RÉPONSES SPATIOTEMPORELLES DE GRANDS MAMMIFÈRES À UN GRADIENT D'INTENSITÉ D'ACTIVITÉS RÉCRÉATIVES DANS QUATRE PARCS NATIONAUX

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RÉSUMÉ

L'utilisation de l'espace par les animaux résulte d'un compromis entre l'acquisition des ressources et le risque de prédation. Dans les paysages contemporains, les activités humaines, incluant les activités récréatives, modifient ce compromis en influençant la perception du risque et en restructurant le « paysage de la peur ». En effet, les activités récréatives peuvent induire diverses réponses anti-prédatrices chez les grands mammifères, influençant ainsi leur répartition spatio-temporelle. Dans les aires protégées, la croissance rapide de la fréquentation par les visiteurs représente un défi important pour la conservation, en particulier pour les grands mammifères, en raison de l'étendue de leurs besoins en espace et de leur sensibilité aux perturbations humaines. Mon mémoire évalue l'influence des activités r écréatives sur l'utilisation de l'espace par de grands mammifères dans quatre parcs nationaux du Québec, en tenant compte des traits d'histoire de vie des espèces et du contexte écologique. J'ai posé l'hypothèse selon laquelle les activités récréatives, perçues comme un risque, induisent des réponses comportementales variant selon le statut de proie ou de prédateur, le niveau de fréquentation des parcs et le contexte paysager, et modifiant la répartition spatio-temporelle des espèces. Les parcs étudiés (Mont-Orford, Grands-Jardins, Jacques-Cartier et Monts-Valin) couvrent un gradient de superficie, d'intensité de fréquentation et d'anthropisation du paysage. Un total de 517 pièges photographiques a été déployé sur une période de deux étés, générant 34 984 jours-caméras et près de 5 millions d'images. Ces données ont permis de quantifier à la fois les détections animales et l'intensité des activités récréatives. Les détections des espèces de grands mammifères, lorsque suffisantes, ont été modélisées en fonction de la distance au sentier le plus proche, de l'intensité d'utilisation humaine des sentiers et de covariables environnementales, en distinguant, lorsque possible, les périodes diurnes et nocturnes pour capter des réponses temporelles à fine échelle. Mes résultats révèlent des réponses propres à chaque espèce et fortement dépendantes du contexte. L'orignal (*Alces alces americana*), un grand herbivore à histoire de vie lente et faible tolérance aux humains, présentait des occurrences plus élevées loin des sentiers, ce qui suggère une perte fonctionnelle d'habitat à proximité des sentiers. À l'inverse, le cerf de Virginie (*Odocoileus virginianus*) présentait des réponses non linéaires et une grande plasticité comportementale. Ses détections étaient maximales à des distances intermédiaires et une forte fréquentation diurne des sentiers par les humains était associée à une diminution des occurrences nocturnes à proximité de ceux-ci. Les modèles analytiques des données d'ours noir (*Ursus americanus*) n'ont révélé aucune relation avec les variables associées à notre hypothèse. Finalement, le nombre de détections d'autres espèces (coyote *Canis latrans*, loup *Canis lupus*, caribou *Rangifer tarandus caribou*) était insuffisant pour effectuer des analyses statistiques. Les réponses obtenues suggèrent que les perturbations récréatives interagissent avec les traits d'histoire de vie des espèces et le contexte local pour

structurer l'utilisation de l'espace. Mon mémoire montre que les activités récréatives agissent comme un processus spatio-temporel interactif, où l'intensité et la phénologie de l'activité humaine façonnent l'utilisation de l'espace par les grands mammifères. En intégrant des analyses multi-espèces, multi-sites et spatio-temporelles à fine échelle, mon travail suggère que les activités récréatives peuvent agir comme un filtre écologique, favorisant les espèces tolérantes aux perturbations et modifiant la dynamique des communautés animales. Mes résultats fournissent des paramètres clés pour améliorer la gestion des activités récréatives afin de favoriser une coexistence durable entre les usages récréatifs et la conservation de la faune dans les aires protégées.

Mots clés : aires protégées, *Alces alces americana*, caméras à détection automatique, réponses comportementales, *Odocoileus virginianus*, perception du risque, utilisation de l'espace

ABSTRACT

Animal space use reflects a trade-off between resource acquisition and predation risk. In contemporary landscapes, human activities, including outdoor recreation, are increasingly embedded within this trade-off by reshaping risk perception and modifying the "landscape of fear." Disturbances from recreational activities can induce a range of anti-predator responses in large mammals, thereby influencing their spatiotemporal distribution. In protected areas, the rapid growth of recreational use poses important conservation challenges, particularly for large mammals, considering their extensive spatial requirements and sensitivity to human disturbance. My thesis investigates how recreational activities influence space use by large mammals in four of Quebec's national parks, while accounting for species' life-history traits and ecological context. I hypothesized that recreational activities are perceived as a risk, inducing behavioural responses that vary with predator–prey status, the intensity of human trail use, and landscape context, thereby altering the spatiotemporal distribution of large mammals. The parks surveyed (Mont-Orford, Grands-Jardins, Jacques-Cartier, and Monts-Valin) represent a gradient in park area, recreational pressure, and land use intensity. I deployed an extensive camera-trap network (517 cameras, 34,984 camera-days) and collected ~5 million images over two summers to quantify wildlife detections and recreational intensity. Species detections, when sufficient, were modelled as a function of distance to the nearest trail, human trail use and environmental covariates, while distinguishing between daytime and nighttime periods whenever possible, to capture fine-scale temporal responses. My results revealed strong context-dependent and species-specific responses. Moose (*Alces alces americana*), a large herbivore with a slow life-history strategy and low tolerance to humans, exhibited higher detection rates further from recreational trails, suggesting functional habitat loss near trails. On the other hand, white-tailed deer (*Odocoileus virginianus*) exhibited non-linear responses to trail proximity and high behavioural plasticity, with peak detection rates at intermediate distances and carry-over effects, whereby high daytime recreation was associated with lower detection rates near trails at night. Candidate models for black bear (*Ursus americanus*) did not reveal any relationship with the variables linked to our hypothesis. Finally, detection numbers of other species (coyote *Canis latrans*, grey wolf *Canis lupus*, caribou *Rangifer tarandus caribou*) were insufficient to perform statistical analyses. These species-specific responses suggest that recreational disturbance interacts with species traits and local context to structure wildlife space use. Conceptually, my thesis advances our understanding of recreation as an interactive spatiotemporal process in which the intensity and timing of human use shape space use by large mammals. By integrating multi-species, multi-site and fine-scale spatiotemporal analyses, my work suggests that recreational activities act as an ecological filter, favouring disturbance-tolerant species and altering animal community dynamics. These findings

provide key parameters to improve our management of recreational activities and favour long-term coexistence between recreation and wildlife conservation in protected areas.

Keywords: *Alces alces americana*, behavioural responses, camera traps, *Odocoileus virginianus*, protected areas, risk perception, space use

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INTRODUCTION GÉNÉRALE

Les changements environnementaux induits par l'activité humaine, tels que les changements climatiques, la perte et la fragmentation des habitats, la pollution et la propagation d'espèces exotiques, constituent aujourd'hui l'un des principaux moteurs du déclin de la biodiversité à l'échelle mondiale (Chen et al., 2022 ; Dirzo et al., 2014 ; Ipbes, 2019 ; Newbold et al., 2015 ; Sih, 2013). L'expansion rapide des infrastructures de transport, l'urbanisation, l'agriculture et l'exploitation forestière transforment les paysages naturels en mosaïques de milieux fragmentés, dans lesquelles les milieux faiblement perturbés deviennent de plus en plus rares (Haddad et al., 2015 ; Tucker et al., 2018). Cette perte de continuité spatiale réduit la disponibilité d'habitats fonctionnels, c'est-à-dire des zones offrant les ressources et conditions nécessaires à la survie, à la reproduction d'individus, ce qui réduit la connectivité du paysage, c'est-à-dire les échanges d'individus et de gènes entre les populations (Crooks et al., 2017 ; Newbold et al., 2015 ; Polfus et al., 2011).

Plusieurs espèces de grands mammifères sont particulièrement vulnérables à l'altération des paysages naturels car leur grande capacité de déplacement s'accompagne d'exigences spatiales élevées, notamment de vastes domaines vitaux et une dépendance à des habitats peu fragmentés ainsi que de faible densité de population (Crooks et al., 2011 ; Hubbard et al., 2022 ; Tucker et al., 2018). À titre d'exemple, les populations boréales du caribou des bois (*Rangifer tarandus caribou*) nécessitent de grandes étendues ininterrompues de forêt mature peu perturbée. Leur déclin illustre clairement comment la fragmentation de leur habitat essentiel par la coupe forestière, le réseau routier qui y est associé de même que par d'autres infrastructures anthropiques (p. ex. mines, exploration sismique) a réduit la qualité et l'étendue des zones favorables, compromettant ainsi la viabilité de ses populations (Leblond et al., 2013 ; Polfus et al., 2011 ; St-Laurent et al., 2022). De tels changements rapides ont altéré la structure et la composition des paysages naturels depuis quelques

décennies, ce qui se répercute directement sur la répartition spatiale de la faune et sur les processus écologiques qui en découlent, notamment les interactions trophiques (Haddad et al., 2015 ; Miller et al., 2022).

La répartition spatiale, modulée par les traits d'histoire de vie

Pour de nombreuses espèces, la répartition spatiale découle des patrons individuels de sélection de l'habitat, eux-mêmes dictés par un compromis entre l'acquisition de ressources et la réduction du risque de prédation (Borregaard et al., 2009 ; Fortin et al., 2005 ; Lesmerises et al., 2017 ; Smith et al., 2024). Lorsqu'un individu perçoit un niveau de risque de prédation élevé, il adopte généralement des comportements tels qu'une vigilance accrue ou un déplacement vers des secteurs jugés plus sécuritaires, ce qui entraîne des coûts énergétiques et réduit le temps disponible pour l'alimentation (Frid et Dill, 2002 ; Lima et Dill, 1990). Dans des cas extrêmes, ceci peut avoir des conséquences démographiques sur la proie (Smith et al., 2024). À l'inverse, un compromis favorisant l'utilisation d'habitats riches en ressources peut accroître l'exposition aux prédateurs, illustrant l'arbitrage fondamental entre sécurité et accès à la nourriture (Duchesne et al., 2000 ; Gill et al., 2001). Toutefois, la position exacte de ce « point de compromis » varie selon les espèces, et plus précisément en fonction de traits d'histoire de vie tels que la taille corporelle, la longévité, le rythme de reproduction et la vulnérabilité à la prédation (Blumstein, 2006). Il est en effet reconnu que ces traits déterminent la manière par laquelle les individus tentent de trouver un point d'équilibre entre sécurité et acquisition de ressources (Geffroy et al., 2020; Suraci et al., 2021).

Les espèces à histoire de vie lente — caractérisées par une grande taille corporelle, une maturité tardive et de faibles taux de reproduction — tendent à privilégier la survie des adultes et adoptent des stratégies plus intolérantes au risque (Blumstein, 2006 ; Fritz et al., 2009 ; Gamelon et al., 2014). À l'inverse, les espèces à histoire de vie plus rapide, de plus petite taille et à renouvellement démographique rapide, peuvent tolérer davantage de risques si l'accès aux ressources est accru (Gaillard et al., 2000 ; Oli, 2004). Par exemple, Suraci et al. (2019) ont montré que l'exposition à des voix humaines modifiait l'utilisation de l'habitat

selon les traits des espèces : les grands prédateurs comme le couguar (*Puma concolor*), à histoire de vie lente, évitaient ces zones, tandis que de petites espèces à reproduction rapide comme la souris sylvestre (*Apodemus sylvaticus*) y augmentaient leur recherche de nourriture. Dans ce cadre, la théorie du risque de prédation prédit que les individus adoptent des stratégies anti-prédateurs ajustées aux variations spatiales et temporelles du danger perçu (Laundré et al., 2010), ce qui donne à la sélection de l'habitat un caractère fondamentalement contextuel, dépendant à la fois des conditions environnementales et des caractéristiques intrinsèques des espèces (Blumstein, 2006 ; Gaynor et al., 2019).

Le « paysage de la peur » et ses effets sur l'utilisation de l'espace

Selon l'hypothèse du '*risk-disturbance'*, les mammifères réagissent aux perturbations soudaines, bruyantes ou imprévisibles en adoptant des comportements analogues à ceux observés face aux prédateurs naturels (Frid et Dill, 2002). Cette réponse s'inscrit dans le cadre théorique du « paysage de la peur », selon lequel la distribution spatiale des animaux reflète leur perception du risque de prédation (Gaynor et al., 2019 ; Laundré et al., 2010). Dans ce contexte, les activités humaines, incluant les activités récréatives, peuvent être perçues comme des sources supplémentaires de risque. Les humains peuvent ainsi être perçus comme des super-prédateurs, générant dans le paysage des gradients de risque qui influencent les déplacements, l'utilisation de l'habitat et l'activité quotidienne de nombreuses espèces (Burton et al., 2024 ; Gaynor et al., 2019 ; Suraci et al., 2019). Les effets de la chasse illustrent clairement cette dynamique : dans les paysages où la mortalité anthropique est historiquement élevée, les individus, en particulier chez les grands carnivores, manifestent une forte aversion pour les zones anthropisées (Ciuti et al., 2012 ; Guimarães et al., 2025 ; Hubbard et al., 2022 ; Muhly et al., 2011). Par exemple, les loups et les ours évitent les secteurs à forte activité humaine et se déplacent vers des habitats plus isolés dans les régions où ils sont chassés, adoptant des comportements typiques d'évitement du risque (Baillie-David et al., 2024 ; Kays et al., 2016 ; Ordiz et al., 2016).

