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Research article

Occupancy modeling of habitat use by white-tailed deer after more than a decade of exclusion in the boreal forest

Aimie Baribeau, Jean-Pierre Tremblay and Steeve D. Côté

A. Baribeau (https://orcid.org/0000-0003-0158-2906) ✉ (aimmiee21@hotmail.com), Biology Dept, Univ. Laval, Quebec, QC, Canada. – J.-P. Tremblay, Center for Northern Studies and Centre for Forest Research, Biology Dept, Univ. Laval, Quebec, QC, Canada. – S. D. Côté, Center for Northern Studies, Biology Dept, Univ. Laval, Quebec, QC, Canada.

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The exclusion of herbivores in forest areas is a strategy used to reduce the impact of selective browsing and increase the regeneration of desired plant species. On Anticosti Island (Québec, Canada), selective browsing by white-tailed deer prevents the regeneration of balsam fir – white birch forests leading to their conversion into white spruce forests. Large deer exclosures were established for ca 10–12 years in clear-cuts with patches of residual forest from 2001 to 2006 to assist in the natural regeneration of fir stands and to provide shelter and food resources for deer. Our objective was to assess how deer use exclosures after the removal of fences according to their spatial configuration and habitat composition. We randomly distributed automatic cameras for periods of 14 days during summer in six exclosures ranging from 3.1 to 11.2 km^2 (n = 25 cameras per exclosure) from which deer were reduced for 10–12 years. We compared candidate occupancy models that included spatial configuration and food resource variables while simultaneously controlling for variables affecting detection probability. We obtained weak evidence that deer habitat use increased by 19% when forage resources, represented by the cover of *Cornus canadensis*, increased from 0 to 100%. None of the other variables (distance between the border of exclosures and cameras and distance between forest patches and cameras) was retained, suggesting that the use of regenerating forests by deer in summer after a period of exclusion is related to forage availability and therefore, any forest management that improves food production during summer should help maintain or increase habitat use by deer.

Keywords: Anticosti Island, camera traps, *Cornus canadensis*, exclosure, habitat use, management, occupancy models, white-tailed deer

The impact of chronic herbivory on plant communities has been extensively studied over the past decades. Heavy selective browsing on plant species can alter natural regeneration, plant communities and forest functions (Rooney 2001, Kuijper et al. 2010). For instance, some large herbivores can affect seedlings' regeneration of palatable species by altering their growth (Frelich and Lorimer 1985, Kaien 2006). A study on browsed scots pine *Pinus sylvestris* by herbivores (goat *Capra hircus*, ibex *Capra*

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pyrenaica and sheep *Ovis aries*) showed that a constant browsing pressure on tree saplings can delay their reproduction and growth by 12 years (Zamora et al. 2001).

Exclusion or partial exclusion following harvesting can be used to prevent the negative effects of large herbivores on forests. Some studies have shown the efficiency of this strategy to achieve forest management objectives and to identify herbivore densities compatible with the natural regeneration dynamics of managed forests (Kay and Bartos 2000, Horsley et al. 2003, Persson et al. 2007). Exclosures are a management strategy that leads to exclusion of consumers and that has been used to document the impact of large herbivores on individual plant growth and survival (Kaien 2006, Hidding et al. 2012), changes in community composition (Horsley et al. 2003, Tremblay et al. 2006), forest dynamics (Hidding et al. 2013, Nuttle et al. 2013, De Vrient et al. 2020) and ecosystem functions (Persson et al. 2005, Vuorinen et al. 2020). Some studies have used this management strategy as a tool to enhance biodiversity and conservation and yielded similar results: less browsing on selected species and higher density of mature trees and saplings (Birhane et al. 2006, Leonardsson et al. 2015).

Reclaiming of previously excluded areas by deer is likely influenced not only by the availability of resources, but also by their distribution over the management area and the surrounding matrix of heavily browsed and unmanaged forests. Large herbivores require a minimum area of forest for foraging, resting and social functions (Cargnelutti et al. 2002). Forest management can contribute to provide such habitat, but can also lead to fragmentation between habitat types, such as forest cover and cuts, thus influencing habitat use by deer (Cargnelutti et al. 2002, Dechen Quinn et al. 2013). Evaluating habitat use following exclosure removal can help assess how landscapes created by this management approach influence the behavior and distribution of large herbivores. In this context, habitat use can be considered as one of the indicators of the effectiveness of this management approach in combination with other indicators of forest attributes in the frequent context where both sustainable forest and wildlife management are the overall goal (Beguin et al. 2016).

