abundance of deer forage, visibility of the deer from the hunter's point of view, further referred to as visibility, and land access) and the spatial distribution of kill sites, and modeled the probability of harvesting a deer during a hunting day. We also assessed how weather conditions, hunter characteristics (e.g., age and experience), deer density, and the date of hunting influenced harvest success (Nugent and Choquenot 2004).

STUDY AREA

Anticosti Island (49°28′N, 63°00′W) covers 7,943 km^2 and is located in the Gulf of St. Lawrence, Québec, Canada. The topography was relatively flat, with an average elevation of 126 m above sea level (Côté et al. 2008). The sub-boreal maritime climate was characterized by relatively long, mild winters with abundant snow precipitations (annual average = 328 cm, Environment Canada 2006). The average temperature was −11.0° C in January and 16.0° C in July (Environment Canada 2006).

Forest on the island belonged to the balsam fir (*Abies balsamea*)-white birch (*Betula papyrifera*) domain of the eastern bioclimatic region of Québec (Tremblay et al. 2005), and dominant tree species were white spruce (*Picea glauca*), balsam fir, and black spruce (*P. mariana*). Paper birch, aspen (*Populus tremuloides*), and larch (*Larix laricina*) also occurred sporadically. Various natural (e.g., insect outbreaks, fire, and windfalls) and anthropogenic (e.g., clearcuts and roads) disturbances also shaped the landscape. Following a 25-year interruption, logging has occurred in the western portion of the island since 1995.

Five outfitters held exclusive hunting rights on approximately 91% of Anticosti Island (Fig. 1). For logistical reasons, we conducted the study in 3 of these 5 areas (Fig. 1). During the first year of the study (2007), we only sampled the Lac Genevieve Outfitter (located on the west part of the island, 706 km^2). In 2008, we also sampled Sepaq Anticosti (central part, 923 km^2) and Cerf-Sau Inc. Outfitter (southeast, 485 km^2).

METHODS

Field Methods

During the 2007 and 2008 hunting seasons (1 Sep to 23 Nov), we sought the cooperation of hunters from the Lac Genevieve, Sepaq Anticosti, and Cerf-Sau Inc. Outfitters. At the beginning of each 4- or 5-day hunting trips, we met hunters in their camp to explain the project objectives, and deliver portable Global Positioning System (GPS) units (Garmin Venture HC model; Garmin International, Inc., Olathe, KS). We asked hunters to carry the GPS unit, and turn it on and off at the beginning and end of each day (Broseth and Pedersen 2000). We configured GPS units to take locations every 150 seconds. In addition, we asked hunters to record the coordinates of harvested deer when the hunter initially shot, and to complete a questionnaire at the end of each hunting day. At the end of their hunting trip, we could estimate daily active hunting time and the number of deer observed with the possibility of shooting, and obtained information relative to weather conditions prevailing during hunting, hunter age, and years of deer hunting experience.