RÉPONSES SPATIALES DE LA FAUNE FACE AUX ACTIVITÉS RÉCRÉATIVES

Longtemps sous-étudiée par rapport à la chasse, l'écologie de la récréation est aujourd'hui reconnue comme un champ essentiel de la conservation (Fennell et al., 2023 ; Larson et al., 2016 ; Miller et al., 2022 ; Naidoo et Burton, 2020). De nombreuses études montrent que les activités telles que la randonnée, le vélo de montagne ou le ski hors-piste peuvent modifier l'utilisation de l'espace par les grands mammifères, souvent par des comportements d'évitement ou une augmentation de la vigilance (Larson et al., 2016 ; Lesmerises et al., 2018 ; Neumann et al., 2011 ; Taylor et Knight, 2003). Les carnivores, par exemple, sont généralement très sensibles à la présence humaine. Le loup gris (*Canis lupus*) tend à éviter les zones fréquentées, bien qu'il puisse utiliser les sentiers comme corridors de déplacement lorsque les humains sont absents (Malcolm et al., 2020 ; Oriol-Cotterill et al., 2015 ; Whittington et al., 2005). De même, les coyotes (*Canis latrans*) évitent les secteurs à forte intensité d'activités récréatives (Patten et Burger, 2018), tandis que chez les espèces plus sensibles comme le caribou forestier, la présence humaine accroît la vigilance et réduit le temps consacré à l'alimentation (Duchesne et al., 2000). Ces réponses peuvent mener à une perte indirecte ou fonctionnelle d'habitat lorsque les zones adjacentes aux sentiers sont délaissées (Polfus et al., 2011).

Dimensions temporelles des réponses aux activités récréatives

Les effets des activités récréatives ne se manifestent pas uniquement dans l'espace, mais également dans le temps. La peur des humains peut modifier la phénologie de l'activité des grands mammifères, plusieurs espèces adoptant un mode de vie plus nocturnes afin d'éviter la présence humaine diurne (Gaynor et al., 2018 ; Lewis et al., 2021 ; Millien et al., 2024 ; Nickel et al., 2020). L'ours noir (*Ursus americanus*), par exemple, devient plus actif la nuit à proximité des sentiers et des secteurs résidentiels (Zeller et al., 2019), tandis que le coyote ajuste son activité quotidienne afin de réduire les rencontres avec les randonneurs (Nickel et al., 2020 ; Procko et al., 2022). Ces décalages temporels peuvent toutefois avoir des conséquences sur la valeur adaptative des individus, notamment lorsqu'ils

adoptent des rythmes d'activité pour lesquels leurs traits morphologiques et physiologiques ne sont pas optimaux (Gaynor et al., 2018 ; Ordiz et al., 2016).

L'intensité des réponses de la faune varie également selon le type d'activité récréative (Ciuti et al., 2012 ; Lesmerises et al., 2017 ; Lewis et al., 2021). Les activités motorisées génèrent généralement des effets plus marqués que les usages non motorisés en raison du niveau de bruit et d'une vitesse d'approche plus élevés (Ciuti et al., 2012 ; Naylor et al., 2009 ; Smith et al., 2024). Chez les wapitis, par exemple, la distance de fuite est plus grande en présence de véhicules tout-terrain (≈ 1000 m) qu'en présence de randonneurs (≈ 400 m ; Rogala et al., 2011 ; Wisdom et al., 2018) et les déplacements sont plus importants à proximité des voies motorisées (Beaupré et al., 2025). La présence de chiens peut également amplifier l'évitement des sentiers chez certains petits mammifères, herbivores et carnivores (Lenth et al., 2008), ceux-ci étant perçus comme des prédateurs potentiels ou des perturbateurs imprévisibles (Doherty et al., 2017 ; Granados et al., 2024 ; Parsons et al., 2016).

Au-delà des perturbations humaines intermittentes, plus diffuses et mobiles, les infrastructures récréatives constituent des sources de dérangement plus localisées et souvent spatialement fixes, mais persistantes, susceptibles de fragmenter l'habitat et de modifier durablement l'utilisation de l'espace (Dertien et al., 2021 ; Patten et Burger, 2018). Certaines études montrent que de grands carnivores réduisent leur activité dans les zones à forte densité d'infrastructures, tandis que des espèces plus opportunistes peuvent au contraire être plus actives à proximité de ces structures, notamment pour éviter les secteurs à forte fréquentation humaine (Nickel et al., 2020). Une exposition répétée aux structures humaines ou à la présence humaine sans conséquences immédiates pour la survie peut favoriser des processus d'habituation. Celle-ci se traduit par une diminution de la vigilance et une augmentation du temps consacré à l'alimentation, mais elle s'accompagne aussi de coûts potentiels : perte de comportements anti-prédateurs, hausse des conflits avec l'humain et augmentation de la mortalité anthropique (Geffroy et al., 2015 ; Smith et al., 2005). Le rapprochement observé chez plusieurs espèces vers des infrastructures désertées durant la pandémie de Covid-19

(Burton et al., 2024) suggère que ces réponses sont davantage liées à la présence humaine elle-même qu'aux structures en tant que telles (p. ex., Suraci et al., 2019).

L'exemple de l'ours noir illustre bien les compromis adoptés lorsque certains individus moins méfiants fréquentent les campings ou les habitations pour exploiter des ressources alimentaires anthropiques (George et Crooks, 2006 ; Zeller et al., 2019). Lorsque les animaux continuent d'utiliser des milieux attractifs mais dégradés, ou lorsqu'ils évitent les zones perturbées sans disposer d'habitats alternatifs adéquats, l'activité récréative et les infrastructures associées peuvent ainsi constituer des pièges écologiques, dans lesquels la sélection d'habitat ne maximise plus la survie ou la reproduction (Gill et al., 2001 ; Tucker et al., 2018). De tels contextes peuvent également induire un stress chronique, susceptible d'entraîner des effets démographiques négatifs, notamment une diminution de la survie ou de la fécondité (Clinchy et al., 2012 ; Corradini et al., 2024 ; Fennell et al., 2023).

La variabilité des réponses aux perturbations humaines s'explique par une combinaison de facteurs intrinsèques et extrinsèques. D'une part, la plasticité comportementale permet à certaines espèces de modifier leur stratégie d'utilisation de l'espace en fonction des conditions locales, modulant ainsi leur sensibilité aux perturbations (Burton et al., 2024 ; Gaynor et al., 2018). Les omnivores généralistes comme l'ours noir peuvent tantôt éviter les perturbations, tantôt utiliser les zones anthropisées la nuit ou s'habituer progressivement à la présence humaine (Costello et al., 2013 ; Smith et al., 2005 ; Zeller et al., 2019). D'autre part, les traits d'histoire de vie influencent également cette sensibilité aux perturbations. Chez les herbivores, la taille corporelle, la vulnérabilité à la prédation et la capacité à évaluer correctement le risque conditionnent les réponses comportementales (Gaynor et al., 2025 ; Suraci et al., 2021). Enfin, ces réponses sont modulées par le contexte paysager. Par exemple, la sensibilité face à une perturbation tend à être plus marquée dans les environnements où le contraste d'intensité de l'activité humaine est élevé, par exemple entre la semaine et la fin de semaine, ou le long de gradients de densité d'usage (Burton et al., 2024 ; Nix et al., 2018). Ainsi, les effets des perturbations humaines

ne peuvent être adéquatement interprétés qu'en tenant compte simultanément des caractéristiques des espèces et des conditions locales dans lesquelles elles évoluent.

Activités récréatives en milieux protégés : limites actuelles et perspectives de recherche

Les aires protégées jouent un rôle central dans la conservation en offrant des habitats relativement épargnés par le développement anthropique (Baker et Leberg, 2018 ; Chen et al., 2022 ; Schulze et al., 2018). Dans un contexte où les espaces naturels à l'extérieur des parcs sont de plus en plus perturbés et fragmentés, il devient crucial de conserver des secteurs exempts d'infrastructures et d'activités humaines afin de maintenir des habitats de qualité pour une multitude d'espèces et des services écologiques, et ainsi assurer la persistance des populations animales, particulièrement de grands mammifères utilisant de vastes domaines vitaux (Balmford et al., 2015 ; Cooke et al., 2023 ; Geffroy et al., 2015). Toutefois, la fréquentation des parcs connaît une croissance rapide à l'échelle mondiale (Balmford et al., 2015 ; Dertien et al., 2021 ; Schulze et al., 2018), ce qui soulève des enjeux quant à la capacité des parcs à concilier leur double objectif de conservation des milieux naturels et d'accessibilité au public. Bien que les parcs nationaux soient reconnus pour leur contribution fructueuse à la conservation des habitats et au maintien de la biodiversité, l'augmentation des activités récréatives à l'intérieur et à la périphérie des parcs pourrait compromettre leur rôle de refuge faunique, d'autant plus que ces aires protégées deviennent de plus en plus isolées les unes des autres dans des matrices fortement anthropisées (Fennell et al., 2023 ; Tucker et al., 2018).

Malgré l'intérêt croissant pour l'écologie de la récréation, plusieurs lacunes persistent dans nos connaissances. Plusieurs études portant sur l'influence des activités récréatives sur la faune sont menées sur une seule espèce focale ou dans un seul site, ce qui limite la portée des conclusions (Costello et al., 2013 ; Fennell et al., 2023 ; George et Crooks, 2006 ; Procko et al., 2022). Par ailleurs, les effets du dérangement sont fréquemment abordés de manière ponctuelle, sans considérer explicitement les gradients d'intensité de fréquentation humaine ni les variations fines de la réponse des animaux en fonction de la distance aux infrastructures. De plus, les dimensions temporelles des réponses demeurent encore peu

intégrées. Les ajustements comportementaux selon les phases du jour et les effets différés du dérangement sont rarement analysés conjointement aux patrons spatiaux. Enfin, il reste difficile de déterminer dans quelle mesure les mécanismes observés sont généralisables entre espèces, ce qui limite la capacité à évaluer les différences de sensibilité au dérangement. Dans ce contexte, une approche intégrée, combinant analyses multi-espèces, gradients de fréquentation et dimensions spatio-temporelles, apparaît nécessaire pour mieux comprendre comment les activités récréatives influencent la distribution de la grande faune en milieux protégés.

OBJECTIF ET PRINCIPAUX RÉSULTATS

Mon projet de maîtrise visait à évaluer l'influence des activités récréatives sur la répartition spatiale des grands mammifères présents dans quatre parcs nationaux du Québec. Ces parcs ont été sélectionnés de manière à obtenir un gradient écologique, de superficie et de fréquentation humaine afin d'examiner la variabilité des réponses comportementales selon l'intensité de la fréquentation humaine et le contexte paysager. Mon étude ciblait les principales espèces de grands mammifères du Québec méridional, soit le cerf de Virginie (*Odocoileus virginianus*), l'orignal (*Alces alces americana*, sous-espèce de l'est de l'Amérique du Nord), le caribou forestier, le loup gris, le coyote et l'ours noir. J'ai posé l'hypothèse selon laquelle les activités récréatives sont perçues comme un risque, induisant des réponses comportementales qui, modifient la répartition spatiale et temporelle des espèces, ces réponses variant selon le statut proie-prédateur, le niveau de fréquentation des parcs et le contexte paysager. Afin d'atteindre mon objectif, j'ai déployé un total de 517 caméras à détection automatique en-deçà de 500 mètres de sentiers récréatifs selon un dispositif aléatoire stratifié par type d'activité (randonnée, randonnée avec chiens, vélo) dans les quatre parcs nationaux. J'ai ensuite traité ~5 millions d'images à l'aide d'un algorithme d'intelligence artificielle et réalisé des régressions visant à caractériser les liens entre l'intensité d'utilisation d'un milieu par chacune des espèces cibles et le niveau de fréquentation humaine, la distance au sentier le plus proche et plusieurs covariables environnementales (p. ex. couverture de forêt, élévation, position topographique, occurrence

de compétiteurs), tout en distinguant les périodes diurnes et nocturnes afin de tenir compte d'éventuels ajustements temporels du comportement.

Mes résultats mettent en évidence des réponses variables, qui varient à la fois selon l'espèce, le moment de la journée et l'interaction entre la distance aux infrastructures et l'intensité de la fréquentation humaine. Le taux photographique du cerf de Virginie était relié de manière non-linéaire à la proximité des sentiers, avec des taux plus élevés à des distances intermédiaires. Des effets de report marqués dans les parcs les plus achalandés ont également été observés, c'est-à-dire qu'une forte fréquentation diurne se traduisait par une diminution des taux de détection nocturnes près des sentiers. L'orignal quant à lui, présentait systématiquement des taux de détection plus faible à proximité des sentiers, particulièrement durant le jour, ce qui témoigne d'une sensibilité élevée au dérangement associé aux activités récréatives. Dans l'ensemble, mes analyses révèlent que les activités récréatives induisent des réponses comportementales dépendantes du contexte et modulées par les traits d'histoires de vie des espèces, l'intensité de la fréquentation humaine et la structure du paysage. Mes résultats montrent également que le dérangement associé aux activités récréatives n'agit pas de manière uniforme au sein de la communauté de grands mammifères, mais qu'il engendre plutôt des réponses propres à chaque espèce, reflétant des différences de sensibilité au dérangement (c.-à-d. une vulnérabilité comportementale face à la présence humaine). Mon étude met ainsi en évidence l'importance de considérer la variabilité interspécifique des réponses des grands mammifères aux activités humaines dans la planification des infrastructures récréatives et des niveaux d'utilisation autorisés afin de concilier les objectifs de conservation de la faune et d'accessibilité au grand public des aires protégées.