On Anticosti Island, selective browsing induced by the high density of white-tailed deer *Odocoileus virginianus* prevents the regeneration of native balsam fir forests leading to their conversion into white spruce *Picea glauca* forests and parklands (Beaupré et al. 2005). Large management exclosures, in which clear cuts and patches of residual forest are intermingled, have been established since 2001 to assist in the natural regeneration of fir stands and to provide shelter and food resources for deer during winter. Deer densities in exclosures were reduced through sport hunting. Several exclosures were considered a success in terms of balsam fir regeneration after 10–12 years of reduced deer density. An evaluation of the habitat use by deer is needed to provide insights about the efficiency of the management strategy.

Our study objective was to evaluate summer habitat use by white-tailed deer in six former management exclosures dismantled eight years ago. Based on our knowledge of feeding habits and movements of white-tailed deer on Anticosti Island that revealed the establishment of deer home ranges in habitats that present higher forage abundance (Massé and Côté 2009, Coulombe et al. 2011), we hypothesized that habitat use would be determined by forage resources in response to the need for deer to replenish body reserves for the winter season. We predicted that deer would use more frequently areas with a higher basal area of balsam fir and white birch as opposed to areas with a higher basal area of black and white spruces. We also predicted that deer would more frequently use areas with a higher percentage of ground forage. We also hypothesized that the integration of formal exclosures into deer habitat use would be a function of their spatial configuration in terms of regenerating cut blocks and mature forest patches. We predicted that deer would use areas closer to residual forest patches and exclosure borders representing continuous protective cover to minimize the tradeoff between food resources and exposure to elements (Mysterud and Østbye 1999, Coulombe et al. 2011). We used presence and absence data obtained from camera traps to model habitat use while controlling for variables affecting detection probability. We discuss how the use of restored habitat by deer inform on the sustainability of exclosures as a deer and forest management method.

Material and methods

Study area

Anticosti Island (49°30′N, 63°00′W) is located in the Gulf of St-Lawrence in Quebec, Canada within the eastern balsam fir-white birch bioclimatic forest zone (Saucier et al. 2009). The vegetation is dominated by balsam fir, white and black spruces, as well as white birch (Saucier et al. 2009). The long fire cycle makes spruce budworm *Choristoneura fumiferana* outbreaks and windthrows the main disturbances leading to cyclic regeneration of balsam fir stands (Baskerville 1975). The island is characterized by a maritime south-boreal climate with fresh summers and long winters (Saucier et al. 2009), and by the lack of any deer predators. The last known predator, the black bear *Ursus americanus*, has not been seen on the island since the 1990s. White-tailed deer density on Anticosti Island is normally > 20 deer km^{-2} (Huot and Lebel 2012), but in 2017–2019, it dropped to < 5 deer km^{-2} locally due to harsh winter conditions (Ayotte 2019). The high deer density maintained over several decades induced heavy browsing pressure on balsam fir, the main food resource of deer during winter (Lefort et al. 2007). The high deer density on the island attracts ca 4000 hunters from September to December. Our study area included six exclosures of 3.1–11.2 km^2 built from 2000 to 2006 and dismantled from 2012 to 2017 (Fig. 1).