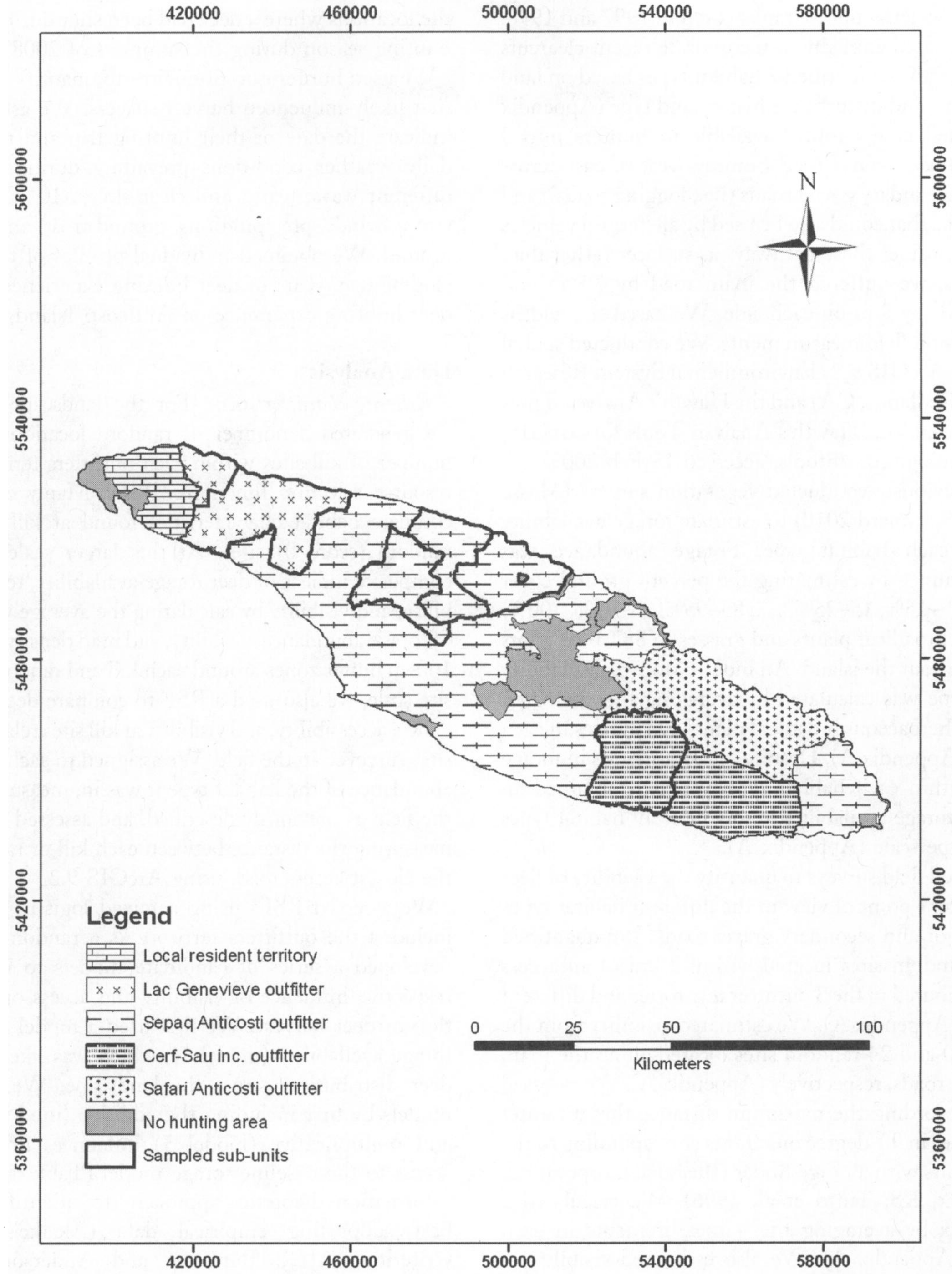

Figure 1. Distribution of the different outfitter territories on Anticosti Island, Quebec, Canada. Areas sampled in this study within outfitters territories are denoted by solid black lines. Grid coordinates are UTM NAD83.

We first determined habitat characteristics at sites where deer were shot in terms of availability of deer forage, visibility of the deer from the hunter's point of view, and accessibility for the hunter. We compared the characteristics of kill sites with that of random sites at 2 spatial scales. At the larger scale (hereafter referred to as the landscape scale), we estimated habitat characteristics from forest maps within a radius of 100 m around the observed and random locations. At the finer scale (hereafter referred to as the site scale), we measured habitat characteristics at the kill sites and random locations by conducting field surveys and using information from forest maps. We also determined habitat characteristics that affected the number of deer seen by hunters per day while taking into account weather conditions prevailing during the hunting day, individual characteristics of the hunter, the date of the hunting trip, and a local index of deer density. Finally, we assessed whether certain habitat characteristics were associated with the successful harvest of deer by comparing sites where a deer was shot and killed with sites where hunters devoted their hunting effort during that day.

We described available habitat types using forest maps at a scale of 1:20,000 from the ministère des Ressources naturelles et de la Faune du Québec that were based on interpretation of aerial photographs taken in 1997 and 1998. Maps were updated annually to incorporate recent clearcuts and access roads. We identified 7 habitat types based on land type, cover type, and disturbance history and type (Appendix A). We divided access routes available to hunters into 3 types: 1) the major gravel road running west to east across the island, 2) secondary gravel roads (i.e., logging roads), and 3) walking trails that could also be used by all-terrain vehicles (ATVs). To consider these pathways as surfaces rather than lines on maps, we buffered the main road by 7.5 m and secondary roads by 5 m on each side. We based the widths of buffer zones on field measurements. We conducted spatial analyses using ArcGIS 9.2 (Environmental System Research Institute Inc. Redlands, CA) and the Hawth's Analysis Tools for ArcGIS extension (Hawth's Analysis Tools for ArcGIS, www.spatialecology.com/htools, accessed 15 Feb 2009).