CHAPITRE 1
LES ACTIVITÉS RÉCRÉATIVES FAÇONNENT L'UTILISATION DE L'ESPACE PAR LES GRANDS MAMMIFÈRES LE LONG D'UN GRADIENT DE FRÉQUENTATION DANS QUATRE PARCS NATIONAUX

RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

Les activités récréatives constituent une source croissante de perturbations anthropiques dans les aires protégées susceptible de modifier l'utilisation de l'habitat par la faune en fonction de sa perception du risque. Les grands mammifères peuvent répondre à ces perturbations en ajustant leur répartition spatio-temporelle, les prédateurs évitant fréquemment les secteurs situés à proximité des sentiers par peur des humains, tandis que certaines proies utilisent la proximité de ces infrastructures comme refuge contre la prédation. Toutefois, la constance de ces réponses entre les espèces, les phases du jour et l'intensité des activités récréatives reste peu documentée. Afin d'évaluer les impacts des activités récréatives sur la répartition spatiale des grands mammifères, nous avons estimé l'occurrence des individus et l'utilisation des sentiers par les humains à l'aide de 517 caméras à détection automatique déployées à proximité de sentiers récréatifs dans quatre parcs nationaux du Québec (Mont-Orford, Grands-Jardins, Jacques-Cartier et Monts-Valin). Ces parcs couvrent un gradient de superficie et d'intensité de fréquentation et ils sont situés dans différents domaines bioclimatiques. Au total, 34 984 jours-caméras ont permis de récolter près de 5 millions d'images, que nous avons traitées à l'aide d'un algorithme d'intelligence artificielle pour quantifier les détections de la faune et la fréquentation humaine des sentiers. Nous avons analysé la variation des détections des espèces en fonction de la distance au sentier le plus proche, de l'intensité d'activité humaine sur les sentiers et de covariables environnementales, tout en distinguant, lorsque possible, les phases du jour (jour et nuit). Les réponses aux activités récréatives se sont révélées propres à chaque espèce et sensibles au contexte et à la

phase du jour. Le cerf de Virginie (*Odocoileus virginianus*) présentait des réponses non linéaires à la proximité des sentiers, avec des taux de détection maximaux à des distances intermédiaires, et a montré un délai de réponse dans le parc le plus fréquenté, où une forte pression récréative de jour étaient associée à une faible occurrence près des sentiers durant la nuit. D'autre part, l'orignal (*Alces alces americana*) présentait de faibles taux de détection dans les secteurs situés à moins de 400 à 500 m des sentiers dans tous les parcs-phases, particulièrement durant le jour, suggérant une sensibilité élevée aux perturbations humaines. Le nombre de détections d'autres espèces (coyote *Canis latrans*, loup *Canis lupus*, caribou *Rangifer tarandus caribou*) était insuffisant pour permettre des analyses détaillées et aucune relation n'a été mise en évidence entre les variables associées à nos hypothèses et les détections d'ours noir (*Ursus americanus*). Dans l'ensemble, nos résultats suggèrent que les activités récréatives génèrent des réponses comportementales qui varient selon le contexte et sont façonnées par les traits d'histoire de vie des espèces, l'intensité de l'utilisation humaine des sentiers et la structure du paysage. Ces résultats soulignent l'importance de maintenir des secteurs exempts de perturbations et d'intégrer une planification spatiale fine dans la gestion des activités récréatives afin de soutenir les efforts de conservation de la grande faune au sein des aires protégées.

Cet article, intitulé « *Recreational activities shape large mammal space use across a visitation gradient in four national parks* », a été rédigé en collaboration avec mon directeur de recherche, Martin-Hugues St-Laurent, professeur à l'UQAR, et mon codirecteur, Marc-André Villard, biologiste à la SÉPAQ. Il sera soumis pour publication à l'été 2026 dans un journal scientifique à comité de lecture. En tant que première auteure, j'ai contribué à l'élaboration de la méthodologie, à la collecte et à la gestion des données, au développement de l'algorithme WildlifeNet, aux analyses statistiques et géomatiques, ainsi qu'à la rédaction et révision de l'article. Frédéric Lesmerises et Kimberly Malcolm, biologistes pour l'équipe de recherche en gestion de la faune terrestre ont contribué à la réalisation partielle des analyses statistiques. Mes directeurs de recherche sont à l'origine de la conception du projet et ont assuré son encadrement scientifique et sa supervision générale, en plus de coordonner les travaux, d'en garantir le financement et de contribuer activement à la rédaction et à la

révision du manuscrit. L'INO a assuré le développement de l'algorithme « *WildlifeNet 2.0* », utilisé pour le traitement des données. Des résultats préliminaires ont été présentés sous forme d'affiche au 17e colloque annuel de la Société québécoise pour l'étude biologique du comportement (SQÉBC) en mai 2024. Une version abrégée de l'article a également été présentée au congrès de la British Ecological Society (BES) à Liverpool en décembre 2024, ainsi qu'au 18e colloque annuel du Centre d'étude de la forêt (CEF) en mai 2025.

Mots-clés : aires protégées, *Alces alces americana, Odocoileus virginianus,* perception du risque*;* pièges photographiques, répartition spatiotemporelle

RECREATIONAL ACTIVITIES SHAPE LARGE MAMMAL SPACE USE ACROSS A VISITATION GRADIENT IN FOUR NATIONAL PARKS

ABSTRACT

Recreational activities are a growing source of anthropogenic disturbance in protected areas and can alter habitat use by wildlife as a function of perceived predation risk. Large mammals may respond to recreation by adjusting their spatiotemporal distribution, as predators may avoid areas near trails due to "fear" of humans, whereas prey species may use these areas as refuges from predation. However, the consistency of these responses across species, diel periods, and recreational intensity remains poorly documented. To assess the impacts of recreational activities on the spatiotemporal distribution of large mammals, we estimated wildlife detection rates and human trail use using 517 camera traps deployed near recreational trails in four national parks (Mont-Orford, Grands-Jardins, Jacques-Cartier, and Monts-Valin) of Quebec, Canada, spanning gradients in park area, recreational intensity, and bioclimatic context. Over 34,984 camera-days, we collected approximately 5 million images and processed them using an artificial intelligence algorithm to quantify wildlife detections and human trail use. We examined how species detection rates varied as a function of distance to the nearest trail, human trail use, and environmental covariates, while distinguishing between daytime and nighttime periods whenever possible. Responses to recreation were species-specific as well as diel- and context-dependent. White-tailed deer (*Odocoileus virginianus*) showed non-linear responses to trail proximity, with peak detection rates at intermediate distances, and exhibited carry-over effects in the most visited park, whereby high daytime recreation led to lower detection rates in proximity to trails at night. In contrast, the eastern moose (*Alces alces americana*) consistently showed lower detection rates in areas within 400–500 m of trails, particularly during daytime, indicating a higher sensitivity to recreational disturbance. The number of detections for other species (coyote *Canis latrans,* grey wolf *Canis lupus*, and caribou *Rangifer tarandus caribou*) was insufficient to allow for detailed analyses, and no relationship was found between the

variables associated with our hypothesis and black bear (*Ursus americanus*) detection rates. Our results suggest that recreational activities generate context-dependent behavioural responses shaped by species life-history traits, human trail use, and landscape structure. These findings underscore the importance of maintaining disturbance-free areas and managing recreational intensity at finer spatial scales to support wildlife conservation in protected areas.

Keywords**:** *Alces alces americana,* camera traps, *Odocoileus virginianus,* protected areas**,** risk perception*,* spatiotemporal distribution.

INTRODUCTION

Anthropogenic activities are major drivers of global biodiversity loss, fragmenting natural landscapes and altering wildlife distribution (Candolin & Wong, 2012; Dirzo et al., 2014; Sih, 2013). Rapid urbanization and industrial expansion continuously change landscape structure, challenging the ability of individual animals to find habitat free from the influence of humans (Beaupré et al., 2025; Granados et al., 2024). Outside protected areas, habitat for large mammals is often altered by human activities such as agriculture, forestry, urban development, and hunting (Chen et al., 2022; Sarmento & Berger, 2017; Schulze et al., 2018). Hence, national parks may play a critical role as refuges for wildlife (Procko et al., 2022), especially for wide-ranging species such as the moose (*Alces alces*) and black bear (*Ursus americanus*), threatened species sensitive to disturbances (e.g. caribou, *Rangifer tarandus caribou*) or apex predators (e.g. wolf, *Canis lupus*) (Naidoo & Burton 2020; Hubbard et al., 2022; Lesmerises et al., 2018; Tucker et al., 2018).

For several species, spatiotemporal distribution results from individual habitat selection and space use patterns, which highlight trade-offs between resource acquisition and predator avoidance (Borregaard et al., 2009; Mao et al., 2005; Smith et al., 2024). Individuals must then forego resource-rich areas when the perceived predation risk is high, a compromise well documented in populations such as Rocky Mountain elk (*Cervus canadensis*) in Yellowstone National Park and woodland caribou in Charlevoix, where elk give up high

quality foraging sites while caribou avoid some of their preferred wintering sites to escape wolf predation (Duchesne et al., 2000; Fortin et al., 2005). These case studies illustrate how fear can shape space use ecology.

According to the risk-disturbance hypothesis, animals adopt anti-predator behaviour in response to loud or rapidly approaching stimuli (Frid & Dill, 2002). Disturbances such as hiking or mountain biking, although intuitively less intense than those associated with motorized vehicles (Ciuti et al., 2012; Ladle et al., 2019; Naylor et al., 2009), may be interpreted as potential threats, increasing vigilance, displacement, and stress (Arlettaz et al., 2007; Larson et al., 2016; Weterings et al., 2024). These behavioural responses can modify predator–prey dynamics, altering the "landscape of fear" where humans indirectly influence trophic interactions (Laundré et al., 2010). For example, cougars (*Puma concolor*) reduced their activity and avoided areas where human voices were broadcasted, resulting in increased use of those same sites by their prey (Suraci et al., 2019). Indeed, predator–prey co-occurrence may decrease in sites with intense human use, with prey three times more abundant than predators (Muhly et al., 2011). Although non-consumptive recreation is generally viewed as less harmful to wildlife (Grooms & Urbanek, 2018; Reed & Merenlender, 2008; Taylor & Knight, 2003), evidence increasingly shows strong ecological effects. A meta-analysis reported negative impacts in 93% of studies reviewed: non-motorized activities reduced species richness and the abundance of both carnivores and herbivores in protected areas (Larson et al., 2016). Moreover, global analyses indicate that recreation can influence animal movement more strongly than habitat modification such as logging or agriculture (Doherty et al., 2021).

Recreational disturbance influences wildlife at multiple spatial scales, from local effects near trails to those of other infrastructure extending 40–1000 m and are often overlooked in studies focusing on landscape patterns (Dertien et al., 2021; Larson et al., 2016; Taylor & Knight, 2003). Predators such as wolves and coyotes (*Canis latrans*) typically avoid areas up to 400 m from trails, reflecting a broad spatial perception of human-associated risk (Patten & Burger, 2018; Rogala et al., 2011), whereas herbivores often exhibit the opposite

response by occupying areas vacated by predators to benefit from reduced predation risk, a phenomenon better known as the human-shield hypothesis (HSH) (Berger, 2007; Gaynor et al., 2025a). Moose, for instance, have been observed calving near roads where predators are scarce (Berger, 2007), while lactating caribou showed reduced vigilance within 500 m of trails, in contrast to females that were not lactating, which exhibited strong avoidance of trails (Lesmerises et al., 2017). Such relationships can also be nonlinear, with some herbivores, such as elk (*Cervus canadensis*), seeking refuge at intermediate distances to escape predation during periods of low human trail use, consistent with HSH (Rogala et al., 2011). These spatiotemporally mediated shifts in habitat use can alter predator-prey dynamics, sometimes leading to trophic imbalances such as overgrazing in areas avoided by predators, with potential repercussions amounting to permanent habitat loss and a decreased carrying capacity in certain areas (Miller et al., 2022; Rowland et al., 2000; Taylor & Knight, 2003).

Fear of humans can also induce temporal adjustments in wildlife activity (Gaynor et al., 2018; Lewis et al., 2021; Millien et al., 2024). Many diurnal or crepuscular species, including the black bear and coyote, shift towards nocturnal activity patterns to avoid daytime human presence along trails and near residential areas (Costello et al., 2013; Nickel et al., 2020; Zeller et al., 2019). In the absence of human activity, large mammals may increase nighttime trail use for ease of movement (Oriol-Cotterill et al., 2015; Tattersall et al., 2023). Such diel adjustments can modify predator-prey interactions, as predators exploit quieter periods to hunt while prey may increase nighttime activity in areas perceived as safe. Yet, reduced vigilance near humans can create ecological traps (*sensu* Gates & Gysel, 1978) when predators gain a temporary advantage as human activity declines, elevating predation risk at dusk or during low-disturbance periods (Ordiz et al., 2016; Patten et al., 2019). These spatiotemporal shifts underscore the complex nature of wildlife responses to human disturbance.

Differences in sensitivity to human disturbance occur both within and between species. For instance, black bears in lower human density areas exhibited stronger avoidance of human activity by shifting to more nocturnal space use following minimal disturbance

compared to individuals inhabiting areas with higher human density (Zeller et al., 2019). Elk exhibited stronger spatial avoidance of trails than mule deer (*Odocoileus hemionus*) under the same recreational intensity levels, reflecting interspecific differences in responses to recreational intensity (Beaupré et al., 2025).

National parks provide relatively undisturbed habitat within otherwise disturbed landscapes, making them ideal sites to study wildlife responses to human activity. Parks have a dual mandate to conserve nature while providing public access. However, recreational activity has increased rapidly over the past decades, in North America and globally. For example, visitation to the U.S. National Park System reached 318 million in 2018, an increase of about 16 % compared to a decade earlier, potentially exerting acute pressure on wildlife (Balmford et al., 2015; Jenkins, 2019; Larson et al., 2016; Schulze et al., 2018). Evaluating the sensitivity of large mammals to human presence is therefore essential to inform management practices that balance these objectives. Despite growing evidence of recreational impacts on wildlife, many studies have focused on single species or sites (Costello et al., 2013; Duchesne et al., 2000; Fennell et al., 2023; Procko et al., 2022), limiting the ability to generalize findings. Behavioural responses are variable and context-dependent, influenced by factors such as predation risk (real and perceived), habitat quality, and intensity of human trail use. Furthermore, it remains unclear whether mechanisms like the human shield operate consistently across species and along disturbance gradients (Granados et al., 2023; Marion et al., 2024; Zong et al., 2023).