Estimation of habitat use from camera traps

Camera traps can be used non-invasively to measure habitat use by animals (O'Connell et al. 2011). The presence/

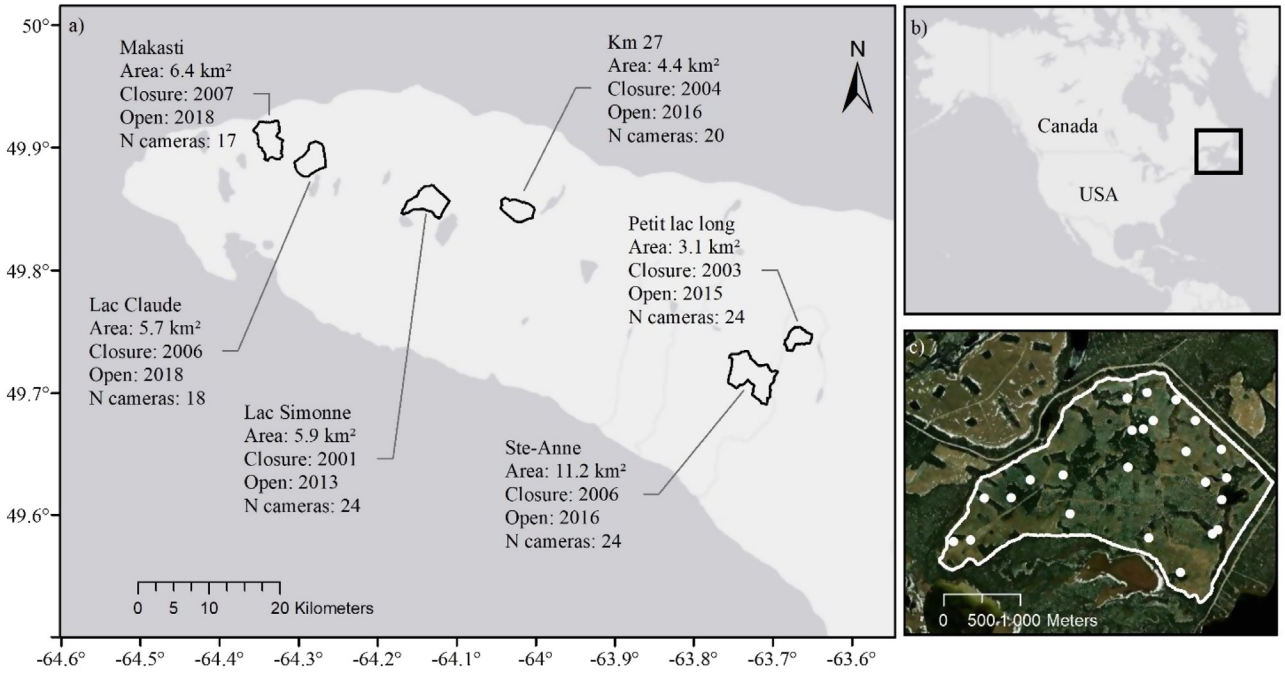


Figure 1. Location of the study area and attributes of the six exclosures under study on Anticosti Island, Québec, Canada. In (a) the specific information of every exclosure and their position on the western part of the island, (b) the location of Anticosti Island on the North American continent and (c) magnification of the km 27 exclosure to show the camera distribution.

absence data collected from cameras can be analyzed using an occupancy model framework that assess the probability of occupancy while controlling for the detection probability. Because we measured occupancy in an open system, occupancy estimates must be interpreted as the percentage of sites 'used' by a species rather than 'occupied' (MacKenzie and Nichols 2004). To assess the effort needed to obtain unbiased estimates of habitat use of white-tailed deer from camera traps (Hamel et al. 2013), we performed a pilot study during all of July 2019 during which we deployed 32 camera traps programmed to take a picture every 5 min in the Lac Claude exclosure (Fig. 1). We resampled the dataset to simulate sampling designs ranging from 5 to 30 days with 5 day steps and different time intervals between pictures (5, 10, 15, 20, 30, 45, 60, 120, 180, 240 min). We ran occupancy models without covariates and holding the detection rate constant to estimate occupancy rates for each sampling design and to determine the minimum requirement (number of cameras, number of days and time interval) for stabilized occupancy rates (see 'Statistical analyses' and Supporting information). A minimum of 20 cameras programmed to take a picture every 5 min during 14 days was sufficient to stabilize the precision of the estimates obtained from occupancy models (Supporting information).