We used previously conducted vegetation surveys (Massé and Côté 2009, Simard 2010) to estimate forage availability for deer in each habitat type. Forage abundance was visually determined by estimating the percent ground cover (<1%, 1–5%, 5–15%, 15–25%, . . ., 85–95%, 95–99%, 100%) of herbaceous broadleaf plants and grasses in 882 1-m^2 plots located throughout the island. An index of forage availability per habitat type was calculated by averaging the estimated availability of herbaceous broadleaf plants and grasses in each habitat type (Appendix A). Despite local variations in forage abundance within each habitat type, we then obtained an index of deer forage availability in the different habitat types at the landscape scale (Appendix A).

We conducted field surveys to quantify the visibility of deer from the hunter's point of view in the different habitat types and along major and secondary gravel roads. We quantified visibility at random sites located within 2 km of an access road and distributed in the 3 outfitter territories and different habitat types (Appendix A). We estimated visibility from the roads using 20 and 24 random sites located along the main and secondary roads, respectively (Appendix A). We assessed visibility by recording the maximum distance that a hunter might see a deer in 90-degree quadrants corresponding to the 4 cardinal points with a range finder (Bushnell Corporation, Overland Park, KS; Tufto et al. 1996). We calculated a visibility index by averaging the 4 measurements in each sample plot (Appendix A). We also estimated visibility at the locations where a deer had been shot during the previous hunting season during the summers of 2008 and 2009.

We used hunter questionnaires to quantify other variables that likely influenced harvest success. We asked hunters to indicate the date of their hunting trip and to describe the daily weather conditions prevailing during their hunt in different ways: warm and clear sky (>10° C), presence of strong winds, precipitations, ground frost, and snow on the ground. We obtained individual profiles of the hunters including age, years of deer hunting experience, and years of deer hunting experience on Anticosti Island.

Data Analysis

Kill-site characteristics.—For the landscape-scale analysis, we generated a number of random locations equal to the number of kill sites within each outfitters territory and used resource selection functions (RSFs; Manly et al. 2002) to compare habitat characteristics found at kill (score 1) and random (score 0) sites. At this larger scale, we obtained composite indices of deer forage availability, territory accessibility, and visibility by calculating the average weighted index of forage abundance, visibility, and road density (m/ha) within 100-m buffer zones around each kill and random sites. At the site scale, we also used a RSF to compare deer forage abundance, accessibility, and visibility at kill sites relative to random sites surveyed in the field. We assigned to each site the forage abundance of the habitat type it was in, measured visibility in the field as previously described, and assessed accessibility by measuring the distance between each kill or random site and the closest access road, using ArcGIS 9.2.

We assessed RSFs using a mixed logistic regression and included the outfitters territory as a random variable. We developed a series of candidate models to investigate the respective influence of visibility and access on the distribution of deer harvest. We first used a model including only forage availability (model 1), which was likely to influence deer distribution across the landscape. We created other models by first including the additive (models 2, 3, and 4) and multiplicative (model 5) influences of visibility and access to the baseline forage model (Table 1). We used an information-theoretic approach to identify the model best supporting empirical data (Akaike's Information Criterion [AIC]; Burnham and Anderson 2002). We

Table 1. Model selection used to describe the relationship between habitat attributes in terms of deer forage abundance, visibility of the deer from the hunter's point of view, density of access roads, and spatial distribution of white-tailed deer harvested on Anticosti Island, Québec, Canada, during the 2007 and 2008 hunting seasons. Models are listed with their number of parameters including the intercept (K), difference in AIC compared to the best model (ΔAIC), and AIC weight (ω). The AIC values of the best model were 1231.42 and 352.4 at the landscape and site scales, respectively.

			Landscape scale		Site scale	
No.	Model[a]	K	ΔAIC	ω	ΔAIC	ω
1	Forage	3	419.6	0.00	242.4	0.00
2	Forage + access	4	109.0	0.00	121.0	0.00
3	Forage + visibility	4	257.4	0.00	137.7	0.00
4	Forage + access + visibility	5	5.6	0.06	14.4	0.00
5	Forage + access + visibility + visibility × access	6	0.0	0.94	0.0	1.00
6	Null model	1	483.8	0.00	321.5	0.00

[a] Appropriate variable transformation determined using polynomial fractions (Hosmer and Lemeshow 2000). Landscape scale = visibility ($1/x^2$), forage (x^2), access (none); site scale = visibility (log), forage (x^2), access ($\sqrt{}$).

considered models with a ΔAIC ≤ 2 equivalent and used multimodel inference if necessary (Burnham and Anderson 2002). We assessed the robustness of the best model using k-fold cross-validation with 10 iterations (Boyce et al. 2002).