To address these gaps, we investigated the effects of recreational activities on the spatiotemporal distribution of multiple large mammal species in four national parks of Quebec, which were selected to capture variation in park area, human trail use, and landscape context. We hypothesized that human disturbance associated with recreational activities will trigger risk-associated behavioural responses in large mammals, altering their spatiotemporal distribution, and that these responses will be mediated by the predator-prey status of each species and human trail use. We predicted that predators would avoid areas with high recreational activity due to fear of humans (i.e. the “landscape of fear” hypothesis, Laundré

et al., 2010). However, at low human trail use, perceived risk associated with humans may be reduced, allowing predators to use areas near or on trails more frequently for access to resources and ease of movement. Hence, we expected predator detection rates near trails to be low during periods of high human presence, but higher during periods of low human presence. In contrast, as posited by the human shield hypothesis (Berger, 2007), prey species would be more likely to occur near recreational trails during periods of high human activity due to reduced predator presence. At low human trail use, prey detection rates near trails should instead reflect avoidance of natural predators and selection of habitat features associated with safety and access to resources, maximizing risk–resource trade-offs rather than human presence alone.

MATERIAL AND METHODS

Study area

This study was conducted in four national parks (Monts-Valin, hereafter MVNP; Grands-Jardins, GJNP; Jacques-Cartier, JCNP; Mont-Orford, MONP) spanning a north-south gradient from boreal and mixed-wood forests to temperate deciduous forests (Figure 1). On the north shore of the St. Lawrence River, MVNP, GJNP and JCNP host populations of the large mammals targeted by this study: the white-tailed deer (*Odocoileus virginianus*), Eastern moose (*Alces alces americana*, i.e. the North American subspecies found in eastern Canada and the United States), black bear, coyote and grey wolf. MONP is primarily inhabited by coyotes, bears, moose and most notably, white-tailed deer as the southeastern portion of MONP overlaps with a deer wintering area (Lalande, 2001). The grey wolf is absent from MONP, as elsewhere south of the St. Lawrence River. Prior to this study, the Charlevoix woodland caribou herd ranged across JCNP and GJNP. However, individuals from this herd are now restricted to enclosures within GJNP. As for MVNP, it lies within the Pipmuacan caribou population range (Ministère des Forêts, de la Faune et des Parcs, 2021a).

The four parks were selected to form a gradient in area, number of visitors and ecosystem type (Table 1). All parks are embedded within or adjacent to multi-use landscapes

with major roads just beyond their boundaries. In MONP, the surrounding matrix is dominated by urbanized areas of varying density and agricultural fields, while the three other parks are embedded within public lands managed through forest harvesting and where controlled hunting takes place. The primary forms of anthropogenic disturbance within the parks are recreational trails, service roads, derelict logging roads (often used as trails), park infrastructure (e.g. campgrounds, visitor centers, parking lots) and, in some instances (MONP), a golf course and a ski station (Crépin et al., 2021; Lalande, 2001; Ministère des Ressources naturelles et des Forêts, 2018; Moisan, 2016; Picard et al., 2021). Recreational use and intensity (Table 1) vary among parks, both in terms of trail density and trail type, including hiking, biking and multi-use trails, with leashed dogs permitted on at least some trails. MONP, located in the Appalachian lowlands, has higher visitation rates and denser infrastructure than MVNP, which is more remote, being located in the Saguenay highlands. JCNP and GJNP experience moderate recreational intensity, which is concentrated at the eastern edge for the latter, where the most popular trails are located.

Table 1. Characteristics of the four national parks surveyed. MVNP: Monts-Valin National Park, GJNP: Grands-Jardins National Park, JCNP: Jacques-Cartier National Park, MONP: Mont-Orford National Park

National park	Area (km^2)	Max. Elev. (m)	Surrounding human disturbances	Summer trail characteristics, length (km) and density (km/km^2), all activities confounded	Number of visitors during study year (May to October)*	Types of recreation (dogs allowed on some trails)
MVNP	154	980	Timber harvesting and hunting on adjacent public land and outfitter territories	Single boundary-to-boundary trail ~ 28; 0.18	26 000 (2023)	Hiking, fishing, canoeing/kayaking
GJNP	318.9	1010	Timber harvesting and hunting on adjacent public land and outfitter territories	Trails broadly dispersed ~ 86; 0.27	135 000 (2022)	Hiking, fishing, canoeing/kayaking
JCNP	670	1082	Park bordered by highways; timber harvesting and hunting on adjacent public land and outfitter territories	Trails concentrated in valleys ~ 122; 0.18	296 000 (2023)	Hiking, cycling, fishing, canoeing/kayaking
MONP	58.4	853	Park bordered by highways, agricultural fields, and low-density residential development	High trail density ~ 135; 2.31	680 000 (2022)	Hiking, mountain biking, cycling, fishing, canoeing/kayaking

*Source: SÉPAQ. Represents number of visitors multiplied by the duration of their stay.

Parks vary in forest composition and structure as a function of latitude, topography, bioclimatic factors, and natural disturbance history. JCNP, MVNP, and GJNP have experienced spruce budworm (*Choristoneura fumiferana*) outbreaks, while beech bark disease and the emerald ash borer (*Agrilus planipennis*) are present in MONP, leading to canopy gaps and regeneration of varying age. Historic wildfires, particularly in GJNP (1991 and 1999), and windthrows have also shaped the current forest structure (Lemieux, 2001; Moisan, 2016). JCNP is characterized by boreal plateaus with a steep valley along the Jacques-Cartier River, where recreation is concentrated. Finally, GJNP has a rolling topography and features large areas undergoing post-fire natural regeneration.

Located within the American basswood (*Tilia americana)* bioclimatic domain (Ministère des Forêts, de la Faune et des Parcs, 2014) of southern Québec, MONP is characterized by a temperate humid continental climate. At around 200 m in elevation, valleys are dominated by basswood, ironwood (*Ostrya virginiana*) and American beech (*Fagus grandifolia*). Below 670 m, sugar maple (*Acer saccharum*) and yellow birch (*Betula alleghaniensis*) are most abundant, whereas conifers such as red spruce (*Picea rubens*) dominate the summits, above 760 and up to 850 m (Gauvin, 1983; Lalande, 2001). Despite its small area, MONP has an extensive trail network (~135 km; Table 1) that supports hiking and mountain biking, with several trails allowing dogs on leashes, contributing to the highest recreational pressure among the four parks.

JCNP boreal plateaus range from 240 to 1140 m in elevation. They are dominated by forest stands of the balsam fir – white birch (*Betula papyrifera*) bioclimatic domain. In river valleys, forest composition transitions from mixed-wood stands of yellow birch and balsam fir to sugar maple/yellow birch stands with a striped maple (*Acer spicatum*) understory to the south. JCNP features a humid continental climate and steep topography that occasionally constrained camera deployment along trails in the valley (Picard et al., 2021). The park receives a moderate number of visitors (Table 1) and includes ~122 km of trails, mostly concentrated in river valleys. Recreational activities include hiking, biking and watercraft sports.

GJNP is characterized by a subarctic continental climate and a rolling topography with elevations ranging from 350 to 1,010 m (Duchesne et al., 2000; Moisan, 2016). Past wildfires (1991 and 1999) have shaped a large portion of the current landscape, which is now dominated by young paper birch and a dense shrub cover dominated by *Vaccinium* species and regenerating black spruce – moss *Bryophyta* forests (Lemieux, 2001). Located within the balsam fir – white birch bioclimatic domain, the park is mainly characterized by mature stands of black spruce and balsam fir with an understory of ericaceous shrubs and mosses (Ministère des Forêts, de la Faune et des Parcs, 2021b). The park's trail network is sparse (~86 km), making it one of the least disturbed of the four parks in terms of trail density.

Located furthest north, MVNP features rugged terrain (120–980 m) but is characterized by cool, humid highland conditions driven by its high elevation and mountainous topography. At the interface between balsam fir – yellow birch and balsam fir – white birch bioclimatic domains, the park is shaped by recurring wildfires and spruce budworm outbreaks. Forest cover is a mosaic of coniferous, mixed and deciduous stands. Balsam fir and black spruce dominate higher elevations, whereas lower elevations are mainly characterized by white birch, yellow birch and trembling aspen (*Populus tremuloides*) (Crépin et al., 2021). MVNP is the least visited of the four parks and has limited infrastructure, including a continuous ~28 km trail traversing the park from end to end.

Sampling design

During the summers of 2022 and 2023, we operated a total of 517 camera traps across the four national parks (Figure 1). From May to August 2022, 148 cameras were set in MONP (108 Spypoint Force 20, 40 Spypoint Force Dark) and 114 (100 Spypoint Force 20, 14 Force Dark) in GJNP. From May to August 2023, 147 camera traps (126 Spypoint Force 20, 21 Force Dark) were active in JCNP and, from June to September 2023, 108 camera traps (90 Spypoint Force 20, 18 Force Dark) were operational in MVNP.

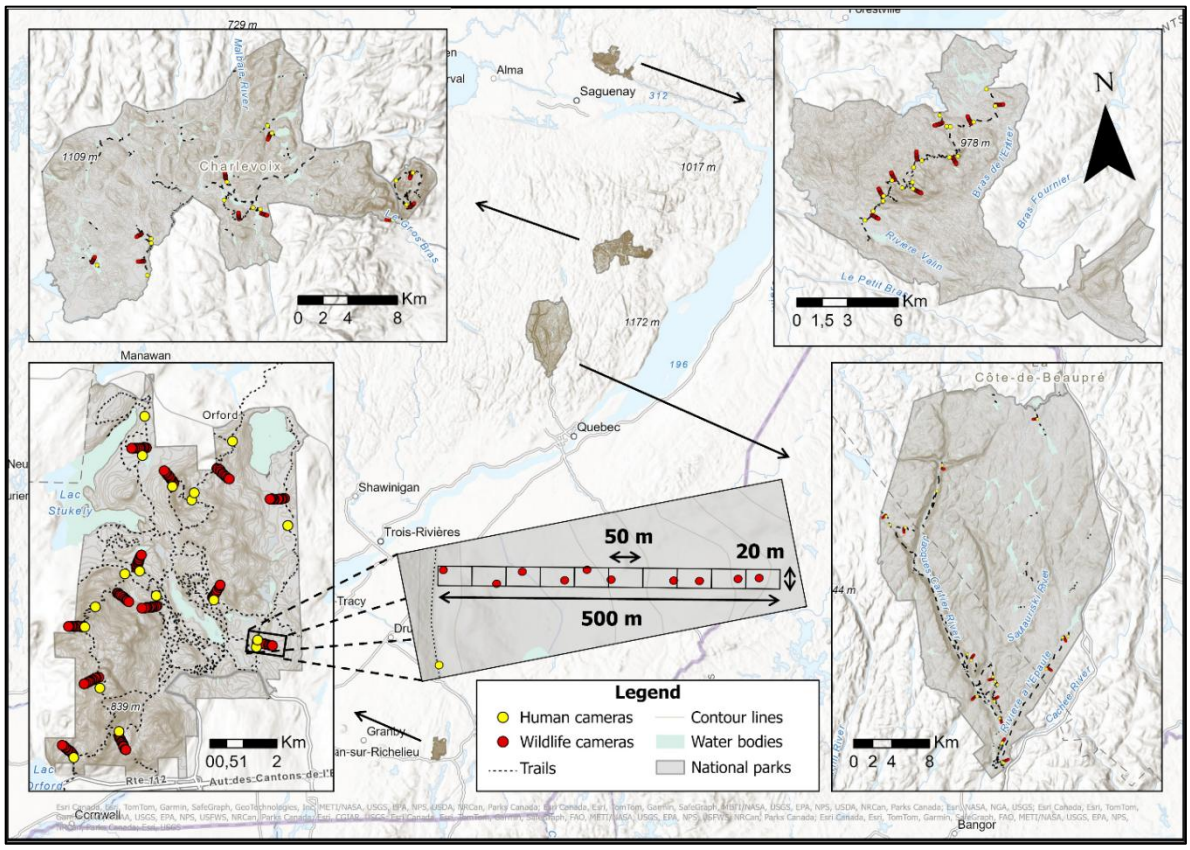

Figure 1. Study area and camera-trap sampling design across four Quebec national parks. Insets show park-specific camera deployments (top left: GJNP; bottom left: MONP; top right: MVNP; bottom right: JCNP). Red circles indicate wildlife camera transects (10 cameras per transect) installed within 500 m of recreational trails, while yellow circles indicate cameras placed directly on trails to quantify human activity. The transect design is illustrated in the schematic inset.

Camera traps were distributed among parks in proportion to total trail length and evenly allocated across the three recreational trail types. This stratification ensured standardization of sampling effort among sites while capturing variations in human disturbance levels. Moreover, we minimized detection biases by ensuring that distinct camera models were used for wildlife and human-related images, respectively. A minimum of 40 camera traps were set per park for the detection of wildlife to obtain a statistically reliable estimate of large mammal detection rates (Rovero & Zimmermann, 2016).

To document large mammal presence near trails, we used a stratified-random sampling design, deploying cameras along 20 × 500 m transects oriented perpendicular to three recreational trail types: biking, hiking, and hiking with dogs. To increase statistical independence, neighboring transects were placed ≥ 2 km apart (as suggested by Rovero & Zimmermann, 2016; Shannon et al., 2014a; Figure 1), except in MONP, where high trail density only allowed for a ≥ 250 m spacing between some of our transects. Transects were also set ≥ 250 m from service roads, neighbouring recreational trails, buildings, and other infrastructure to minimize the influence of disturbances other than the designated trail use on wildlife presence (Shannon et al., 2014a). Each transect was divided into 10 (20 × 50 m) cells, with a camera randomly placed in each cell using ArcGIS Pro 3.3.1 "random points" tool (ESRI, 2024). Wildlife cameras were located at least 25 m apart (Figure 1, transect inset).

Wildlife cameras were secured to trees at a height of 1.3 m to maximize large mammal detections (Gagnon-Labrosse, 2022). To minimize glare, cameras were oriented to the north, and larger, more stable trees were selected to prevent false triggers caused by tree movement. Cameras were set to high sensitivity and automatic detection, triggering continuously until the focal element moved out of the detection zone. To account for imperfect detection, we conducted walking tests at various distances and postures to ensure reliable triggering. We cleared low vegetation to minimize false positive events. We also delineated each camera's detection zone to correct detection-rate differences based on effective detection area (Nakashima et al., 2022). This zone corresponds to the space between the leftmost (a) and rightmost (b) diagonals where the sensor detected our movements, as indicated by the red flash in setup mode, and we measured the length of these diagonals for each camera (Appendix 1).