During the summer of 2020 (25 June–16 August), we distributed 25 cameras (Bushnell Trophy, Spypoint Force 10, Reconyx PC800 and Spypoint Force 20) in each of the six exclosures according to a stratified random distribution in three different habitat types (regenerating cuts, residual mature forest without balsam fir [representing forest cover] and residual mature forest with balsam fir [representing forest cover and food resources]). Those categories were defined using data from Données Québec forestry map with disturbances collected in 2012 (DonnéesQuébec 2017). We randomly distributed the 25 cameras among those three habitat types (eight points per habitat, one with nine points) using ArcGis ver. 10.4 (ESRI 2016). We deployed each camera as accurately as possible to the random locations. We mounted cameras at level, 75 cm from the ground on trees with a diameter at breast height of 8–10 cm and facing the north quadrant. We removed vegetation obstructing the camera's lens. Cameras recorded pictures for 14 days in each exclosure, taking a systematic picture every 5 min for a total of 288 pictures per day. Because of some camera failures, the number of camera traps varied from 17 to 24 among exclosures (Fig. 1). We measured visibility in front of the camera, a variable that could influence deer detection probability at each camera trap site (Meek et al. 2014, Kolowski and Forrester 2017). The probability of detection is defined as the 'probability that the species of interest is present at the time of the survey and detected at used units' (MacKenzie et al. 2018). It can impact the probability of habitat use, which is the probability the units are used by the target species (MacKenzie et al. 2018). To estimate visibility and model the detection probability of each camera, we used a profile board composed of four panels of 50 × 25 cm to estimate the lateral cover in front of the camera. We took a measure at 5 and 10 m in front of each camera, and then estimated the percentage of visibility at each site, following the approach in Ferron et al. (1996). The approach consist of averaging the grade of lateral cover of four squares on a blanket held vertically in front of the evaluator (1: 0–19% of visibility, 2: 20–39%, 3: 40–59%, 4: 60–79%,

5: 80–100%), then multiplying it by 20 and deducing 10, for example: $((1+3+4+4)/4) \times 20 - 10 = 50\%$ of lateral cover visibility at 5 m in front of the camera. The same approach was used at 10 m. We also recorded whether the camera was pointing at a deer trail or not.

To classify automatically the presence and absence of white-tailed deer, we analyzed 485 338 pictures collected during 2100 camera trap days using an artificial intelligence from Tan and Le (2019). We classified the pictures with the neural network/architecture *EfficientNet* from the EfficientNet-Pytorch library (Melas-Kyriazi 2020). We used a sample of 2968 pictures pre-classified as deer presence (n = 1484) and absence (n = 1484) to train the model and 636 pictures to validate the model efficiency. The model classified the pictures with a degree of precision of 94%.

Vegetation and spatial configuration variables

At each camera trap site, we surveyed all saplings and merchant trees present per species in a circular area of 100 m^2 (5.64 m radius) centered on the camera. We tallied saplings per species and diameter at breast height (DBH, 1.3 m) classes to compute basal area per species.

We measured vegetation of the ground layer in a 4 m^2 circular plot located at 2 m in front of each camera. We estimated the percentage of cover of common herbaceous plants regularly browsed by deer on the island: *Cornus canadensis*, *Maianthemum canadense*, *Chamaenerion angustifolium*, *Clintonia borealis*, *Rubus* sp. and Poaceae sp. We kept only two species for the analysis (i.e. *C. canadensis* and *Rubus* spp.) because the global presence of the other species at all camera trap sites was less than 4%, and therefore their availability was not high enough to include these species in the analysis.

To define spatial configuration, we used ArcMap tools (ArcGIS ver. 10.4), to measure the distance of the closest forest cover and the shortest distance to the exclosure border (m) for each camera trap site. When the camera was located under forest cover, we set the distance at 0.