Number of deer seen during a hunting day.—In a situation of overabundance, a hunter may be selective and not shoot the first deer seen. We used the number of deer seen in a day with the possibility of shooting as a more sensitive index of hunter success. We used data from hunters who had successfully completed their questionnaire and for whom we had data from at least 1 7-hour-hunting day (an average daily hunt). We partly validated the quality of the information provided by hunters on the questionnaires by comparing reported active hunting time to the data from the GPS units. Hunting start and end time on the questionnaires corresponded to GPS records in 96% of the occasions.

To address our main objective of identifying habitat characteristics associated with successful deer harvests, we first identified potentially confounding variables that may also influence the number of deer observed per day, such as weather conditions, hunter experience, and date. We conducted a principal component analysis (PCA) to reduce the number of correlated variables among the 5 weather variables obtained through questionnaires. The first 2 axes explained 63% of the variance, with the first axis (hereafter cloud cover) discriminating between sunny and warm rainy days, and the second axis (hereafter temperature) discriminating warm days from rainy days with frost and/or snow on the ground (Appendix B). We also performed a PCA to synthesize the 3 variables related to hunter's experience, but these variables were highly correlated and we decided to use only the number of years of deer hunting experience (Gratson and Whitman 2000).

Although this is not the conventional approach of information-theoretic model selection (Burnham and Anderson 2002), we first assessed 15 candidate models that included every combinations of weather conditions (the 2 PCA axes of cloud cover and temperature), years of deer hunting experience, and date, because we aimed at finding the best combination of these variables and could hardly build candidate models based on a priori knowledge. Then, we developed a set of 5 candidate models by adding the same explanatory variables that we included in the candidate models of kill-site analyses (i.e., forage, visibility, and access) to the best model obtained in the first step (Table 2).

To characterize habitats used by hunters, we calculated an area-weighted index of deer forage availability and visibility, as well as road density (m/ha) in a 50-m buffer zone around each location recorded during the day. We used the average number of deer seen per hunter per day to obtain a relative index of local deer abundance (Simard et al. 2010), an indicator that was found to be reliable on Anticosti Island (Pettorelli et al. 2007, Simard 2010) and that is not influenced by the selectivity of hunters compared to other hunting statistics (Solberg et al. 2004). It should be noted, however, that the relationship between density indices and real density could be non-linear (MacFarland and Van Deelen 2011). Because the outfitters' territories were divided into sub-units 126–485 km^2 (Fig. 1), we calculated a relative density index for each of the sub-units (Pettorelli et al. 2007). We forced the density index into all models as a potentially confounding factor likely to influence the number of deer seen by hunters.

We modeled the number of deer seen per hunter-day using a regression analysis with negative binomial distribution and generalized estimating equations (GEE; PROC GENMOD), which allowed us to take into account repeated observations of the same hunters. We used a compound-symmetry covariance matrix for the repeated effect (i.e., the correlation between observations of a single hunter was considered constant; Gillies et al. 2006), and the logarithm of hours hunted in a day as an offset variable (Agresti 1996). We used the quasi-likelihood under independence criterion (QICu) developed by Pan (2001) to rank candidate models. Similar to AIC, we calculated the ΔQICu and QICu weights

Table 2. Model selection used to describe the relationship between the number of white-tailed deer seen with the possibility of shooting during a hunting day and (A) weather conditions, hunter's experience, and date of hunting trip; and (B) habitat attributes in terms of visibility of the deer from the hunter's point of view, deer forage abundance, and density of access roads, Anticosti Island, Québec, Canada, 2007 and 2008. Models are listed with their number of parameters including the intercept (K), difference in quasi-likelihood information criterion (QIC) compared to the best model (ΔQICu), and QIC weight (ω). The QICu values of the best model were −3711.97 for (A) and −4002.25 for (B).