To monitor human trail use, cameras were positioned to face the focal trail at an angle and height optimized for detecting humans, bikes, and dogs. Each wildlife transect was paired with two cameras monitoring trail use but, for analytical purposes, only one of these two cameras was retained, i.e. the one with the highest operability (no corrupted images, full study period coverage) and located closest to the transect. This approach ensured that human

trail use data reflected activity levels nearest to wildlife detections, as visitation typically declined with distance from the entry point of the trails. Retaining data from the trail camera closest to the wildlife transect thus allowed for a more representative estimation of disturbance experienced by wildlife. SD cards and batteries were replaced every 3 weeks for cameras on trails.

Image processing

Human- and wildlife-related image sets (~5 million images) were processed using WildlifeNet 2.0 (Shannon, 2023), an algorithm trained on local data sets (manually sorted and annotated using Timelapse; Greenberg, 2025) and designed for automatic recognition of large mammals, humans, and recreational activities. For wildlife images, the algorithm was used to identify which species was captured by wildlife cameras. We considered images of the same species separated by ≥30 minutes as distinct events (Nickel et al., 2020; Procko et al., 2022; Rovero & Zimmermann, 2016), except if we had evidence that these photos refer to different individuals (e.g. male with antlers vs. female; see Gagnon-Labrosse 2022). If two or more individuals of the same species appeared in the same image, we counted every individual. We then cross-checked our annotations for all wildlife-related images using the algorithm's output to improve accuracy.

For trail use by humans, WildlifeNet 2.0 was trained to distinguish between objects (e.g. truck, stroller, hiker, biker, dog) and generate accurate recreational activity counts (Shannon, 2023). Humans can be distinguished from each other more reliably than wildlife (e.g. using clothes), but this task was very time-consuming, and our algorithm was not trained to reach this level of precision. Therefore, we estimated the time it took for hikers and bikers to pass through the camera's field of view across different weeks and cameras during the study period to identify a threshold useful to distinguish independent events. While several studies define independent events using longer time intervals (e.g. 1 minute, Procko et al., 2022; 5 minutes, Fennell et al., 2022; 30 minutes, Nickel et al., 2020), the high levels of recreation in some of our parks (i.e. MONP and JCNP) required a shorter window to maximize count precision. For that reason, we applied a 5-second interval to define a single

detection for individual hikers and hikers with dogs and applied a ≥ 75% precision filter. WildlifeNet 2.0 had a 91% accuracy rate in identifying hikers and 98% for dogs (Shannon, 2023). Hence, there was a ≥ 90% probability that an individual would be accounted for at least once within the ~5 second interval of traversing the camera frame.

Applying the precision filter reduced overestimation by eliminating blurry or peripheral images of the same person or dog. We did not apply the precision filter to bikers considering the increased likelihood of motion blur when detecting fast-moving objects, often leading to lower precision scores. In addition, the camera captured fewer images per individual because bikers passed quickly through the frame. We therefore retained all bike-related images regardless of precision score. Within each 5-second window, we selected the image with the highest predicted human count, regardless of activity type, to maintain a reliable estimate of the maximum number of visitors passing within that time window. This calibration was applied consistently among parks, standardizing human counts and correcting for the algorithm's overestimation. Before this correction, algorithm-generated counts were inflated by a factor of 2 to 10 times, whereas following calibration, overestimation was reduced to just 1.5 to 2 times the actual counts. To further minimize bias, and for each camera, we excluded the first and last hour of data collection (i.e. following camera installation and preceding its retrieval, respectively) to eliminate repeated detections of the field team. Cameras that recorded their first detection past the installation date were assumed to have functioned from the moment of installation. However, cameras that failed to trigger during retrieval were assumed to have stopped functioning after their last detection, and any data from the following weeks were consequently removed. All post-image processing was performed in R 4.4.1 (R Core Team, 2024).

Landscape characterization

To account for the influence of environmental variables on the spatial distribution of large mammals, we extracted the following covariates (Appendix 2). We calculated elevation and the Topographic Position Index (TPI) from LiDAR-based digital terrain models (1m spatial resolution; Ministère des Ressources naturelles et des Forêts, 2016a), as elevation of

a camera site and topography can influence site accessibility and ease of movement by animals (Nickel et al., 2020; Sultaire et al., 2023). We also extracted the proportion of mixed-wood forest from digital forest cover maps (1:20,000; Ministère des Ressources naturelles et des Forêts, 2016b) to account for the potential influence of vegetation cover on large mammal detection rates (Procko et al., 2022). For the TPI and proportion of mixed-wood forest, we conducted a multiscale analysis across 25, 50, and 100 m buffers, while treating elevation and distance to water as baseline variables, and retained the most parsimonious radius for each variable using the AIC_c (Borcard et al., 2004; see Appendix 3). We calculated the Euclidean distance from each camera to the nearest permanent water body to account for access to drinking water and riparian resources for herbivores (Ministère des Ressources naturelles et des Forêts, 2019). Roads were derived from AQRéseau+ (Ministère des Ressources naturelles et des Forêts, 2018), whereas park infrastructure and other linear features, used for transect placement, were sourced from SÉPAQ shapefiles. All covariate extraction was performed in ArcGIS Pro 3.3.1 (ESRI, 2024) and further analyzed in R 4.4.1 (R Core Team, 2024).

Response variable and covariate specifications

We measured recreation as the cumulative trail use of hikers, bikers, and dogs per station-week, excluding all other annotated elements (e.g. strollers), which were used solely for training the detection algorithm. This approach was necessary given limited sample sizes, which precluded testing activity types independently. We standardized detections by effort (detections per camera-hour) to ensure comparability between full and partial weeks. We evaluated a log transformed version of the variable to account for skewness in human trail use and to assess potential non-linear relationships between recreational disturbance and large-mammal detection rates. This transformation was retained only when it improved model fit, using a baseline model with environmental covariates only (i.e. distance to the nearest permanent water body, elevation), relative to the untransformed version as determined by AIC_c (Borcard et al., 2004). This approach allowed us to test whether small increases in human trail use at low levels exert stronger effects than equivalent increases at

higher use (Dertien et al., 2021; Sytsma et al., 2022). We included the Euclidean distance to the nearest transect-associated recreational trail as a secondary proxy for human disturbance. We also ensured that this distance was always calculated relative to the same trail for which visitor counts were obtained, rather than to an adjacent trail that could fall within 500 meters (as was the case in MONP, where some transects were < 250 m apart).

To control for potential spatial autocorrelation in species detection rates associated with our sampling design, we conducted a principal coordinate of neighborhood matrix (PCNM) analysis separately for each species and phase of day (Dray et al., 2006; Lacerte et al., 2022). A maximum of two significant eigenvectors, at different spatial scales, were retained following a pre-analysis selection process where a baseline model with environmental covariates (i.e. distance to the nearest permanent water body, elevation) was compared across PCNM combinations, and the most parsimonious set was retained using AIC_c (Borcard et al., 2004; Appendix 4).

Statistical analyses

We used negative binomial mixed models (GLMMs) to evaluate whether recreational disturbance represented a key driver of large mammal spatial distribution using the glmm*TMB* package (Brooks et al., 2017), as these models are appropriate for count data exhibiting overdispersion and can accommodate moderate levels of zero-inflation (Zuur et al., 2009). Our dependent variables were species-specific counts of independent detections per camera-week and phase of day (day/night), with effort (i.e. no. of camera-hours) included as an offset to standardize counts, effectively modelling detection rates (O'Brien 2011). Independent variables included human trail use, distance to human trail, interspecific interactions and environmental covariates (see candidate models, Table 2). Transect ID was included as a random effect to account for pseudo-replication, and PCNM eigenvectors were incorporated when spatial structure was detected. The temporal sampling unit was the week (Monday to Sunday), which allowed us to balance fine-scale daily variation (prone to zero inflation and temporal autocorrelation) and coarse-scale monthly aggregation (which could mask patterns; Fennell et al., 2023; Naidoo & Burton, 2020; Procko et al., 2022). Counts

were further partitioned by phase of day where “day” was defined as the interval between dawn and dusk, and “night” as the interval between dusk and dawn, with civil twilight times obtained from the National Research Council Canada (2024) sunrise/sunset calculator. When detections were insufficient within a given phase, data were pooled across phases, which was the case for bears in GJNP and moose in MONP. For species with insufficient variability in detection counts (i.e. too few non-zero frequency classes) to support negative binomial modeling, counts were converted to binary presence–absence data (detections = 1, non-detections = 0), and fitted logistic regression models using the lme4 package (Bates et al., 2015); this was the case for moose in MONP. Finally, some species-phase combinations (i.e. bear in MONP, deer in GJNP, bear and deer in MVNP and coyote in all parks) were not modelled, as there were insufficient detections to test candidate models.

Table 2. Candidate models for weekly species detection rates within 500 m of recreational trails in the Mont-Orford, Grands-Jardins (May–Aug 2022), Jacques-Cartier, and Monts-Valin (June–Sep 2023) national parks, Québec, Canada. Models may include one or two PCNMs as fixed effects to account for spatial autocorrelation (depending on species and diel period), with transect as a random factor and effort as an offset. Description of variables can be found in Appendix 2.

Model #	Covariates
1	Elevation + distance to water + % mixed-wood forest + TPI + competitor species
2	Elevation + distance to water + % mixed-wood forest + TPI + competitor species + distance to trail
3	Elevation + distance to water + % mixed-wood forest + TPI + competitor species + distance to trail^2
4	Elevation + distance to water + % mixed-wood forest + TPI + competitor species + distance to trail + cumulative trail use (raw or log-transformed)
5	Elevation + distance to water + % mixed-wood forest + TPI + competitor species + cumulative trail use (raw or log-transformed) x distance to trail
6	Elevation + distance to water + % mixed-wood forest + TPI + competitor species + cumulative trail use (raw or log-transformed) + distance to trail^2
7	Elevation + distance to water + % mixed-wood forest + TPI + competitor species + cumulative trail use (raw or log-transformed) x distance to trail ^{2}
8	Elevation + distance to water + % mixed-wood forest + TPI + competitor species + predators
9	Elevation + distance to water + % mixed-wood forest + TPI + prey

We initially included Julian date of installation to account for potential variation in vegetation phenology, as progressive spring green-up can alter understory and canopy cover, influencing both animal movement and their detectability by cameras (Chataigner et al., 2025). Distance to park infrastructure was also considered, since proximity to roads or buildings can affect wildlife presence (Nickel et al., 2020). However, both variables showed limited potential to explain species detection rates in our study: all cameras were located more than 500 m from permanent infrastructure, and preliminary models indicated that Julian date did not contribute to a reduction in AIC_c across species-phase combinations. Given our limited sample size, we prioritized model parsimony by excluding variables that did not improve model fit, as assessed by AIC_c (Arnold, 2010). We did not apply exponential decay functions for trail distance because all cameras were located within 500 m of recreational trails and distances never extended beyond this threshold, making the assumption of a continuous decay over larger distances less likely (Dertien et al., 2021). Moreover, we accounted for potential variation in detection rates among sites by incorporating each camera's detection depth into sampling effort (see section: sampling design).

Candidate models and selection process

For each species and phase of day, we tested a set of candidate models designed to evaluate the hypotheses in line with our objective about the drivers of large mammal species distribution (Table 2). All models included the following environmental covariates: elevation, distance to the nearest water body, proportion of mixed-wood forest, and TPI. Candidate models differed in their inclusion of distance to trails (linear or quadratic), cumulative trail use (raw or log-transformed), and interactions between trail distance and recreational activity to explore potential non-linear and synergistic effects, whereby the influence of recreation could vary with proximity to trails (Rogala et al., 2011). Although human trail use was concentrated during the day, we also included human trail use in night models to test for lagged effects of daytime recreation on nocturnal wildlife activity (Nix et al., 2018).

The most parsimonious model for each species and phase of day was retained as the best-supported, while competing models within $\Delta AIC_c \leq 2$ were also examined (following Burnham & Anderson, 2002). When competing models contained different predictors, both were considered supported and their predictors were reported as possible drivers (e.g. models 6 and 8 for white-tailed deer in MONP; Table 2). When a model only differed by the addition of one predictor, we interpreted that predictor only if its inclusion lowered the AIC_c relative to the simpler model (Arnold, 2010). Otherwise, it was considered uninformative, even if statistically significant. As advised by Arnold et al. (2010) for small model sets, we did not conduct model averaging, as our objective was to identify drivers of species distribution patterns based on detection data rather than maximize predictive accuracy. All predictors were standardized (mean = 0, variance = 1), and we evaluated assumptions using the DHARMa package (Hartig, 2024), which provides simulation-based diagnostics for residuals in mixed models, with diagnostics confirming that overdispersion and zero-inflation were adequately addressed by the negative binomial family. We calculated marginal (R^2_m) and conditional (R^2_c) R^2 values following the approach of Nakagawa & Schielzeth (2013) and implemented in the MuMIn package. MuMIn estimates observation-level variance using multiple methods (delta, log-normal, and trigamma) for computing R^2 (Bartoń, 2026), and we report log-normal estimates because they provide stable estimates in negative binomial mixed models and closely matched R^2 values from Performance while delta and trigamma estimates were consistently lower due to near-zero transect variance. For logistic regression models of moose in MONP, model fit was assessed using the area under the curve (AUC), and we compared the model to the null model. Variance inflation factors (VIF) were also examined for all predictors, with values < 3 indicating no multicollinearity issues.

RESULTS

Across the four parks, we analyzed a total of 34,984 camera-days of sampling (range: 6,385–9,973 per park; Appendix 5). White-tailed deer was the most frequently detected species (day: 1,542; night: 338), followed by moose (day: 362; night: 170), black bear (day: 161; night: 15), and coyote (day: 45; night: 16) (Appendix 6). Camera failures occurred

mainly due to device malfunction, displacement by bears, battery drainage from excessive false triggers, or image corruption.