Statistical analyses

We estimated deer use of restored habitat following the opening of exclosures using the single-season single-species occupancy model with the function *unmarkedFrameOccu* of the package 'unmarked' (ver. 1.1.1) (Fiske and Chandler 2011) in R (<www.r-project.org>). This model structure allowed us to determine deer habitat use based on different variable combinations while accounting for detection probabilities across all sites. The main initial assumptions for this type of model were respected (MacKenzie et al. 2018) (Supporting information). We included eight variables in our models: the percent ground cover of *Rubus* sp. and of *Cornus canadensis*, the basal area for white spruce, black spruce, balsam fir and white birch saplings ($m^2\ ha^{-1}$), the distance between a camera trap site and the border of the exclosure (m) and the shortest distance to forest cover (m). To obtain convergence, we scaled all the covariates (MacKenzie et al. 2018) (Supporting information). Pairwise correlations between all variables were all below 0.48. Our data were organized in a matrix that included, for all camera sites (127), the daily detection (24 hours) of the presence (1) or absence (0) of deer during 14 days combined with the table containing all the variables used for modelling occupancy.

We first computed a null model, holding occupancy (Ψ; measuring habitat use in our study) and detection (p) constant. We then made a preselection of detection models holding occupancy (Ψ) constant, to find which combination of variables was the best to account for the probability of detection. In those models, we included combinations of four variables: the presence or absence of a deer trail at the camera site, the percentage of visibility at 5 m in front of the camera, the percentage of visibility at 10 m in front of the camera, and the camera model. We then included the best supported detection model among the 15 occupancy models built with combinations and interactions of variables that could affect deer occupancy based on our hypotheses.

The residuals of the models for occupancy and detection were normal according to the Dunn and Smyth method (Dunn and Smyth 1996, Warton et al. 2017). The c-hat value of the goodness-of-fit test indicated a lack-of-fit in the data (Supporting information). We used parametric bootstrap for the goodness-of-fit to determine whether the observed value was unusually large. We ran this test on all models using 999 bootstrap resamples (MacKenzie and Bailey 2004). We then compared all the models according to the corrected Quasi Akaike's information criterion (QAICc) that corrects over dispersed data (MacKenzie and Bailey 2004) to determine which model(s) had the heavier QAICc weight, a delta QAICc < 1 and explained most of the deer occupancy variance using the aictab function of the AICcmodavg package in the program R ver. 4.0.3 (<www.r-project.org>).

Results

The best supported model for the detection probability had a weight of 39% and was a combination of the percentage of visibility at 5 and 10 m in front of the camera (Table 1). The detection varied between 12 [5; 28] (95% confidence interval (CI)) and 19% [14; 24], increasing when the percentage of visibility was higher at 5 and 10 m in front of the camera (Supporting information).

Only one competitive model was found (Δ AICc < 1 and a weight of 24%), but this model was nested within the best supported model, including only the percentage of visibility at 10 m (Table 1). Therefore, the best supported model was used in all the occupancy models as the best combination of variables to account for the detection probabilities among camera sites.

For the probability of occupancy, the goodness-of-fit test on the complete model revealed overdispersion ($\chi^2 = 90300$, $p = 0.03$, $\hat{c} = 2.57$; Supporting information) so we used QAICc to compare models after correction for overdispersion. The model with the lowest QAICc was the null model

Table 1. Model comparison for variables influencing the detection probability (p) of white-tailed deer using camera traps in former management exclosures (n = 6) on Anticosti Island, Canada. The occupancy (Ψ) is fixed at 1 (null). View_5m and view_10m are the percentage of visibility at 5 and 10 m in front of the camera, trail is the presence of a deer trail near a camera trap site and mod_cam is the model of the camera used. AICc is the value of each model and AICcWt is the weight of each model.

Model	Parameters	AICc	AICcWt	Δ AICc
p (view_5m + view_10m) Ψ (1)	4	1602.81	0.39	0.00
p (view_10m) Ψ (1)	3	1603.79	0.24	0.98
p (trail + view_5m + view_10m) Ψ (1)	5	1604.88	0.14	2.07
p (view_5m) Ψ (1)	3	1605.35	0.11	2.53
p (trail + view_10m) Ψ (1)	4	1605.66	0.09	2.85
p (trail + view_5m) Ψ (1)	4	1607.47	0.04	4.66
p (1) Ψ (1) (null model)	2	1611.70	0.00	8.89
p (mod_cam) Ψ (1)	3	1613.61	0.00	10.80
p (trail) Ψ (1)	3	1613.77	0.00	10.96

(Table 2). A second model with a similar weight and QAICc < 1 included only the percentage of *Cornus canadensis* cover (Table 2). According to this model, the probability that deer use restored habitat following the opening of exclosures was high at all sites and increased slightly when the percentage cover of *C. canadensis* increased. When *C. canadensis* was absent (0%), the probability that deer use restored habitat was on average 78% [65; 88], but it increased to 97% [74; 100] when the cover of *C. canadensis* reached 100% (Fig. 2).

