



# OPEN White-tailed deer limit their spatio-temporal overlap with hikers in a protected area

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The pressure on ecosystems resulting from outdoor recreational activities is increasing globally. Protected areas offer to large mammals refugia free of hunting with greater access to food resources, but the presence of humans for recreation in these areas may induce changes in behaviour, activity pattern, and habitat use. We used camera traps to model the spatial distribution and temporal activity of the white-tailed deer (*Odocoileus virginianus*) in a nature reserve located close to Montreal, the second largest metropole in Canada. We showed that deer limit their overlap with the public both across space and over time. White-tailed deer exhibited their highest activity level early in the morning, prior to the reserve's opening hours, indicating temporal avoidance of the public. Deer were also detected at a higher rate when further away from the hiking trail, although in less suitable habitat, indicating spatial avoidance. Human recreational activities in nature reserves open to the public may thus have an indirect effect on ecosystems, by altering the habitat use and behaviour of wildlife.

**Keywords** Movement behaviour, Temporal activity, Recreational human activities, Nature reserve, White-tailed deer

Nature reserves serve an important purpose in conservation biology by contributing to the preservation of biodiversity and the protection of ecosystems, while providing opportunities for people to connect with nature<sup>1,2</sup>. However, outdoor recreational activities are increasing globally<sup>3,4</sup>, resulting in increasing pressure on ecosystems and wildlife<sup>5</sup>. The response of wildlife to human disturbance and infrastructure related to outdoor recreation is highly variable, and it depends on the type of human activity<sup>1,6</sup> and level of human presence<sup>1,7–10</sup>. In response to intensified contacts with humans, mammals may adjust their behaviour, most notably by increasing their nocturnality and avoiding human presence temporarily<sup>2,11–14</sup>. Conversely, animals may become habituated to human presence and increase their tolerance, decrease their vigilance, or even respond inadequately to human disturbances<sup>7,15–18</sup>. Trail infrastructures may also have an impact on the spatial distribution of mammals by limiting the habitat use of some species in the vicinity of a trail or by facilitating the movement of other species along trails<sup>1</sup>.

Protected areas offer large ungulate mammals refugia free of hunting, with greater access to food resources<sup>19</sup>. Human presence in protected areas may, however, be perceived as a predation risk<sup>20,21</sup>, inducing a fear response in large ungulate species<sup>11,22</sup>. For example, ungulates may alter their pattern and/or level of activity, habitat selection, and space use<sup>8,12,23–25</sup>, leading to a less efficient use of the habitat and reduced fitness<sup>15</sup>. In protected areas with a high and recurrent level of human activity, ungulates may alternatively become habituated to human presence<sup>7,16,17</sup>. There are few studies documenting the behavioural adjustment of ungulates in response to the level of human recreational activity in protected areas at various spatial scales (from a few square km up to a regional scale). Some studies showed that mule deer (*Odocoileus hemionus*) can exhibit different adjustments of their activity pattern, such as becoming more crepuscular in a protected area in British Columbia<sup>26</sup>, reducing their activity during the day in protected areas in California<sup>27</sup>, or becoming more nocturnal in the presence of human disturbance with a high level of recreational activities in Colorado<sup>13</sup>. In addition to shifting their diel activity pattern, avoidance of humans may be achieved by ungulate species through a change in habitat use and a displacement to otherwise less suitable areas. For example, caribou (*Rangifer tarandus*) avoided areas occupied by skiers in a protected area in the Gaspésie National Park in Quebec, instead using habitats with a higher risk of encounters with coyotes, their main predator in this area<sup>9</sup>. Similar findings were reported for Tatra chamois (*Rupicapra rupicapra*) in response to increasing tourism in protected high-altitude habitats of the Tatra

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mountains in Poland<sup>28</sup>. Finally, both a spatial and temporal displacement in response to hikers was observed in red deer (*Cervus elaphus*) in Scotland<sup>24,29</sup>.

The white-tailed deer (*Odocoileus virginianus*) is the most widely distributed species of large mammal in North America. Its abundance has drastically increased over the last decades, reaching historical levels throughout much of its distribution range<sup>30,31</sup>; it is now considered as the most abundant wild large herbivore in northeastern North America<sup>30</sup>. However, it is not well established how the presence of humans is affecting deer activity and space use. This is particularly relevant in protected areas opened to the public since white-tailed deer, as selective feeders favouring some tree essences over others for forage, can have profound effects on plant communities in forested habitats<sup>31–33</sup>, limiting recruitment and preventing regeneration in some species<sup>34</sup>, and ultimately, impacting the species composition of tree and understory plant communities<sup>35</sup>.