White-tailed deer – daytime

In MONP, predicted daytime deer detection rates were best explained by the predator model (model 8), although models including trail use and distance to trail (model 6 & 7) received comparable support ($\Delta AIC_c < 2$; Table 2; Appendix 7). Hence, we present results from models 6 and 8, considering that they capture distinct hypotheses relevant to deer detections rates and are among the closest competing models in terms of ΔAIC_c, while avoiding redundancy with model 7 (Appendix 8). In model 6, predicted detection rates were negatively associated with quadratic distance to trail (β= -0.15 [-0.25 : -0.06] 95% CI; Figures 2 and 3a) and positively associated with moose detections (β= 0.08 [0.01 : 0.15]). Cumulative trail use had no detectable effect, and this model had low explanatory power (pseudo-R^2_m = 0.046; R^2_c = 0.094). In model 8, deer detection rates increased with daytime predator detections (β= 0.10 [0.04 : 0.16]), but model fit was low (pseudo-R^2_m = 0.043; R^2_c = 0.091). Environmental covariates across top models showed consistent patterns: detection rates decreased with distance to water and increased with TPI as well as with the proportion of mixed-wood forest, while both PCNMs had a significant effect on detection rates (Appendix 7).

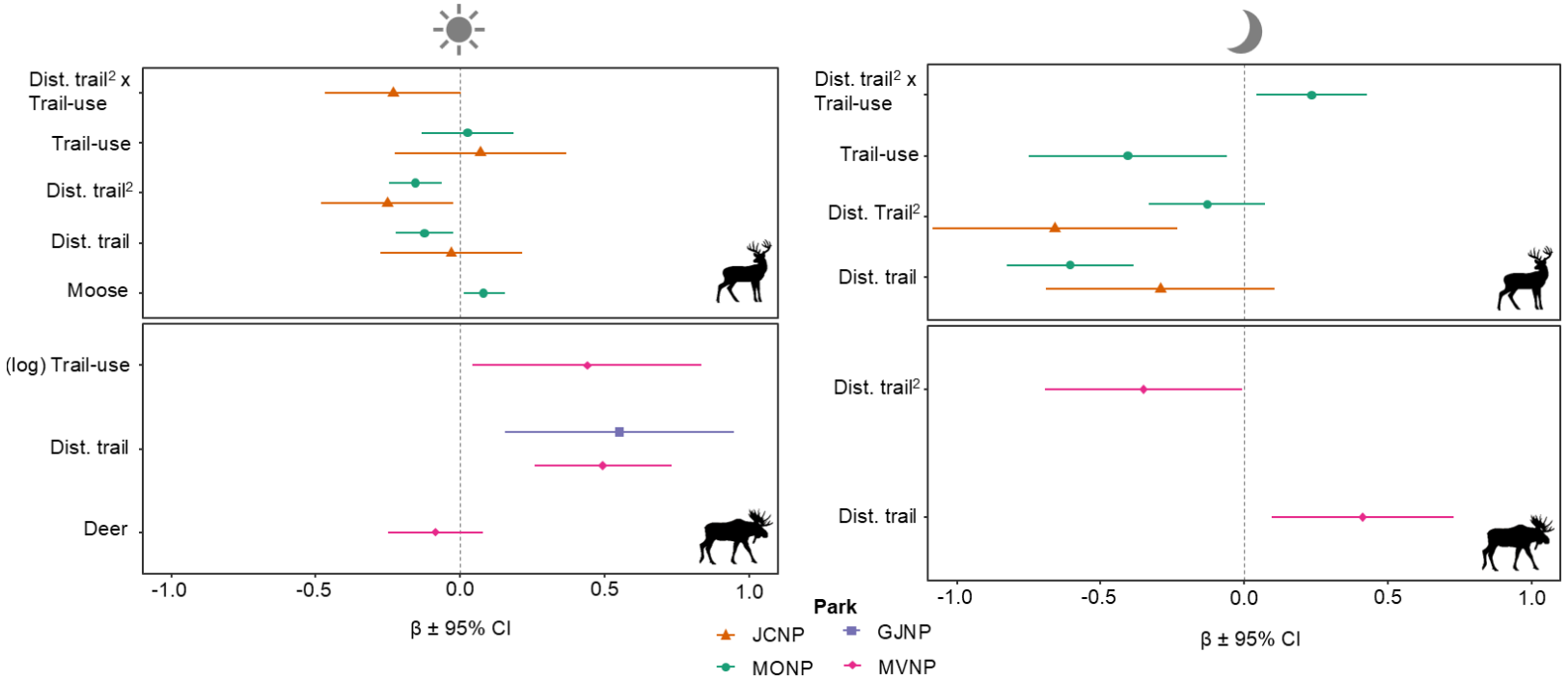

Figure 2. Coefficient estimates (±95% CI) from top-ranked (AIC_c) negative binomial models for daytime weekly detection rates (left) of white-tailed deer (top; MONP: n = 1286, JCNP: n = 199) and moose (bottom; GJNP: n = 74; MVNP: n = 191) and nighttime weekly detections rates (right) of white-tailed deer (top; MONP: n = 242, JCNP: n = 88) and moose (bottom; MVNP: n = 103) in four national parks of Quebec, Canada. Only coefficients relevant to the study hypotheses (distance to trail, trail-use, their interaction, and competitor presence) are shown. Effects are statistically significant when confidence intervals (horizontal lines) do not overlap zero (vertical line). Full model outputs are provided in the appendices (Appendices 7, 9–14).

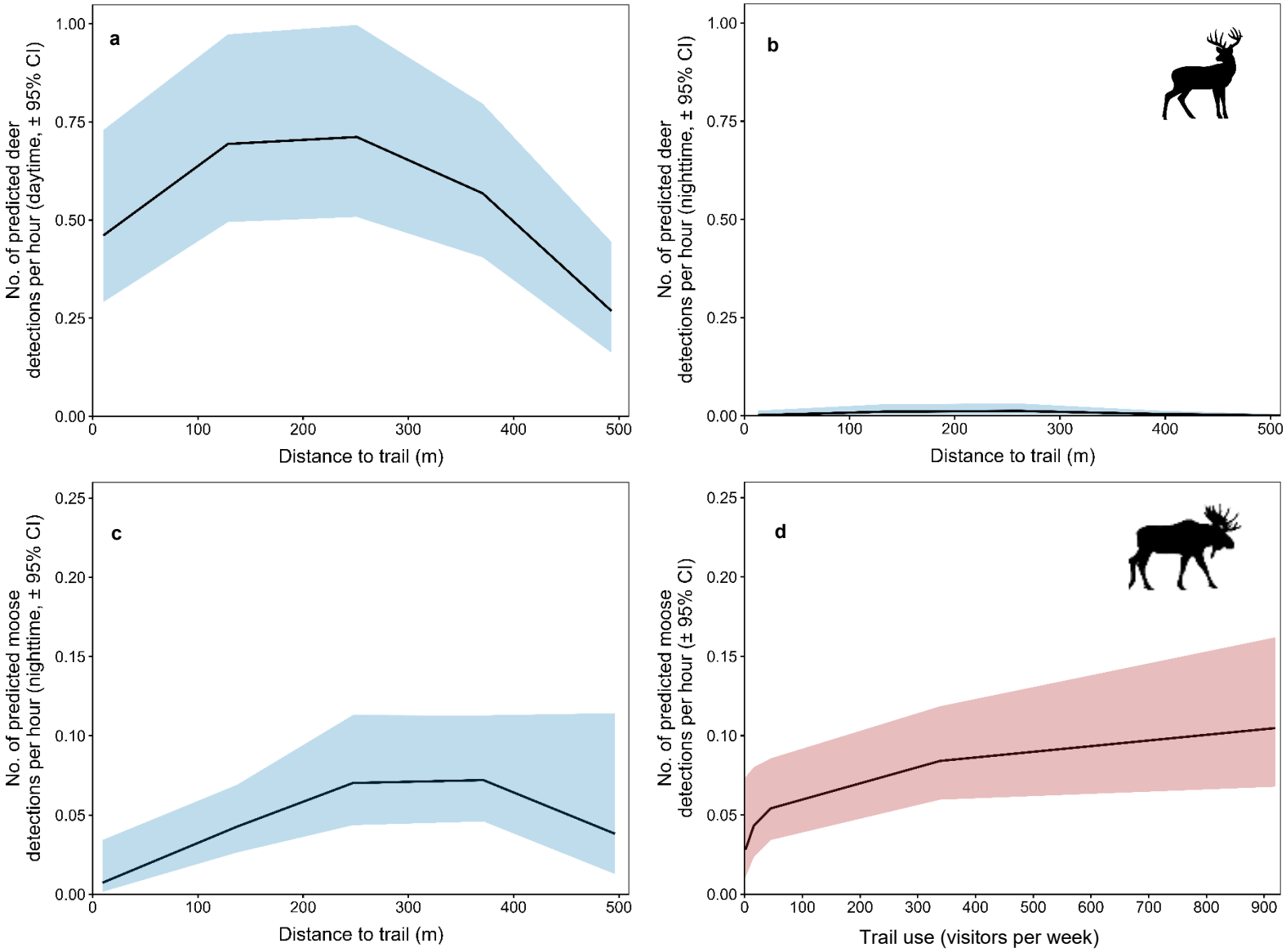
a
No. of predicted deer detections per hour (daytime, ± 95% CI)
1.00
0.75
0.50
0.25
0.00
0
100
200
300
400
500
Distance to trail (m)
b
No. of predicted deer detections per hour (nighttime, ± 95% CI)
1.00
0.75
0.50
0.25
0.00
0
100
200
300
400
500
Distance to trail (m)
c
No. of predicted moose detections per hour (nighttime, ± 95% CI)
0.25
0.20
0.15
0.10
0.05
0.00
0
100
200
300
400
500
Distance to trail (m)
d
No. of predicted moose detections per hour (± 95% CI)
0.25
0.20
0.15
0.10
0.05
0.00
0
100
200
300
400
500
600
700
800
900
Trail use (visitors per week)

Figure 3.Predicted quadratic relationships between distance to trail and herbivore detection rates within three national parks in Quebec, Canada. Panels show white-tailed deer daytime detection rates in Mont-Orford National Park (a), deer nighttime detection rates in Jacques-Cartier National Park (b), and moose nighttime detection rates in Monts-Valin National Park (c) as a function of distance to trail. Panel (d) shows the predicted response of moose daytime detection rates to cumulative trail use in Monts-Valin National Park. Distance to trail is shown in meters (standardized in models), and cumulative trail use represents the number of visitors per week. In all panels, the response variable represents predicted detections per camera-hour, with solid lines indicating fitted values and shaded areas (blue for distance to trails and red for cumulative trail use) representing 95% confidence intervals.

In JCNP, detection rates were best explained by the interaction between trail use and quadratic distance to trail (model 7), with the simpler distance to trail model (model 3) receiving similar support ($\Delta AIC_c < 2$; Appendix 15). The interaction term was statistically supported ($\beta = -0.23$ [−0.47 : 0.00]; Figure 2) and comparable in magnitude to other covariates in the model. However, due to the strongly negative intercept, predicted detection rates remained extremely low (< 0.005 detections per hour) across the full distance gradient under both minimal and maximal trail-use conditions (Appendix 16). Consequently, although the interaction altered the shape of the predicted response (i.e. producing a parabolic relationship under high trail use and a relatively flat response under low trail use), absolute differences in predicted detection rates were small and associated with high uncertainty on the response scale, as indicated by overlapping confidence intervals (Appendix 16). Despite this uncertainty, the quadratic distance to trail term alone was statistically supported in model 7. At mean trail-use levels, quadratic distance to trail was negatively associated with deer detection rates ($\beta = -0.25$ [−0.48 : −0.02]), indicating a parabolic relationship with distance to trail. Deer detection rates declined with elevation and, unlike in MONP, increased with distance to water (Appendix 9). Model 7 explained a large proportion of the variance (pseudo-$R^2_m = 0.78$; $R^2_c = 0.81$).

White-tailed deer – nighttime

In MONP, predicted nighttime deer detection rates were best explained by the same interaction (model 7; Table 2; Appendix 17) as in JCNP, but the effect was positive ($\beta = 0.24$ [0.04 : 0.43]; Figure 2 and 4). Detection rates also increased with the proportion of mixed-wood forest and TPI (Appendix 10). Model fit was low (pseudo-$R^2_m = 0.097$; $R^2_c = 0.13$). In JCNP, nighttime detection rates were driven primarily by the quadratic distance to trail model (model 3), and models including trail use (model 6 and 7) fell within $\Delta AIC_c < 2$ (Appendix 18). Nighttime detection rates were negatively associated with quadratic distance to trail ($\beta = -0.66$ [-1.08 : -0.23]; Figures 2 and 3b), mirroring the daytime pattern in MONP. Predicted nighttime detection rates increased with distance to water but decreased with

elevation, and the model had moderate explanatory power (pseudo-R^2_m = 0.35; R^2_c = 0.40; Appendix 11).