Discussion

By integrating deer presence/absence data, estimates of forest composition and structure, and spatial configuration variables in single-season single-species occupancy models, we evaluated factors influencing the use of habitat of white-tailed deer in former management exclosures during summer in the boreal forest. None of the variables representing the spatial configuration of the formal exclosures contributed to explain the use of restored habitat. The second best model after the null model suggested a trend for an increase in the habitat use by deer in areas with higher ground cover of *Cornus canadensis*, a ubiquitous forb consumed by deer in summer that we interpret as an indicator of favorable foraging conditions, providing support for the role of summer forage in determining habitat use by deer.

Camera trap sites that presented a higher percentage of forage cover were initially hypothesized to increase deer habitat use due to food availability and the need for deer to maximize summer food intake to replenish body reserves in preparation for the following winter. Deer usually feed on newly grown leaves of hardwood trees and forbs that are nutrient rich (Chamrad and Box 1968, Everitt and Drawe 1974, Crawford 1982). Because *C. canadensis* can be found in mixed and coniferous forests (Marie-Victorin et al. 1995), it was present in most of our sampling sites at different levels of abundance, making it an indicator of summer forage availability. This species of the field layer of boreal forests is heavily used by deer in summer on Anticosti Island (Tremblay et al.

Table 2. All occupancy models (14) and the null model for the probability that white-tailed deer use restored habitat (Ψ) on Anticosti Island (Canada) following 10–12 years of exclusion in clear-cuts and forested areas (n = 6 exclosures). Detection probability (p) was influenced by the percentage visibility of lateral cover at 5 (view_5m) and 10 (view_10m) m in front of the camera. Cornus is the percentage of *C. canadensis* ground cover, Rubus the percentage of *Rubus* spp. ground cover, basal area BF, WB, WS and BS are the basal area of balsam fir, white birch, white spruce and black spruce saplings, fence dist is the shortest distance between a camera and the exclosure border and cover dist is the shortest distance between a camera and a forest cover area.

Models	Parameters	QAICc	Δ QAICc	QAICc Wt
p (view_5m + view_10m) Ψ (1) (null model)	5	630.92	0.00	0.25
p (view_5m + view_10m) Ψ (Cornus)	6	631.22	0.30	0.21
p (view_5m + view_10m) Ψ (Rubus)	6	632.77	1.86	0.10
p (view_5m + view_10m) Ψ (basal area BF)	6	632.97	2.05	0.09
p (view_5m + view_10m) Ψ (cover dist)	6	633.08	2.17	0.08
p (view_5m + view_10m) Ψ (fence dist)	6	633.11	2.19	0.08
p (view_5m + view_10m) Ψ (basal area WB)	6	633.12	2.20	0.08
p (view_5m + view_10m) Ψ (basal area BF + basal area WB)	7	635.21	4.29	0.03
p (view_5m + view_10m) Ψ (basal area WS + basal area BS)	7	635.33	4.41	0.03
p (view_5m + view_10m) Ψ (Cornus + Rubus + basal area BF + basal area WB)	9	637.07	6.15	0.01
p (view_5m + view_10m) Ψ (dist cover * fence dist)	8	637.51	6.59	0.01
p (view_5m + view_10m) Ψ(dist cover + Cornus + basal area BF + basal area WB)	9	637.55	6.64	0.01
p (view_5m + view_10m) Ψ (fence dist + Cornus + basal area BF + basal area WB)	9	637.69	6.77	0.01
p (view_5m + view_10m) Ψ (dist cover + fence dist + Rubus + Cornus + basal area BF + basal area WB)	11	641.75	10.83	0.00
p (view_5m + view_10m) Ψ (dist cover * fence dist + Cornus + basal area BF + basal area WB)	11	642.30	11.38	0.00