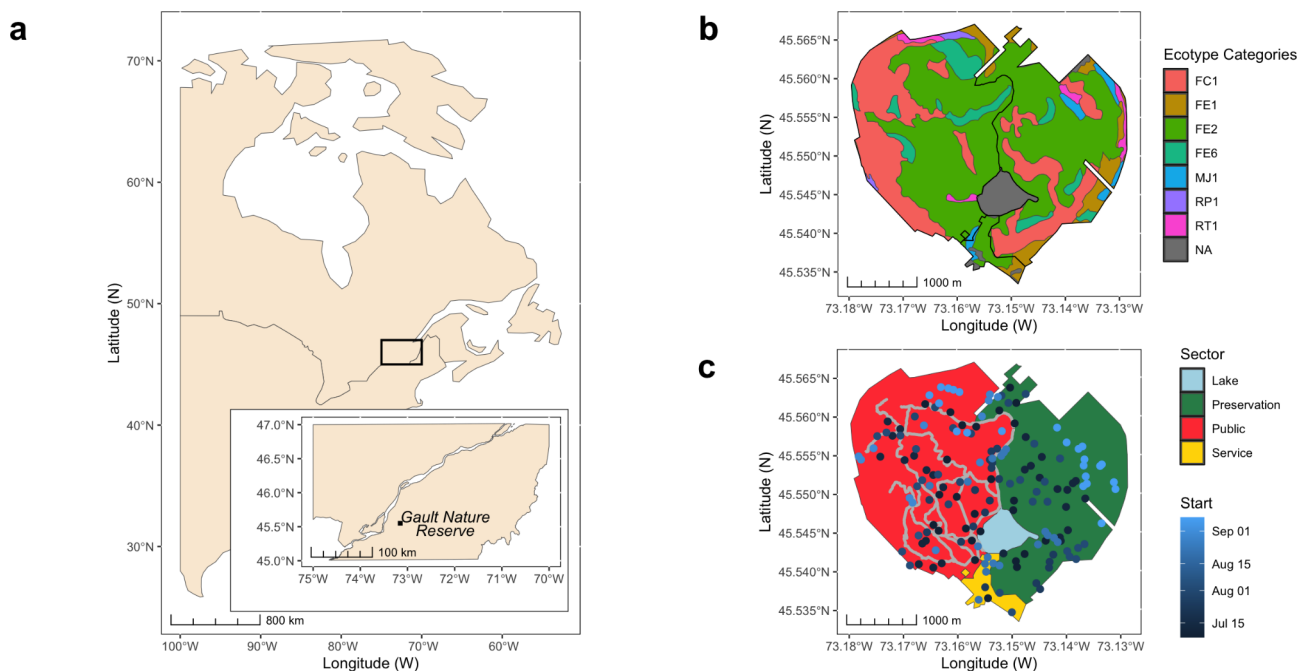
The Gault Nature Reserve of McGill University (hereafter the GNR) is a protected area located south of Montreal (Quebec, Canada). Due to its spatial configuration, it provides a unique opportunity to examine the interaction between humans and wildlife. The GNR territory is split into two main sectors, the first with limited human presence, while the second is open year-round to the public and hosts a well-developed network of hiking trails. A third, smaller sector hosting buildings for public use is also heavily used by hikers. Such a unique design thereby mimics an experimental system where one would have manipulated human activity both in space and time, allowing the study of the effect of the different “treatments” on wildlife.

Here, we examined how the activity pattern, activity level, and spatial distribution of white-tailed deer at the GNR are modulated by human recreation. We first tested the hypothesis of spatial avoidance of the public by deer and predicted that they reduce their use of areas accessible to hikers compared to the preservation sector (limited public access) of the GNR (Prediction 1). At a finer spatial scale, we tested the hypothesis that the availability of favoured forage interacts with the level of disturbance from human activities to determine deer occupancy. We predicted that the deer detection rate is relatively lower at sites that are less isolated and located closer to a trail than at sites that are more isolated and located further away from a trail and at sites that have less favoured forage (Prediction 2). We then tested the hypothesis of a behavioural adjustment of white-tailed deer to levels of disturbance caused by human recreation and predicted that deer reduce their activity level during opening hours in the sectors of the GNR accessible to the public (Prediction 3).

## Results

### White-tailed deer detections (prediction 1)

Camera trapping was conducted at 71 locations in the preservation sector, 81 locations in the public sector and 9 locations in the service sector (Fig. 1). On average, the cameras were active for 30 days, ranging from 10 to 46 days, for a total sampling effort of 4,300 camera-days over the duration of the study (Table 1). The detection zone of each camera ranged from 4.05 to 65.83 m<sup>2</sup>, with an average area of 18.92 m<sup>2</sup> (Table S1).