Model[a]	K	ΔQICu	ω
A) Weather conditions and hunter's experience			
Cloud cover[b]	2	0.0	0.80
Experience[c] + cloud cover	3	2.8	0.20
Experience	2	68.0	0.00
Cloud cover + temperature[d]	3	287.8	0.00
Experience + cloud cover + temperature	4	297.0	0.00
B) Habitat attributes, weather conditions, and deer density			
Deer density + cloud cover + forage	4	43.7	0.00
Deer density + cloud cover + forage + access	5	69.4	0.00
Deer density + cloud cover + forage + visibility	5	0.0	1.00
Deer density + cloud cover + forage + access + visibility	6	24.2	0.00
Deer density + cloud cover + forage + access + visibility + visibility × access	7	38.4	0.00

[a] Appropriate variable transformation determined using polynomial fractions (Hosmer and Lemeshow 2000): visibility (none), forage ($1/x$), access ($1/x$).
[b] Axis 1 of the PCA for weather variables.
[c] Number of years of experience in white-tailed deer hunting.
[d] Axis 2 of the PCA for weather variables.

(w_i) to select the most parsimonious model and considered models with ΔQICu ≤ 2 as equivalent.

Environmental features associated with deer harvest.—We assessed whether certain habitat characteristics were associated with the successful harvest of deer by comparing sites where a hunter harvested a deer with sites frequented by the hunter the same day. We used conditional logistic regression (PROC PHREG with the STRATA statement) to compare a hunter's kill-site location(s) with 10 locations randomly selected from the set of locations collected on the same day. We determined habitat characteristics in terms of deer forage, visibility, and accessibility within a 100-m buffer centered on kill sites and hunter locations. We evaluated the influence of habitat variables using the same candidate models as developed in previous analyses and identified the best model with QICu (Table 4).

Prior to all statistical analyses, we used the polynomial fractions method (Hosmer and Lemeshow 2000, Hardin and Hilbe 2003) to determine the best transformation for each explanatory variable and assessed collinearity within the most complex models using the tolerance index (Allison 2003; PROC REG). When the tolerance index was >0.4, we centered and standardized the collinear variables (Allison 2003). We conducted all statistical analyses using SAS 9.2 (SAS Institute, Inc., Cary, NC).

RESULTS

We sampled 477 hunters in 2007 and 2008, which provided 667 kill-site locations across the 3 outfitter territories. We visited 306 kill sites in the field. We obtained 152 and 530 full-day movements (i.e., $\geq$7 hr) for 59 and 283 hunters in 2007 and 2008, respectively, 172 and 17 of which included 1 and 2 kill-site location(s).

Kill-Site Characteristics

The most parsimonious model describing kill-site habitat characteristics at the landscape scale included the visibility × access interaction (Table 1). Cross-validation confirmed that this model had strong predictive power ($r_s = 0.94 \pm 0.03$ SE). Deer were disproportionately harvested in areas with both a high road density and a high visibility for the hunter, but the positive influence of visibility decreased when the density of access routes was either low or high (Table 3, Fig. 2a). The effect of forage abundance on the spatial distribution of harvested deer was not linear, and suggested that deer had a greater probability of being harvested in locations with greater forage abundance (>50% ground cover; Fig. 2b). The influence of forage abundance, however, was much less than that of visibility and accessibility.

As with the landscape scale, the best performing model (model 5) at the site scale included a significant interaction between visibility and access (Table 1, Table 3), and had high predictive power ($r_s = 0.90 \pm 0.08$ SE). Deer were disproportionately shot in sites with good visibility and access roads, but more deer were killed far from access roads when visibility increased (Fig. 2c). Contrary to the landscape scale, the spatial distribution of deer kill sites was not linked to forage availability (Table 3).

Number of Deer Seen During a Hunting Day

Among the candidate models assessing the influence of hunter experience, weather conditions, and date of the hunting trip, on the number of deer observed per hunter per day, the one including only cloud cover performed the best

Table 3. Estimated parameters (β) of the best models used to discriminate deer kill sites from random sites at landscape a) and site b) scales on Anticosti Island, Quebec, Canada, during the 2007 and 2008 hunting seasons.

			95% CI	
Variable	β	**SE**	**Lower**	**Upper**
a) Landscape scale				
Intercept	−0.2	0.1	−0.4	0.1
Visibility	−1874	220	−2307	−1442
Forage	0.020	0.008	0.002	0.0034
Forage^2	0.0006	0.0005	−0.0005	0.0017
Access	0.039	0.003	0.033	0.045
Visibility × access	12.6	5.0	2.8	22.3
b) Site scale				
Intercept	−0.1	0.6	−1.3	1.2
Visibility	6	1	4	8
Forage	0.04	0.03	−0.03	0.1
Forage^2	−0.001	0.002	−0.003	0.002
Access	−0.7	0.1	−0.9	−0.5
Visibility × access	0.27	0.07	0.13	0.41