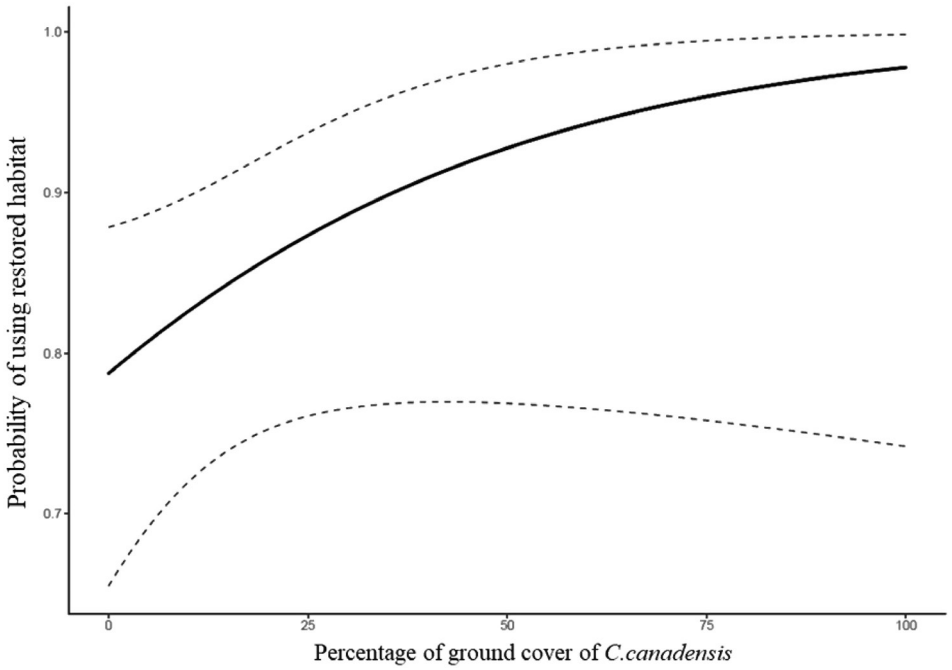


Figure 2. The probability that white-tailed deer use restored habitat after the removal of exclosures on Anticosti Island (Canada) in relation with the percentage of cover of *Cornus canadensis*. The upper and lower dashed lines are 95% confidence intervals.

2006) and the conditions that cause *C. canadensis* to be abundant reflect particularly favorable conditions for deer occupancy. During summer, deer tend to base movements and space use according to forage abundance (Stewart et al. 2000, Coulombe et al. 2011). On Anticosti Island, the size of deer home ranges is influenced mainly by forage abundance, especially forbs and deciduous shrubs, and not by lateral cover because the absence of predators allows deer to move freely among habitats (Massé and Côté 2009, Coulombe et al. 2011). Yet, the probability of using restored habitat reached 78% even in sites where *C. canadensis* was absent, indicating a high overall use of the restored habitat by deer and a limit in our capacity to detect small effects due to relatively low detection rate in our dataset.

The abundance of forage in summer is determinant for white-tailed deer on Anticosti Island, but also for other large herbivores that depend on fat stores accumulated during summer and autumn to survive the winter (Cook et al. 2004, Bishop et al. 2005). For example, yearling mule deer *Odocoileus hemionus* recruitment is influenced by summer nutrition, decreasing when food availability is decreasing (Tollefson et al. 2011). According to Cook et al. (2004), elk *Cervus elaphus* calves and cows were heavier and stored more fat when forage abundance in summer-autumn was higher. On Anticosti Island, female primiparity is earlier, and weaning success is higher in sites with high plant biomass (Simard et al. 2014). Giroux et al. (2014) also reported heavier mass for yearlings inside formal exclosures than outside because forage abundance was higher during spring and summer in the exclosures.