**Fig. 1.** (a) Map of the area surrounding the Gault Nature Reserve of McGill University (Mont-Saint-Hilaire, Quebec, Canada); (b) main ecotype categories (tree essences assemblages) present at the GNR; FC1: red oak stands, FE1: maple/hickory stands, FE2: maple/basswood stands, FE6: maple/red oak stands, MJ1: yellow birch/sugar maple stands, RP1: pine (white or red) stands, RT1: hemlock stands; (c) GNR with sectors, trails in grey, and camera locations coloured by set-up date (Start). This figure was created using the packages *raster*<sup>79</sup>, *rnatuarearth*<sup>80</sup> and *sf*<sup>56</sup> in R<sup>57</sup>.

	Sector		
	Preservation	Public	Service
# Camera locations	71	81	9
# Camera-days	1961	2048	291
# Deer detections			
Adult Female	666 (40.3%)	883 (50.7%)	153 (37.0%)
Adult Male	218 (13.2%)	173 (9.9%)	28 (6.8%)
Juvenile	418 (25.3%)	408 (23.4%)	137 (33.2%)
Unknown	351 (21.2%)	276 (15.9%)	95 (23.0%)

**Table 1.** Number of camera locations, sampling effort (camera-days), and number and proportion of white-tailed deer detections per sex-age class and by sector of the GNR.

Smooth term	edf	Chi.sq	p.value	
s(Sector)	0.0000	0.0000	0.7654	
s(Habitat 1)	1.0000	2.3695	0.1237	
s(Habitat 2)	1.4610	1.8009	0.2481	
s(Habitat 3)	2.9561	11.1545	0.0221	*
s(Elevation)	1.5024	1.2181	0.4386	
s(Trail Distance)	1.0003	17.9951	<0.0001	***
s(Trail Density)	1.0005	0.0000	1.0000	
s(Trail Distance, Trail Density)	3.2195	5.9305	0.0093	**
s(Trail Distance): Sector preservation	1.0004	6.3084	0.0120	*
s(Trail Distance): Sector public	2.4388	47.8486	<0.0001	***
s(Trail Distance): Sector service	1.0000	0.0000	1.0000	
s(Trail Density): Sector preservation	1.0002	0.0000	0.9992	
s(Trail Density): Sector public	1.4716	0.2993	0.8144	
s(Trail Density): Sector service	0.0000	0.0002	0.9897	

**Table 2.** The effects of the Sector, Habitat, Elevation, Trail Distance, and trail density on the number of deer detections of white-tailed deer at the Gault Nature Reserve. Sampling effort was included as an offset. Edf: effective degrees of freedom, Chi. Sq: Chi square statistics. Deviance explained = 34.6%;  $n = 161$ ; \*\*\*:  $P < 0.001$ , \*\*:  $P < 0.01$ , \*:  $P < 0.05$ .

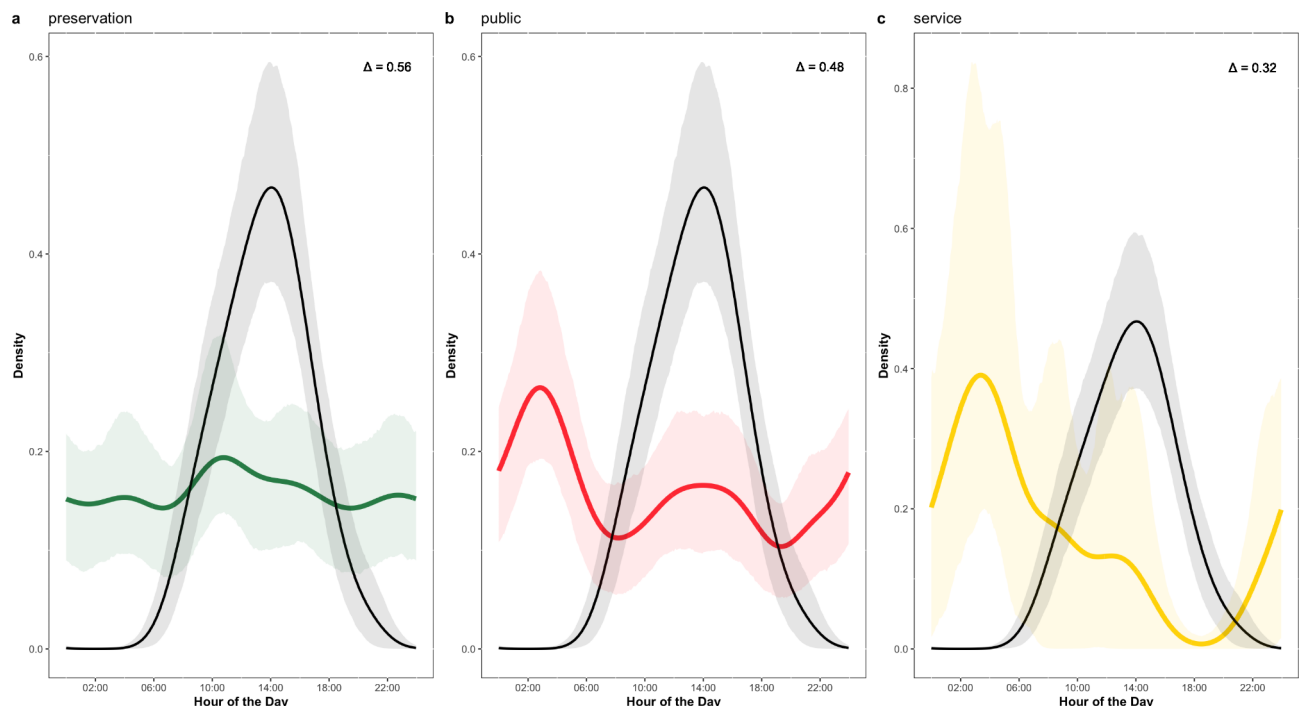
We recorded 3,665 independent detection events categorised into four different sex-age classes (i.e. juveniles, adult males, adult females, and unknown). We detected more adult females (1,702 detections) than any other class (419 adult male and 963 juvenile detections, Table 1). When considering sampling effort, the detection rate was significantly higher for females than for other classes in all three sectors (all  $P < 0.0001$ , Table S2). Juveniles were detected at a higher rate in the service sector than in the public and preservation sectors ( $P < 0.006$  and  $P < 0.004$ , respectively) but the detection rate of adult males and females did not differ across sectors (Table S2).