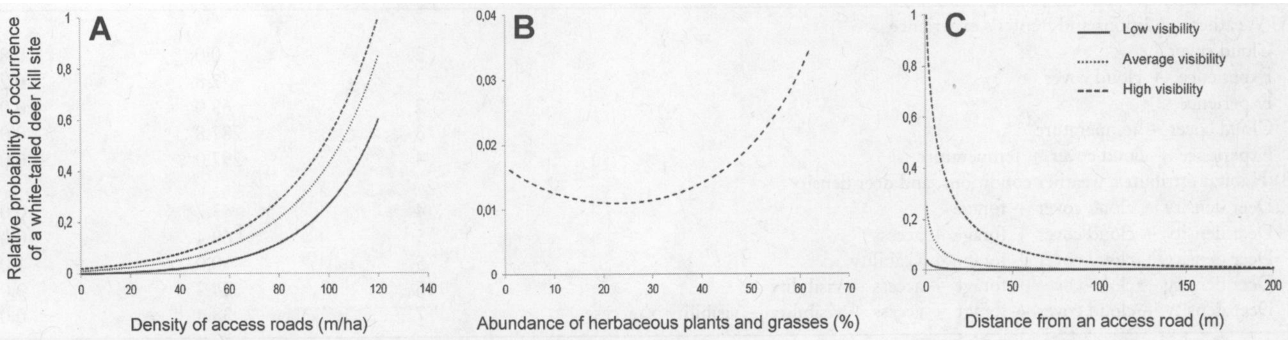

Figure 2. Relative occurrence probability of a white-tailed deer kill site in relation with the density of access routes by visibility interaction (A), abundance of broadleaf herbaceous plants and grasses (B), and distance from access roads by visibility of the deer from the hunter's point of view interaction (C), Anticosti Island, Quebec, Canada, 2007 and 2008. Habitat characteristics were measured in a 100-m radius around each location (A and B). We used the 25th, 50th, and 75th percentiles of observed visibility (respectively 30 m, 38 m, and 47 m for A, and 38 m, 73 m, and 120 m for C) and rated them as low, average, and high visibility.

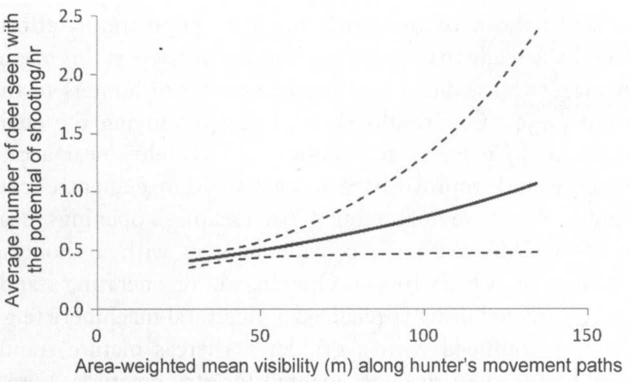

Figure 3. Relationship between the number of white-tailed deer seen with the possibility of shooting per hour and average visibility in the habitat types frequented by a hunter on Anticosti Island, Quebec, Canada, 2007 and 2008. The dashed lines indicate the 95% confidence interval.

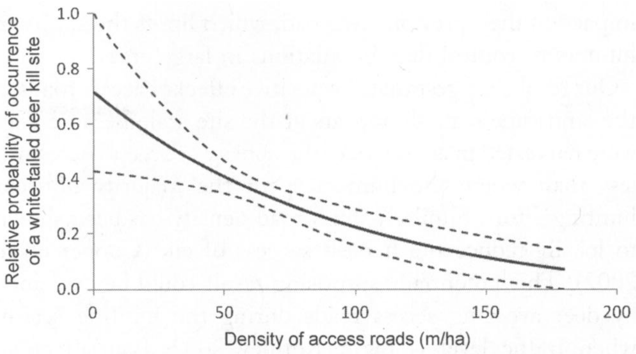

Figure 4. Relationship between the relative occurrence probability of a white-tailed deer kill site and density of access routes on Anticosti Island, Quebec, Canada, 2007 and 2008. The dashed lines are the 95% confidence interval.

(Table 2). However, the 95% confidence interval of the coefficient for cloud cover included 0 ($\beta = 0.04 \pm 0.03$, 95% CI $= -0.02, 0.10$).

The best model assessing the influence of habitat variables on the number of deer seen per hunter per day, and controlling for cloud cover, deer forage availability, and local deer abundance, only included visibility of the deer from the hunter's point of view (Table 2) which had a strong positive effect ($\beta = 0.009 \pm 0.004$, 95% CI $= 0.001, 0.018$, Fig. 3). The 95% confidence interval of all other parameters included 0.