The detection probabilities were influenced by the percentages of visibility at 5 and 10 m in front of the camera. The maximum detection probability varied between 12 and 19%. These relatively low percentages can affect the predictions of the probability of occupancy. According to MacKenzie et al. (2002) and O'Connor et al. (2017), single species data with low survey detection probabilities ($p < 0.15$) may lead to uncertainty in occupancy parameters. O'Connor et al. (2017) suggested to target detection probabilities larger than 0.40. To increase detection probabilities, it is preferable to increase the length of the survey than the number of camera traps (MacKenzie and Royle 2005, Shannon et al. 2014). Using presence-absence data from camera traps sampled in one of the formal exclosures one year prior to our study, we estimated that a 14-day period with a minimum of 20 cameras was enough to obtain unbiased occupancy estimates, but we overlooked the effort required to obtain stabilized detection probabilities. O'Connor et al. (2017) showed in a study aimed at investigating how detectability is influenced by the number of cameras and the season length, that 30 days were necessary to obtain high detection probabilities in a high deer density area (30–80 deer km^{-2}). The year we did our survey in the six exclosures, deer densities were relatively low on the island (< 5 deer km^{-2} $\pm$ 11 locally) (Ayotte 2019). These low densities combined with the 14-day survey length certainly contributed to the low detection probabilities.

Even when considering these two factors, the low detection probabilities and the low deer density on the island during our survey, the probabilities of deer using restored habitat and the detection probabilities were similar to other studies. For example, a study aimed at detecting changes in white-tailed deer occupancy for a survey length of one week reported occupancy (Ψ: 0.60 [0.52–0.67]) and detection (p: 0.24 [0.23–0.26]) probabilities similar to what we obtained

(Steenweg et al. 2019). They also showed that for similar large herbivore species such as elk and mule deer, the occupancy and detection probabilities were similar to what we obtained: (Ψ: 0.56 [0.49–0.64], p: 0.24 [0.22–0.26]) for elk and (Ψ: 0.61 [0.53–0.69], p: 0.18 [0.17–0.20]) for mule deer. When the survey length was extended to a month, occupancy for white-tailed deer was 0.62 [0.54–0.70] and detection probability 0.47 [0.43–0.52], and the same scenario occurred for elk and mule deer (Steenweg et al. 2019). With a 20% detectability, Barata et al. (2017) estimated that they had almost 20% chances of detecting a 15% change in occupancy by the frog *Crossodactylodes itambe*. The power increased to almost 45% for a 30% change in occupancy. The statistical power for a 15% effect size reached a plateau at ~35% at a 50% detectability. Lengthening the duration of the sampling period would likely increase detection rates and thus improve the chance of detecting small changes in occupancy in future studies.

Management implications and conclusions

Together, our results support previously published studies highlighting the contribution of summer forage on habitat use (Massé and Côté 2009) and demographic parameters of white-tailed deer on Anticosti Island (Simard et al. 2014). As regeneration reaches the pole stage, however, forage abundance on the forest floor will likely decline (Massé and Côté 2009). We suggest, based on our results and previous knowledge, that future forest management efforts made to improve forest floor productivity and maximize food resources would help maintain or increase deer habitat use.

Furthermore, estimation of deer habitat use in winter would also be required to evaluate the use of the landscape designed by forest management in formal exclosures. This is a challenging objective because of the incompatibility between the regular inspections required to keep camera traps working in cold and snowy environments (O'Connell et al. 2011) and the necessity to avoid biasing the results by creating access paths in the snow that can lure deer toward camera traps. We can expect the spatial configuration variables to have a larger effect in winter, because deer tend to stay in areas where the impact of wind and the thickness of snow are lower to minimize heat loss (Ozoga and Gysel 1972, Lang and Gates 1985). Thus, the largest forest patches could induce a higher use of sites close to forest patches. Availability of twigs from balsam fir and deciduous trees may also influence habitat use in winter as this type of forage contribute to reduce the use of body reserves (Verme and Ullrey 1984).

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Author contributions

Aimie Baribeau: Conceptualization (supporting); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Resources (supporting); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (supporting). **Jean-Pierre Tremblay**: Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Resources (lead); Supervision (lead); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (lead). **Steeve D. Côté**: Conceptualization (lead); Data curation (supporting); Formal analysis (supporting); Funding acquisition (lead); Methodology (supporting); Project administration (lead); Resources (lead); Supervision (supporting); Validation (supporting); Writing – original draft (supporting); Writing – review and editing (lead).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.1c59zw3zf> (Baribeau et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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