**Spatial distribution (prediction 2)**

The distribution of white-tailed deer varied across the GNR, and our GAM model explained 34.6% of the deviance. Deer at the GNR were more frequently detected when further away from a hiking trail ( $\chi^2 = 17.96$ ,  $P < 0.0001$ ; Table 2). This effect was most significant in the public sector of the GNR (interaction term,  $\chi^2 = 47.85$ ,  $P < 0.0001$ ), as well as in the preservation sector, but not in the service sector (Table 2). We also detected an effect of trail density on deer detections, although only when in interaction with the distance to the trail ( $\chi^2 = 5.93$ ,  $P < 0.0094$ ). Lastly, deer were detected at a higher rate in forest stands dominated by yellow birch (*Betula alleghaniensis*), sugar maple (*Acer saccharum*) and eastern hemlock (*Tsuga canadensis*), as revealed by a significant effect of the Habitat 3 variable ( $\chi^2 = 11.16$ ,  $P < 0.023$ ; Table 2). Most of these habitats were located on the edges of the reserve (Fig. 1). Other covariates included in the model (i.e. Habitat 1, Habitat 2 and elevation) had no significant effect on deer detections (Table 2).

**Diel activity (prediction 3)**

The level of activity of deer in the preservation sector was significantly higher than in the service sector ( $W = 8.84$ ,  $P < 0.003$ ) and slightly higher than in the public sector, although this difference was only marginally significant ( $W = 2.87$ ,  $P = 0.09$ ). The pattern of deer activity did not differ statistically across the three sectors, with coefficients of overlaps of 0.67 (preservation vs. service sectors,  $P = 0.06$ ), 0.76 (public vs. service sectors,  $P = 0.58$ ), and 0.87 (preservation vs. public sectors,  $P = 0.18$ ). Deer activity level remained relatively constant throughout the day in the preservation sector, while in both the public and service sectors, deer showed a peak



**Fig. 2.** Diel activity pattern averaged across the duration of the study for white-tailed deer in the three sectors of the GNR and for hikers in the public sector. **(a)** Preservation sector, **(b)** public sector, **(c)** service sector. Deer activity in **(a)**, **(b)**, and **(c)** is displayed with a coloured curve (green, red and yellow) matching the colours in Fig. 1c, and hiker activity is displayed with a black curve. Shaded ribbons represent confidence intervals for each density curve.  $\Delta$ : coefficient of overlap in activity patterns between deer and hikers.

of activity early in the morning (Fig. 2). In the public sector, the deer activity level peaked at 2:48, reached a minimum level at 8:12, then remained constant at this low level throughout the rest of the day (Table S3). The largest deer activity level observed at the GNR occurred early in the morning in the service sector where it peaked at 3:22, but then decreased constantly throughout the day until it reached the lowest level of activity observed at the GNR by 18:28 (Table S3).

The level of activity of hikers coincided with the opening hours of the GNR, and the activity pattern of visitors throughout the day differed significantly from the activity pattern observed in deer in the preservation (coefficient of overlap = 0.56,  $P < 0.0001$ ), public (coefficient of overlap = 0.48,  $P < 0.0001$ ), and service (coefficient of overlap = 0.32,  $P < 0.0001$ ) sectors of the GNR (Fig. 2).

## Discussion

We presented empirical evidence of the effect of human presence on the activity pattern and space use of white-tailed deer in a unique natural setting, the Gault Nature Reserve in southern Quebec. Consistent with our prediction that human recreation impacts the activity of deer, we detected behavioural adjustments in the response of deer to the presence of the public, both across space and over time.