Environmental Features Associated With a Successful Deer Harvest

Three candidate models had equal ability to discriminate kill-site locations from sites frequented by hunters during a hunting day (Table 4). Only access road density influenced the relative probability of harvesting a deer, with the probability of harvesting a deer decreasing as the density of access routes increased ($\beta = -0.010 \pm 0.003$, 95% CI $= -0.015, -0.005$; Fig. 4). The 95% confidence intervals of all other variables included 0.

Table 4. Model selection used to describe the relationship between habitat characteristics in terms of visibility of the deer from the hunter's point of view, deer forage abundance, density of access roads, and deer kill-site location(s) during a hunting day on Anticosti Island, Québec, Canada, 2007 and 2008. Models are listed with their number of parameters including the intercept (K), difference in quasi-likelihood information criterion (QIC) compared to the best model (ΔQICu), and QIC weight (ω). The QICu of the best model was 947.77. Models 2, 4, and 5 were considered equivalent (ΔQICu ≤ 2).

No.	Model[a]	K	ΔQICu	ω
1	Forage	2	18.6	0.00
2	Forage + access	3	0.6	0.32
3	Forage + visibility	3	14.6	0.00
4	Forage + access + visibility	4	0.0	0.43
5	Forage + access + visibility + visibility × access	5	1.0	0.25

[a] Appropriate variable transformation determined using polynomial fractions (Hosmer and Lemeshow 2000) : visibility (none), forage (none), access (none).

DISCUSSION

In areas where large predators thrive, they often regulate ungulate populations (Flueck 2000) and several studies have linked predation success and environmental features (Kunkel and Pletscher 2000, Thogmartin and Schaeffer 2000). When large predators are scarce or absent, sport hunting may be the only management tool available to control ungulate populations and their potential negative effects. Using an original approach of monitoring hunter movements with GPS (Lyon and Burcham 1998, Broseth and Pedersen 2000, Stedman et al. 2004), we demonstrated that hunters, like predators, are more effective in killing their prey under specific conditions. Results across the landscape and site-scales, although obtained using a different approach, both indicated that the spatial distribution of harvested deer was mainly determined by the presence of access roads in open stands. The abundance of deer forage also influenced the spatial distribution of harvested deer across the landscape, but to a lesser extent. Hunting success, however, did not relate much to weather conditions, date, or hunter experience.

Land Access

Although hunters focus their activity near access roads and trails (Diefenbach et al. 2005, Keenan et al. 2008), non-human predators prefer areas where they are most likely to encounter prey (Mao et al. 2005). For example, roads are not necessarily required by wolves for movement or to catch prey (Whittington et al. 2005); instead, wolves use roads opportunistically to increase their hunting efficiency (James and Stuart-Smith 2000, Whittington et al. 2005).

Several studies have shown the influence of roads and footpaths on the spatial distribution of hunters (Lyon and Burcham 1998, Broseth and Pedersen 2000, Diefenbach et al. 2005). Fuller (1988) observed that deer hunters concentrated their activities within 200 m of roads or trails, and Diefenbach et al. (2005) concluded that 87% of hunters hunted within 500 m of a road. Similarly, about 80% of all hunter movements recorded in our study were located within 100 m of a drivable gravel road or a footpath. Similar to Broseth and Pedersen (2000) for ptarmigan (*Lagopus lagopus*), we conclude that deer hunters had a spatially limited impact on their prey on Anticosti, which limits the ability of hunters to control deer populations in large areas.

Our results suggest that the positive effect of access roads at the landscape scale disappears at the site scale because deer were harvested in areas where the density of access routes was less than where the hunters spent the majority of their hunting effort. Similarly, high road density has been shown to locally reduce the harvest success of elk (Cooper et al. 2002). This potentially surprising result could be explained by deer avoiding access roads during the hunting season when traffic level is high (Rothley 2002, Laurian et al. 2008) or because hunters could harvest their game far away from roads in open sites (Brinkman et al. 2009).

Visibility of the Prey From the Hunter's Perspective

For hunters, as for predators (Creel et al. 2005), prey detection is a key determinant of harvest success. Hunters prefer hunting in habitat types characterized by low vegetation cover and high visibility allowing them to see preys at greater distances and increase their success (Millspaugh et al. 2000, Brinkman et al. 2009). Habitat types that provided the best visibility for hunters were clearcuts, wetlands, and open portions of mature forests (Brinkman et al. 2009).