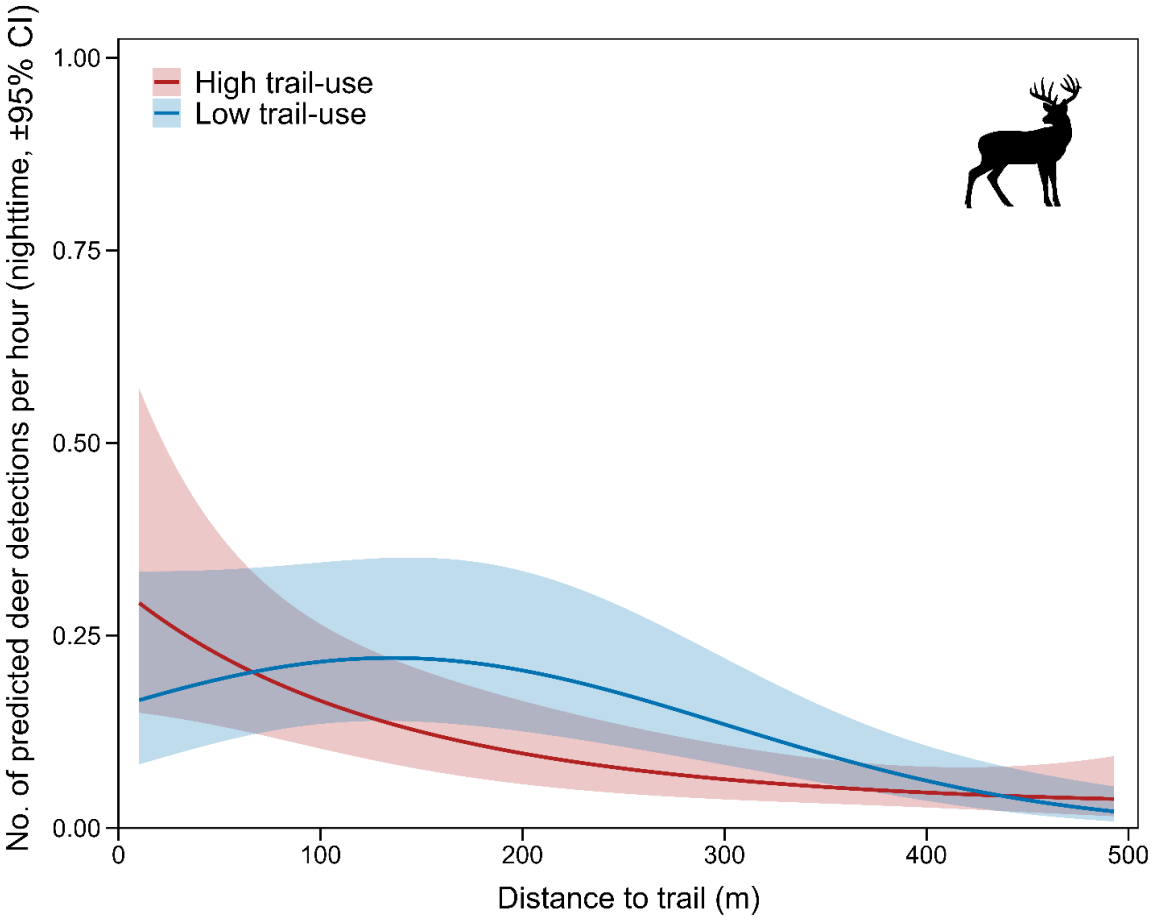

Figure 4. Predicted nighttime detection rates of white-tailed deer as a function of the interaction between quadratic distance to trail (m) and daytime cumulative trail use (visitors per week) in Mont-Orford National Park, Quebec, Canada. The response variable represents weekly predicted detections per camera-hour. The red line shows predictions at maximum daytime trail use, and the blue line shows predictions at minimum daytime trail use. Shaded areas represent the 95% confidence intervals for both curves.

Moose – daytime

In GJNP, the model that best explained moose predicted daytime detection rates included distance to trail (model 2; Table 2), but models (3, 4 and 7) including both trail use and distance to trail were also supported ($\Delta AIC_c < 2$; Appendix 19). Predicted daytime detection rates increased with distance to trail (model 2; β= 0.55 [0.15 : 0.95]; Figure 2).

Moose also responded positively to distance to water, but negatively to TPI (Appendix 12). The PCNM was significant, and model fit was low (pseudo-$R^2_m = R^2_c$ at 0.16). In MVNP, the top model also included distance to trail and trail use (model 4), and competing models within $\Delta AIC_c < 2$ also included these covariates (Appendix 20). Detection rates increased with distance to trail (β= 0.49 [0.26 : 0.73]; Figure 2) and with log-transformed cumulative trail use (β= 0.44 [0.04 : 0.84]; Figure 2 and 3d), while decreasing with elevation (Appendix 13). The PCNM was significant and the model had low explanatory power with an $R^2_m = R^2_c$ of 0.24.

Moose – nighttime

In MVNP, nighttime detection rates were best predicted by quadratic distance to trail (model 3), and model 6 (Trail use + distance to trail^2) was within $\Delta AIC_c < 2$ (Appendix 21). Moose nighttime detection rates were negatively related to the quadratic distance to trail (β= -0.35 [-0.69 : -0.01]; Figure 2 and 3c), and they decreased with elevation, as for daytime detection rates in this park. The PCNM term remained significant, and the model had low explanatory power (pseudo-$R^2_m = R^2_c$ at 0.20) (Appendix 14). Nighttime predicted detection rates in GJNP were best explained by environmental covariates (model 1, Table 2). A model including distance to trail (model 2) was within $\Delta AIC_c < 2$ (Appendix 22), but only the PCNM was significant. Given the low sample size (41 detections; Appendix 6) for this phase in GJNP, we likely had limited power to discern signals for our variables of interest ($R^2_m = R^2_c$: 0.18; Appendix 23).

Moose – day and night combined

The probability of moose detections in MONP was best explained by the interaction between distance to trail and trail use (model 5; Table 2; Appendix 24). Detection probability was positively associated with the interaction between distance to trail and daytime cumulative trail use (β= 0.63 [0.19 : 1.07]; Figure 5 and 6) and increased with deer presence (β= 0.29 [0.05 : 0.52]). Moose detection probability also increased with mixed-wood forests. The PCNM was significant, as well as the effort (integrated as a fixed effect; Appendix 25).

Model fit was good, with an area under the ROC curve of 0.78, and the fixed effects significantly improved the model compared to the null model (LRT: $\chi^2 = 31.47$, df = 10, p > 0.001).

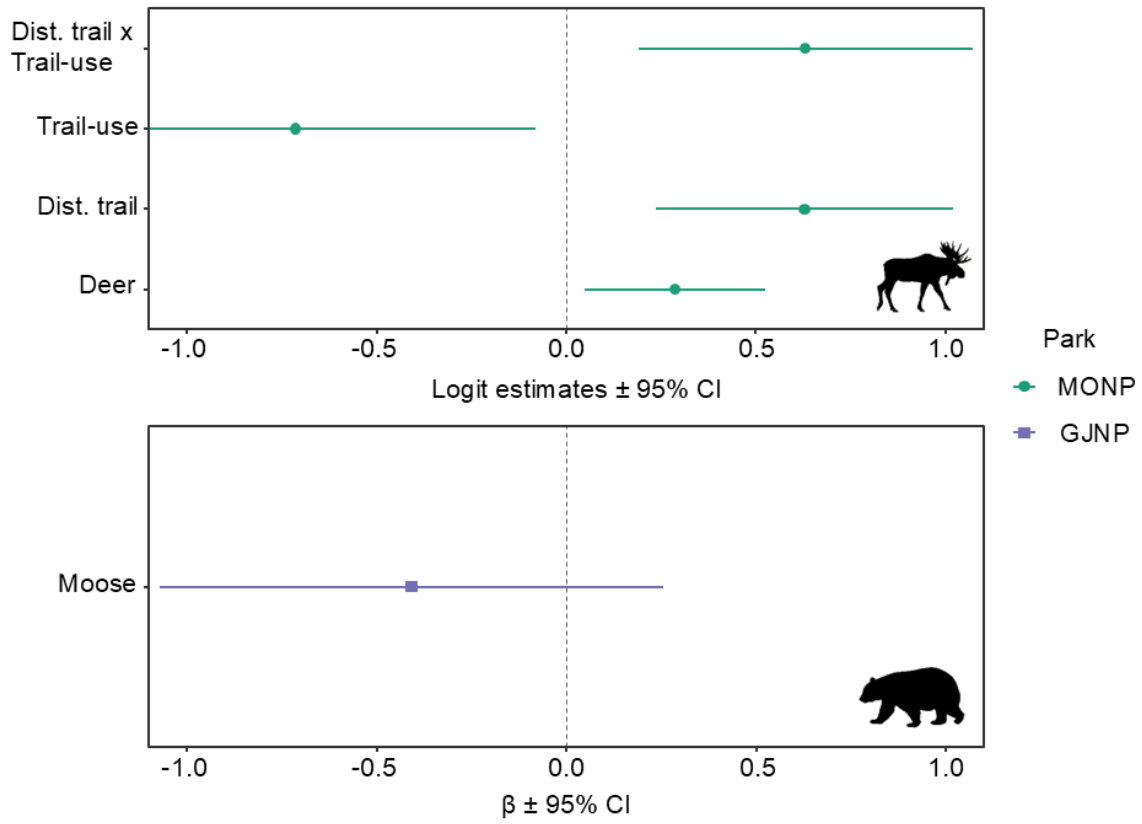

Figure 5. Coefficient estimates (±95% CI) from the top-ranked (AIC_c) logistic model for the combined day–night weekly detection probability of moose (top; MONP: $n = 99$) and from the top-ranked (AIC_c) negative binomial model for the combined day–night weekly detection rates of American black bear (bottom; GJNP: $n = 73$). Only coefficients relevant to our hypotheses (distance to trail, trail use, their interaction, and competitor or prey presence) are shown. Effects are statistically significant when confidence intervals (horizontal lines) do not overlap zero (vertical line). Full model outputs are provided in the appendices (Appendices 25 & 27).

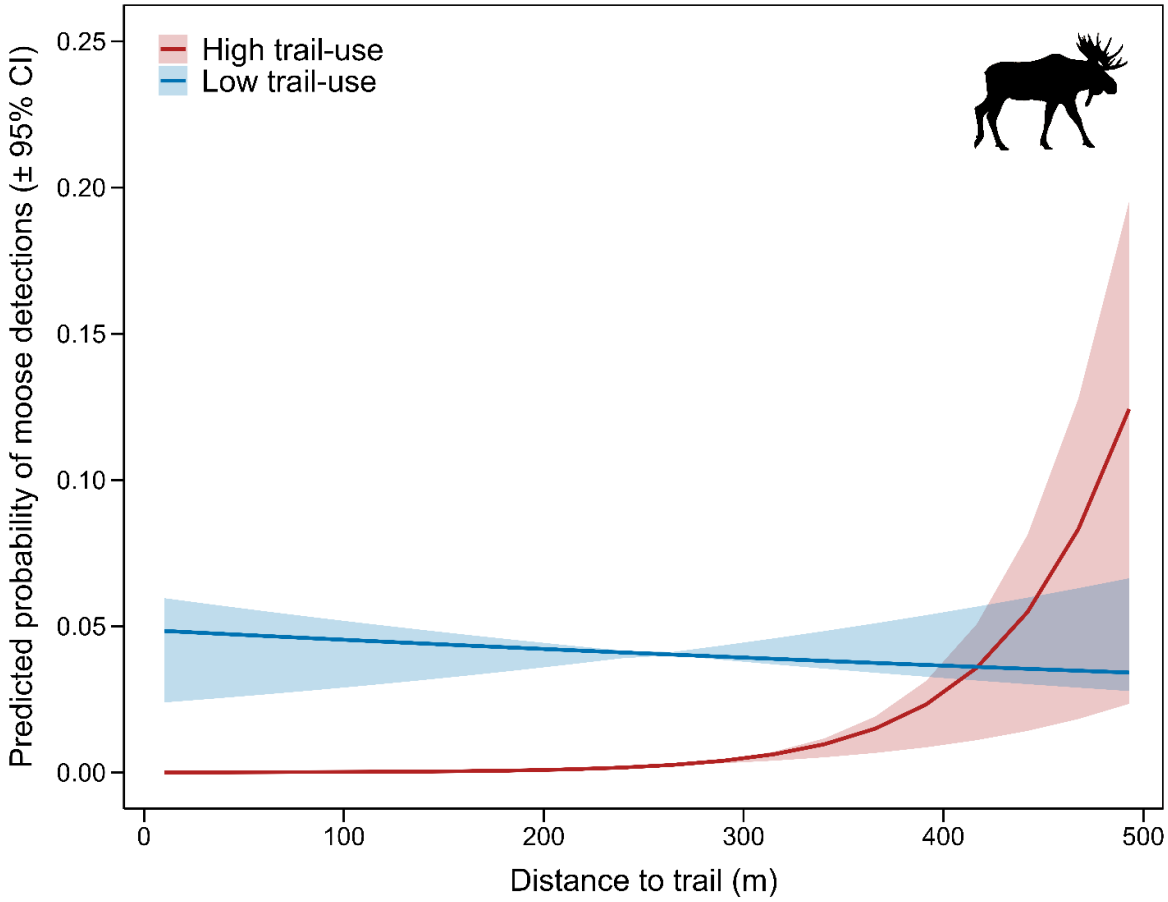

Figure 6. Modelled probability of moose detections (day and night combined) derived from a logistic regression assessing the interaction between quadratic distance to trail (m) and daytime cumulative trail use (log-visitors per week) in Mont-Orford National Park. The red curve illustrates predicted detection probabilities at maximum daytime trail use, while the blue curve shows predictions at minimum trail use, with shaded regions representing 95% confidence intervals.

American black bear – day and night combined

In GJNP, predicted black bear detection rates were best explained by environmental variables (model 9; Table 2), as no trail-related variables were retained in the top-ranked model. However, several competing models including the baseline environmental model (model 1) as well as models incorporating trail-use effects and distance-to-trail terms (models 2, 4, and 5) received comparable support ($\Delta AIC_c < 2$; Table 2; Appendix 26). Bear detection rates declined with increasing elevation and TPI (Appendix 27). Overall explanatory power

was low, with the top model yielding a pseudo-R^2_m of 0.057 and R^2_c of 0.08, indicating that fixed and random effects explained only a small proportion of the variation in detection rates.

DISCUSSION

Trail use and distance to trail were important predictors of white-tailed deer and moose spatiotemporal distribution in the four national parks surveyed. Environmental covariates and, in some cases, predator and competitor presence, also contributed to the most parsimonious models. Importantly, the strength and direction of trail effects varied among parks, indicating that focal species' responses were context dependent. This is consistent with recent studies showing that avoidance of recreational infrastructure by large mammals interacts with recreational intensity and landscape context (Beaupré et al., 2025; Burton et al., 2024; Fennell et al., 2023), and that avoidance is often expressed differently in more intensively used parks compared to "wilder" systems (e.g. Marion et al., 2024). However, we did not detect any effect of trail-use or distance-to-trail variables on black bear detection rates, and coyote, grey wolf or woodland caribou responses could not be evaluated due to insufficient detections.