## Relative abundance and population structure

The GNR is an island of forested habitat surrounded by residential development along its edges<sup>36</sup>, and it is situated within a landscape of suburban and agricultural land<sup>37,38</sup>. Due to these landscape features, the GNR acts as a refuge for wildlife such as white-tailed deer. Furthermore, natural predators such as gray wolf (*Canis lupus*) or mountain lion (*Puma concolor*) are absent from the GNR, making the coyote (*C. latrans*) the only predator able to put some predation pressure on the deer population in this area. However, coyotes mostly prey on fawns and have little effect on the abundance of white-tailed deer<sup>39</sup>. Additionally, hunting is prohibited at the GNR, but not in its vicinity<sup>40</sup>. As a result, the GNR harbours a large population of white-tailed deer estimated at 7.8 to 13.0 deer/km<sup>2</sup>, well above the region's estimated carrying capacity of 5 deer/km<sup>2</sup><sup>41,42</sup>. The population of white-tailed deer at the GNR also differs from the regional population in its structure. We found that the adult sex-ratio was highly skewed towards females, deviating from the theoretical 50:50 ratio expected in vertebrates. Such an unbalanced detection rates between adult males and females may be the result of hunting pressure at the foot hill of the GNR, with the selective removal of adult males, and a resulting increase in female relative abundance, which would be reflected in the population at the GNR. Distinct behaviour between males and females may also result in spatial segregation, for example with males tending to avoid open habitats with a strong hunting pressure to a larger extent than females<sup>43</sup>, or females with a fawn favouring habitats providing more nutritious forage than males<sup>44</sup>, and lactating females being more active than males<sup>45</sup>. Our study overlapped with the breeding season of white-tailed deer, which starts at the end of October and is centred in November,

during which adult females may converge in a larger proportion than males to the GNR. This hypothesis is further supported by our higher detection rate of juveniles than males in all three sectors of the GNR.

### Spatial avoidance

White-tailed deer were not detected at a larger rate in the preservation sector, which is closed to the public, than in sectors of the GNR accessible to the public (Prediction 1). However, at a finer spatial scale, white-tailed deer exhibited behavioural adjustment in space use. The deer detection rate was higher at locations further away from a hiking trail and in forest stands with less suitable forage and located on the edges of the reserve (Prediction 2), confirming our hypothesis of spatial avoidance of the public by deer. Deer at the GNR were consistently detected at a higher rate in forest stands dominated by yellow birches and sugar maples, and to a lesser extent by hemlock trees. The white-tailed deer is a selective feeder<sup>46,47</sup> and while yellow birch may be eaten, it is not a favoured browse of white-tailed deer<sup>48,49</sup>. In addition, the deer detection rate was not significantly larger in tree stands dominated by favoured summer forage such as red oak (*Quercus rubra*) and maple (*Acer* sp.)<sup>46,47</sup>. Finally, the two habitats associated with a higher detection rate of deer at the GNR only cover a relatively small portion of the GNR (3.4% of the total area) and are mostly located on the edge of the GNR, except for a hemlock tree stand located west of the lake. Overall, deer tended to occupy habitat with less favoured forage, away from hiking trails. We thus posit that white-tailed deer at the GNR use locations not for a specific forage, but rather as a mechanism to limit their interactions with hikers at the GNR, a hypothesis in line with previously reported findings. For instance, wild reindeer (caribou) (*R. tarandus*) occur at a lower density in proximity to a ski resort in Norway, although forage quality is relatively lower in habitats located away from human disturbance<sup>50</sup>.

### Temporal avoidance

In addition to this shift in spatial distribution, we also detected the effect of recreation on the diel activity pattern of white-tailed deer at the GNR. Deer exhibited a higher activity level in the sector closed to the public when compared with sectors accessible to the public (Prediction 3), supporting the hypothesis that the level of human activity affects deer behaviour. Furthermore, white-tailed deer are more active at dawn and sunset in areas free of human disturbance (e.g.<sup>51</sup>), but their diel activity followed a different pattern in all three sectors of the GNR. First, the deer activity level remained constant throughout the day on the preservation side of the GNR. Food availability and perceived risk of predation determine the shape of the activity pattern of white-tailed deer and the occurrence of peaks of high activity level during the day<sup>52,53</sup>. As there is no large predator at the GNR, hikers are the sole source of disturbance that could be perceived as a predation risk. As the preservation sector of the GNR is relatively isolated from the public, the constant activity level we report for deer in this sector may thus be the result of a low perceived threat from hikers relative to the availability of forage. Secondly, deer also displayed a pattern of activity deviating from natural conditions in sectors accessible to hikers. While deer showed a peak in activity early in the morning, there was no apparent increase in activity level at dusk, as would have been expected in a deer population<sup>45</sup>. The low level of deer activity we observed at dusk suggests that they may use other habitats outside the GNR after sunset. Such behaviour has been reported for a population of white-tailed deer in Pennsylvania, which forage in open habitats outside the forested area after sunset, before returning to the forest cover by dawn<sup>53</sup>.