In agreement with Sage et al. (1983), our results showed that searching habitat types with good visibility was the only variable that had a positive, and significant, influence on the number of deer seen. Just seeing game and having the opportunity to harvest contribute greatly to hunter satisfaction (Miller and Graefe 2001). In our system, we believe that weather conditions, hunter experience, and the date on which the hunt took place, did not influence observation rates because of the high density of deer. In other systems, weather (Fobes 1945, Curtis 1971) and hunter's experience (Holsworth 1973) were found to influence harvest success.

Deer Forage Abundance

Predators may select habitat types supporting high food availability for their prey to increase hunting success (Courbin et al. 2009, Hebblewhite et al. 2009). On Anticosti Island, productive environments attracted more deer, which increased the likelihood of harvest but we found that visibility and accessibility were better predictors of kill-site distribution than forage availability. Deer were also more likely to be harvested in sites with high forage abundance. Hunters may not only target productive habitat types to increase their harvest success, but also open habitat types (e.g., bogs) or habitat types with low vegetation cover (e.g., recent clearcuts). But in the less productive environments, which likely attract less deer, the ability for a hunter to spot deer over large distances remains a vital asset to increase their probability of harvest.

MANAGEMENT IMPLICATIONS

Sport hunting may not be always an efficient population control method in all instances, for example if the desired reduction in deer density is high over a large area (Nugent and Choquenot 2004). Overall, our study provided a better understanding of hunter behavior and identified variables that influence harvest success. For sport hunting to be an effective mean of managing ungulate populations, efforts should be made to improve the hunters' efficiency; this means managers must direct a sufficient number of hunters to the right places. Our results showed that modifying the environment to increase accessibility and visibility near access roads would improve harvest success. Management efforts should focus on maintaining (or creating) openings near roads and footpaths to provide hunters with a shooting distance of at least 100 m. Openings in regenerating stands can be created using specialized agricultural machinery (e.g., tractors equipped with a grinder), whereas mature stands could be opened through adapted forestry practices. Forest openings, however, are likely to provide deer with abundant forage resources that could ultimately, if habitat management is conducted over large areas, favor the local deer population. That potential influence of increased forage availability on deer population dynamics should not be overlooked. The creation of access routes and high-visibility areas in remote areas would also increase the hunters' impact on deer populations.

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Appendix A. Habitat types used to study environmental attributes influencing white-tailed deer harvest by sport hunting on Anticosti Island, Quebec, Canada, 2007 and 2008. Indices for deer forage abundance and visibility of the deer from the hunter's point of view were measured in the field in each habitat type.

		Browse index (%)			Visibility index (m)		
Habitat type	**Description**	$\bar{x}$	SE	*n*	$\bar{x}$	SE	*n*
Balsam fir	Stand with conifer basal area ≥75%, balsam fir ≥50%	32.9	1.8	302	25.3	1.0	87
White spruce	Stand with conifer basal area ≥75%, white spruce ≥50%	37.8	3.2	81	24.2	1.0	69
Black spruce	Stand with conifer basal area ≥75%, black spruce ≥50%	31.0	3.3	105	16.9	0.9	44
Clearcut	Clearcut <15 yr old	62.3	5.6	49	46.4	7.1	22
Peatland	Fen or bog	53.2	1.7	297	53.9	10.0	39
Disturbances	Burn, total windfall, severe insect epidemics	18.7	3.5	48	29.2	6.1	38
Other	Lake and intertidal zone (50-m buffer zone around stands)	0			250[a]		
Main gravel road	Main road (15-m buffer zone centered on the roadway)	0[b]			178.7	11.5	20
Secondary gravel road	Secondary road (10-m buffer zone centered on the roadway)	0[b]			98.1	13.5	24

[a] We arbitrarily set visibility to 250-m which corresponds to the usual scope of a firearm.
[b] We considered that no forage was available on main and secondary roads. The available browse for deer on roadsides was estimated based on adjacent habitat types.

Appendix B. Results of the principal component analysis for 5 weather condition variables obtained through questionnaires distributed to hunters on Anticosti Island, Quebec, Canada, during the 2007 and 2008 hunting seasons.

Variables	Axis 1	Axis 2
Warm temperature and clear sky (>10° C)	−0.66	0.05
Presence of strong winds	0.27	−0.34
Precipitation	0.58	−0.27
Ground frost	0.10	0.69
Snow on the ground	0.38	0.57