### Conclusions and implications

The increasing populations of white-tailed deer throughout northeastern America, combined with an ever-increasing demand of the public for outdoor activities, raises chances of encounters and interactions between humans and deer. In response, we showed that deer may seek refuge in areas less prone to human disturbances. Such a behavioural adjustment may have management and conservation implications for the GNR, as white-tailed deer browsing is known to have profound and long-lasting impacts on plant communities, especially in areas targeted for conservation<sup>30–35</sup>. Our work illustrates the need for a better understanding of changes in the spatiotemporal distribution of deer in response to human presence and improving efforts in habitat conservation in protected areas open to the public.

### Materials and methods

#### Study area

The study took place at the Gault Nature Reserve of McGill University located on Mont St-Hilaire in southern Quebec (45°33'N, 73°10'W), 30 km east of Montreal (Fig. 1). The GNR covers an area of 9.7 km<sup>2</sup> and occupies a hill peaking at 414 m in elevation. It is dominated by sugar maple and red oak and is the largest untouched remnant of old-growth primeval forest in the St. Lawrence valley<sup>54,55</sup> (Fig. 1).

The GNR is divided into two main sectors (Fig. 1). The preservation sector, covering 4.2 km<sup>2</sup> (~43% of the GNR), has a primary mission of conservation. It is closed to the public and used solely for teaching and research activities, thus supporting a notably low level of human activity. The public sector covers 5.2 km<sup>2</sup> (~53% of the GNR) and hosts more than 250,000 visitors each year on its 25 km hiking trail network. A third smaller service sector covers only 0.3 km<sup>2</sup> (~3% of the GNR) and consists of accommodations for field researchers, administrative offices, as well as public amenities extensively used by hikers at the GNR. This latter area experiences significant vehicle and foot traffic during the day and is usually inhabited throughout the field season (May–September). Access to the study site and camera trapping was approved by the Gault Nature Reserve of McGill University.

#### Sampling design

To establish our sampling design, we used the function `st_sample` in the package `sf`<sup>56</sup> in R<sup>57</sup> to generate 180 random locations covering the whole territory of the GNR (Fig. 1c). We deployed 60 unbaited camera traps and



relocated each of them twice, but as some cameras malfunctioned, we surveyed a total of 163 locations (Fig. 1). Based on empirical evidence, it has been suggested that 20 cameras are sufficient to obtain a precise estimation of occupancy for a common species, and that a deployment duration of 3 to 5 weeks (i.e. 21 to 35 days) is required for an accurate estimation of detection rates<sup>58</sup>. Here, we deployed the cameras over a period of 120 days (30 days on average per location), between July 5th and November 1st, 2018. The number of cameras deployed was relatively constant throughout the study, except towards the end of the sampling. To determine the minimum number of active cameras beyond which no significant improvement in detection rate was achieved, we plotted the curve of the cumulative frequency of detection rate adjusted for the area of the detection zone of each camera trap. Detection rate plateaued at a threshold of 1 detection event/100 trap nights. We thus truncated the dataset from 7 July to 6 October 2018, outside of which the detection rate was significantly lower due to inadequate sampling effort. The truncated dataset comprised detections across 161 out of the original 163 sampling sites (Table 1). The distance between each camera location was on average 1,513 m, and ranged from 33 m to 3,723 m.

We used Spypoint Force-10 infrared motion-activated trail cameras<sup>59</sup> and affixed each camera to a tree at a height of approximately 75 cm above ground. We avoided pointing the camera towards any obvious corridor of animal movement or deer trail, or placing the camera directly in front of understory vegetation or low-hanging branches that could trigger the camera in windy conditions<sup>60,62</sup>. The cameras were set for continuous action throughout the day and night and configured to take a burst of 3 photographs every time they detected movement, with no delay between detection.

Sampling effort varied across cameras depending on their detection zone area and the number of days during which they were active. As camera traps are triggered when motion is detected in their detection zone<sup>63</sup>, we measured the radius and width (angle) of this detection zone for each camera by approaching the camera, walking at different distances perpendicular to where the camera was pointing, and measuring the distance at which the researcher was first detected, a standard method used in camera trap studies<sup>60,64</sup>. We calculated the area of the detection zone (variable *Area*) at each camera location as  $\theta / 360 \times \pi \times r^2$ , where  $\theta$  is the angle of the detection zone, and  $r$  its radius. We also calculated the total number of days when the camera was active (variable *Effort*) and calculated sampling effort as  $(\log \text{Effort} + \log \text{Area})$ .

### Deer detection

We inspected visually the photographs, recorded the total number of animals observed, and categorised the deer detected into one of four sex-age classes (juvenile, adult male, adult female, and unknown). Each detection event was defined as a continuous series of pictures, delimited from the next series of pictures by at least 60 s<sup>65</sup>. Following<sup>66</sup>, we used a threshold of 15 min. to retain the number of independent events per sex-age class for further analyses.

We occasionally detected more than one individual per detection event (up to three individual deer), and we used the deer detections (count of deer) in all analyses. We recorded an initial 3,853 detection events, representing a total of 3,665 independent detection events. The 188 observations filtered out represented a minimum of 166 distinct individuals captured multiple times within 15 min (105 adult females, 16 adult males, 35 juveniles, and 10 individuals of unknown sex-age class).

### Spatial covariates

The camera locations were characterised by distinct habitats and varied in their elevation. We first retrieved the elevation at each camera location using the package *elavatr*<sup>67</sup>. Camera site elevation ranged from 97 to 389 m (Table S1). We then used the 2017 inventory of ecotypes produced by the Government of Quebec<sup>68</sup> to characterise the habitat conditions encountered by deer in our study area (Fig. 1). The ecotype is a categorical variable used to classify forest stands by their dominant tree species composition combined with the type of deposits in forested habitats<sup>69</sup>. As we only needed to characterise the type of forage available to deer at a given location, we aggregated the ecotypes based on their tree species composition only, resulting in 7 distinct ecotype categories represented in the GNR (Fig. 1).

We then used these categories to quantify the types of forage available to deer around each camera location within an area matching its home range size. The home range area of white-tailed deer at the GNR has not been quantified, so we used two published home range sizes from white-tailed deer populations from southeastern Quebec where climatic and habitat conditions were similar to our study system (i.e. limited to the northern portion of the distribution range of the deer). The average summer home range of white-tailed deer in forested habitat east of Quebec City was estimated at 69 ha (i.e. a radius of 469 m)<sup>47,70</sup>, and at 42 ha (i.e. a radius of 365 m) on Anticosti Island, located further east in the mouth of the St. Lawrence River<sup>71</sup>. We thus calculated the proportion of different ecotype categories within a 400 m radius around each camera location to cover an area comparable to that of the home range of each deer detected. Next, we extracted the percent cover of each ecotype category represented within the 400 m radius buffer around each camera location. Finally, we ran a Principal Component Analysis (PCA) on the percent cover of the 7 ecotype categories and retained the first 3 components that cumulatively explained 73% of the variance (Habitat 1, Habitat 2 and Habitat 3) to characterise the habitat around each camera location (Figure S1). The first axis, Habitat 1, was positively correlated with the relative cover of maple and basswood (FE2), and negatively correlated with red oak (FC1). The second axis, Habitat 2, was negatively associated with the relative cover of maple and red oak (FE6) as well as with pine (RP1). The third axis, Habitat 3, was positively correlated with the relative cover of yellow birch and fir (MJ1), as well as with hemlock (RT1). The first two axes (Habitat 1 and 2) were thus both negatively associated with the availability of favoured summer forage for white-tailed deer, namely red oak and maple, while the third axis (Habitat 3) reflected the availability of less favoured forage such as yellow birch.

### Human infrastructure variables

We used measures of the trail infrastructure as a proxy for the distribution of human activity at the GNR. While hikers do not have access to the preservation sector and the hiking trails are all located in the public sector of the GNR, some camera locations in the preservation and service sectors were situated close to the public sector and hiking trails. Furthermore, the service sector is heavily used by hikers, even more so than the public sector, since each hiker will use the service sector, while they will only use a portion of the public sector (i.e. only some of the trails). We thus calculated the degree of isolation from the hiking trails for each camera location in all three sectors of the GNR.

To estimate the degree of isolation, we first calculated the Euclidian distance to the closest trail for each camera location. As the response of wildlife to a disturbance is expected to decline exponentially with the distance to that disturbance (e.g.<sup>9,72</sup>), we calculated seven decay distance variables as  $e^{-\alpha / dist}$ , where  $dist$  is the Euclidean distance in meters between the camera location and the nearest trail and  $\alpha$  was set at 10, 50, 100, 200, 400, 600 and 1,000<sup>73,74</sup>. The decay function transforms and scales the Euclidian distance to values ranging from zero to one, with values reaching one when closest to the trail. Next, we calculated the trail density around each camera as the total length of the trails intersecting with a buffer of 50 m radius around each camera location, as this is the maximum flight initiation distance (FID) reported for the white-tailed deer<sup>11,22</sup>.

Camera locations in the preservation sector were more isolated (located further away from the trails and with smaller trail densities around the camera locations) than in the public sector. As the distance from the trail increased, the trail density around each camera location decreased ( $R = -0.39$ ,  $P < 0.0001$ ). The distance to the nearest trail ranged from 6 to 335 m in the public sector, and from 27 to 1,651 m in the preservation sector. The trail density ranged from 0 to 160 m in the public sector, and from 0 to 88 m in the preservation sector; in the preservation sector, only 4 camera location buffers intersected with a trail (Fig. 1, Table S1).

### Spatial variation in deer detections

To test for an effect of hiker presence on the detection rate of deer at the GNR (Prediction 1), we fit a generalized linear model using the *glmmTMB* package in R<sup>75</sup> with deer detections as a response variable and the factors Sector and Sex-age class as covariates. We included an offset to correct for sampling effort as  $offset(\log Effort + \log Area)$  and the camera location as a random factor. We used a negative binomial family with zero inflation, suitable for count data containing a large number of zeros. We then conducted post-hoc mean comparisons with Bonferroni corrections to assess the significance of the differences in detection rate between the four deer sex-age classes and across the three sectors of the GNR using the package *emmeans* in R<sup>76</sup>.

Next, to test for an effect of proximity to the trail infrastructure and habitat characteristics on deer detection rate at a given camera location (Prediction 2), we modelled deer detections at the camera locations by fitting General Additive Models (GAMs) with a negative binomial family, using the *mgcv* package<sup>77</sup>. In all models, we included covariates that varied at the scale of the GNR, including the sector of the GNR (preservation, public, and service), habitat variables (the first three PCA axes Habitat 1, Habitat 2, and Habitat 3), and elevation. We also included in each model two variables related to human activity: one variable representing the distance to the nearest trail (the Euclidean distance to the nearest trail in the first model, and one of the seven decay distances in the remaining seven models), and the trail density around each camera. The distance to the trail, trail density and elevation were scaled. We tested for variable collinearity, and none of the correlation coefficients between the variables was above a threshold value of 0.7. In each model, sampling effort was included as an offset as  $offset(\log Effort + \log Area)$ <sup>77</sup>. We ran eight distinct models with the same structure, but each with one of the distance variables described above, and used Akaike Information Criterion corrected for small sample sizes (AICc) for model selection to identify the best fitting distance variable. Based on AICc, we used a decay distance with an alpha of 10 to select the best fitting model (Table S4).

### Deer and hiker activity patterns

To test for an effect of the hourly number of visitors at the GNR on the activity of deer (Prediction 3), we analysed the diel activity pattern of deer at the GNR and compared it across the three sectors of the GNR, as well as with the pattern of daily activity of hikers using the package *activity*<sup>78</sup>. We fit a kernel density function with 1,000 bootstrap iterations of the count of deer per hour to the time of the day converted in radian time (ranging from 0 to  $2\pi$ ) to estimate the diel activity level of deer in each sector of the GNR. We corrected the deer count for sampling effort by dividing the number of deer detections by the number of active cameras and by the sum of the detection zone areas for all active cameras at each hour. We then estimated the daily activity of hikers at the GNR using the number of visitors recorded by the GNR for management purpose throughout the year of 2017 with an ecometer, an automatic system triggered by movement which records foot traffic data and allowed us to extract the hourly proportion of hikers at the GNR. We fit a kernel density function to the number of hikers per hour to estimate the activity level of hikers at the GNR over the duration of the study. We then calculated the coefficients of temporal overlap ranging from zero (no overlap) to one (full overlap) and tested for differences in the activity pattern across groups (deer in the three sectors, and hikers) with 1,000 bootstrap iterations. Using a similar method, we also compared deer activity levels at six times throughout the day (0:00, 3:00, 8:00, 13:00, 18:00 and 23:00) within each sector of the GNR. We used the Wald statistics to assess the significance level of all comparisons of activity levels between groups (i.e. deer across the three sectors, deer and hikers, and deer at different times of the day).

All analyses were conducted in R version 4.3.1<sup>57</sup>.

### Data availability

All data used for this study are included in this article as a Supplementary Information file.

Received: 30 May 2024; Accepted: 18 December 2024

Published online: 30 December 2024

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## Acknowledgements

VM was supported by NSERC Discovery Grants #2017-03839 and #2024-04374, MHSL was supported by NSERC Discovery Grants #2016-05196 and #2022-0430, and FT by a fellowship from the Gault Nature Reserve. We thank the staff at the Gault Nature Reserve for access to our field sites, support in field data collection, and sharing visitor statistics with us. We would like to thank K. Malcolm, T. Leslie and two anonymous reviewers for their constructive comments on previous versions of this manuscript.

## Author contributions

VM, FT and MHSL conceived the ideas and designed the methodology; FT collected the data; VM and FT analysed the data; VM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## Declarations

### Competing interests

The authors declare no competing interests.

### Additional information

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1038/s41598-024-84000-3>.

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