Response to trails and trail use modulated by prey vulnerability

Deer, a small ungulate, exhibited a trade-off between human disturbance and refuge from predators

According to the human-shield hypothesis, herbivore space use near recreational infrastructure is expected to vary with intensity of human activity rather than trail proximity per se. Hence, we predicted more intensive use of areas near trails under high human activity. In the case of white-tailed deer, however, we found a consistent quadratic relationship between distance to trail and detection rates, the latter peaking at intermediate distances (~200–300 m) in both parks (MONP and JCNP) and across diel periods. This pattern suggests a reduced use of areas near trails under high human presence rather than an increase, while also indicating that deer response is influenced by recreational intensity and diel period.

In MONP, the park with the highest recreational pressure, deer showed lower detection rates in proximity to trails at night. Specifically, under high daytime human activity, deer shifted nocturnal space use away from trails over most of the distance gradient, suggesting that disturbance during the day carried over into nocturnal space use. Such carry-over effects have rarely been documented but are consistent with evidence suggesting that human presence and recreation can induce shifts in diel activity patterns in mammals (Fennell et al., 2023; Gaynor et al., 2018; Procko et al., 2022). For example, increased nocturnality in response to recreation (Gaynor et al., 2018) as well as temporal avoidance of human trail use by mule deer (*Odocoileus hemionus*) on weekends (the "weekend effect" reported by Nix et al., 2018) have been reported. Furthermore, the COVID-19 "Anthropause" created abrupt reductions in human activity following widespread park closures, providing a quasi-experimental context to assess wildlife responses to changes in human disturbance (Gaynor et al., 2025b). Across systems, these reductions were associated with changes in wildlife spatiotemporal dynamics, including altered movement behaviour and increased use of previously disturbed areas (Procko et al., 2022; Anderson et al., 2023). Within protected areas, the suspension of recreational activities led to increased habitat use and activity for some species compared to pre-closure conditions, whereas the resuming of recreational activity was associated with a contrasting reduction in site use and daytime activity (Anderson et al., 2023). Although these studies do not explicitly test diel carry-over effects, they pointed out that human activity can structure animal space use beyond periods of direct exposure.

The non-linear relationship between distance to trail and daytime deer detection rates observed in MONP may reflect the combined influence of recreational disturbance and predation risk, given the relatively high predator detection rates in this park (0.29 coyote and 0.23 black bear detections per 100 camera-days). Linear features such as trails are frequently used by predators for movement and hunting, particularly during crepuscular and nocturnal periods (Dickie et al., 2016, 2020; Geffroy et al., 2015). This trade-off between human disturbance and predation risk could produce peak detection rates at intermediate distances from trails, as reported for elk, whose spatial response to trails varied with recreational

intensity (Rogala et al., 2011). However, we could not model predator responses and, therefore, any inference regarding predator-mediated effects should be interpreted cautiously.

In JCNP, where recreational pressure and predator detection rates (0.021 coyotes and 0.064 bears per 100 camera-days) were lower than in MONP, deer also showed intermediate-distance peaks at night, while daytime space use was best described by an interaction between trail use and quadratic distance to trail. However, a simpler quadratic distance-only model received similar support. Despite very low absolute detection rates and largely overlapping confidence intervals, higher trail use shifted the shape of the predicted response toward greater use at intermediate distances, whereas detection rates were more evenly distributed across the distance gradient under low trail use (Appendix 16). Nevertheless, the recurrent peaks in deer detection rates at intermediate distances from trails, especially under higher recreational use, suggest that deer adjust space use to balance access to trail-adjacent resources while minimizing both human disturbance and predation risk, rather than simply staying away from trails outright. This interpretation is consistent with findings from Suraci et al. (2021), who reported peak use by several species (including black bear and elk) at low to intermediate levels of human presence, consistent with context-dependent tolerance rather than steering clear of disturbance. As recreational pressure increases, such spatial structuring appears to become more pronounced, as observed in MONP.

Moose, the largest ungulate prey, showed heightened sensitivity to hiker disturbance

Moose detection rates showed a generally positive relationship with distance to trails across parks: individuals were detected more frequently beyond 400–500 m from recreational trails. This pattern suggests a higher sensitivity to human disturbance in moose compared to smaller, more behaviourally flexible ungulates. Where visitation rates were highest (MONP), this relationship was strongly influenced by trail use. The probability of detecting moose remained near zero within ~300–350 m of trails, suggesting markedly reduced use of areas near intensively visited trails (see also Granados et al., 2023; Neumann et al., 2011; Suraci et al. 2021). Even under low recreational intensity, detection probabilities remained low

across the distance gradient, likely reflecting both low overall detections ($n = 99$) and patterns consistent with low use of areas near recreational infrastructure. Given MONP's relatively small area and high trail density (2.31 km of trails/km^2; mean across the 4 parks = 0.74 km/km^2), recreational disturbance is likely experienced across much of the landscape. For a wide-ranging herbivore with annual home ranges of 15–40 km^2 (Courtois & Crête, 1988), such broad-scale patterns translate into substantial indirect habitat loss (Gaudry, 2013; Polfus et al., 2011). Unlike deer, moose may be less likely to benefit from human presence as a refuge from predation, especially in systems where apex predators are absent, such as in MONP, and the remaining predators—coyotes and black bears, in this case—pose low predation risk to adults. The variable responses observed between species are consistent with Granados et al. (2023), who found limited support for the human-shield hypothesis as a general mechanism and instead suggested that its effects, when present, operate at local scales and under specific ecological conditions.

Interestingly, in the park where recreational use was lowest (MVNP), moose detections rates were also lower in areas near trails, but detection rates increased modestly with trail use. Although the magnitude of this effect was small (~0.025 to 0.10 detections per hour across the observed human trail use gradient; Figure 3d), it suggests a weak tendency toward areas with greater human presence. In this context, human activity may function as a partial refuge (see also Sytsma et al., 2022), as wolves are present and the overall recreational intensity remains relatively low (mean number of hikers per week was 437 in MVNP vs. 1254 in MONP. Relative to deer, which primarily exhibited the highest detection rates at intermediate distances from trails during the day and more flexible nocturnal responses depending on daytime recreational intensity, moose showed a clearer diel asymmetry. They presented increased detection rates at intermediate distances from trails when human activity was low, likely to access forage resources, while exhibiting higher detection rates further from trails during periods of high human presence, consistent with higher sensitivity to recreational disturbance.

In a park with intermediate recreational use (GJNP), only a positive relationship between distance to trail and moose detection rates was observed. Low detection rates (n = 74 day; n = 41 night) likely limited our ability to capture interactive effects with trail use, rather than indicating an absence of recreational effects. Lower detection rates within 500 m of trails are consistent with findings for other large, disturbance-sensitive herbivores such as elk, which can be displaced from extensive areas of high-quality habitat by recreational activity (Beaupré et al., 2025; Rogala et al., 2011).

Taken together, these results add to the growing evidence that sensitivity to recreational disturbance varies among ungulates (Brown et al., 2012; Suraci et al., 2021). Across systems, larger-bodied species tend to exhibit stronger behavioural responses to human activity. For example, non-lactating female caribou in Gaspésie National Park moved away from trails in the presence of hikers (Lesmerises et al., 2017), whereas elk increased movement, reduced foraging and resting, and avoided trails during recreational use (Naylor et al., 2009; Wisdom et al., 2018). Experimental studies further demonstrate that recreation noise elevates vigilance and flight responses in large ungulates, elk being among the most sensitive species (Zeller et al., 2024). Non-uniform responses between moose and white-tailed deer are consistent with their life-history differences: as a large-bodied, slow-reproducing species, moose are expected to prioritize survival and exhibit stronger risk aversion, whereas the smaller, faster-reproducing white-tailed deer can tolerate higher levels of human disturbance in their habitat selection (Blumstein, 2006; Gaillard et al., 2000; Oli, 2004; Suraci et al., 2019). These patterns align with our findings that moose display strong, context-dependent reduction in space use near recreational trails, reflecting both their life-history traits and heightened sensitivity to human disturbance compared to deer.

Predators showed no detectable trail-level responses or detections were insufficient

Our hypothesis that black bears would exhibit lower detection rates in proximity to recreational trails under higher levels of human activity received no support, nor did we detect effects of trail use or distance to trail. For black bears, coyotes and grey wolves, low detection rates limited our ability to robustly assess responses to recreational activity. The

absence of detectable effects likely reflected a combination of low predator densities (Mazzarisi et al., 2025; Sinclair et al., 2003) and spatial responses occurring at scales larger than those captured by our sampling design. Large carnivores often avoid human infrastructure over distances approaching or exceeding 1 km (Northrup et al., 2012; Rogala et al., 2011; Shannon et al., 2014b; Theuerkauf et al., 2003), consistent with predictions from the landscape-of-fear framework (Laundré et al., 2010). If bears and coyotes displaced their space use toward remote areas within parks (Smith et al., 2022) or low-access areas beyond trail-adjacent zones, this would result in weak or absent effects within the spatial extent sampled here despite the presence of meaningful behavioural responses at broader scales.

Co-occurrence patterns with predators and competitors reflected spatial overlap rather than behavioural responses

In MONP, positive associations between deer and moose detection rates may reflect spatial and niche overlap driven by limited habitat availability in this small park, where both species can rely on similar forage resources (Lalande, 2001; Ludewig & Bowyer, 1985). In model 8 (see section: White-tailed deer – daytime), positive associations between deer and predator detections likely reflect high overall deer availability within a spatially constrained system rather than active prey attraction to predators, particularly in fragmented landscapes where prey densities may exceed predator densities (Mazzarisi et al., 2025). Predator-prey encounter rates generally increase with prey density due to density-dependent encounter processes, such that higher prey abundances can generate apparent spatial co-occurrence in shared sampling units even in the absence of direct behavioural attraction (Hebblewhite & Pletscher, 2002; Rovero & Zimmermann, 2016). These results should therefore be interpreted as coarse indicators of spatial overlap rather than direct evidence of predator-mediated behavioural responses.

Deer detection rates were generally associated with lower elevations (JCNP) and forest types providing higher forage availability (MONP; Fennell et al., 2023; Procko et al., 2022), consistent with their preference for deciduous-dominated stands (Millien et al., 2024). Moose were also associated with lower elevations and valley positions, particularly in parks where

mixed-wood forests provided greater browse diversity, consistent with habitat selection patterns documented for the species (Leblond et al., 2013). Variation in responses to distance from water among parks likely reflected differences in topography, trail placement, and watercourse density, as recreational trails often follow valley bottoms or riparian corridors (Crépin et al., 2021; Moisan, 2016; Picard et al., 2021). For the black bear, selection for lower elevations and valley positions is consistent with their opportunistic foraging ecology, as these areas often provide a higher availability of berries and other food resources (Fennell et al., 2023; Kays et al., 2016; Naidoo & Burton, 2020).

Limitations

Our inferences were primarily constrained by low detection rates rather than the number of cameras, as the number of cameras was determined by the sampling design and was relatively high across parks. Species occurring infrequently, such as predators, were particularly affected by the limited number of detections during the relatively short sampling period. Low detection rates of moose in MONP and black bears in GJNP required combining day and night phases. This also prevented species-specific analyses of large carnivores, as well as direct inferences about the human shield effect. It was not possible to model the effects of recreational activities separately (e.g. hiking, biking, dog walking, and motorized use), despite them being recorded independently (e.g. Procko et al., 2022), or to evaluate how population structure (e.g. sex or reproductive status) mediates responses to disturbance (Hubbard et al., 2022; Lesmerises et al., 2017). We conducted park-specific analyses rather than pooling data across parks because differences in species densities among parks could not be accounted for, as independent estimates of density were unavailable. Given this limitation, the heterogeneity in environmental parameters and the unbalanced, low detection rates for several species, including the park as a random or fixed effect (with or without interactions) could have confounded the effects of interest with underlying density differences. Thus, it may have led to obscured park-specific relationships and biased parameter estimates. The poor fit of some models suggests that unmeasured covariates, such as vegetation productivity (NDVI), hunting pressure in areas adjacent to the parks that may

influence large mammal space use in parks, logging activity, road density, or distance to park boundaries, may have contributed to variation in detection rates (Granados et al., 2023; Kays et al., 2016; Nickel et al., 2020; Procko et al., 2022; Suraci et al., 2021). Nevertheless, our sampling design partially controlled for confounding effects by placing transects ≥ 500 m from permanent human infrastructure other than trails. Moreover, potential differences in detections between sites related to the camera model used were negligible, as 97% of cameras (parks confounded) were of the same model.

With over 517 cameras and 34,984 camera-days of effort, our study represents one of the most spatially extensive camera-trap assessment of large mammal responses to recreation-related disturbance to date. Most previous work relied on telemetry (Rogala et al., 2011; Lesmerises et al., 2017, 2018) or finer-scaled camera trap surveys (Burton et al., 2012; Fennell et al., 2023; Marion et al., 2024), limiting generalization across landscapes. By integrating fine-scale spatiotemporal analyses with gradients of trail use across several protected areas, we documented context-dependent detection patterns that may contribute to indirect habitat loss.

Conclusion and management implications

Recreational trails and their associated human disturbance influenced large mammal space use across protected areas, although responses were species-specific and varied with diel periods and among national parks. Across species, our results indicate that responses to recreation emerged from the interaction between distance to trails, human trail use intensity, and time of day, rather than from trail proximity alone. While previous studies have documented avoidance of recreational activities by white-tailed deer, along with a displacement to lower-quality habitat (Millien et al., 2024; Nix et al., 2018), we found rare evidence of fine-scale carry-over effects of daytime recreation on nocturnal space use. Moreover, our results suggest that life-history traits and vulnerability differences among prey species shape their responses, whereby a large-bodied ungulate prioritizes minimizing exposure to disturbance over potential reductions in predation risk (Suraci et al., 2021). Although disturbance thresholds were not explicitly quantified, the observed spatial and

temporal shifts in space use, particularly the strong daytime reduction in use of areas near trails by moose, suggests that such thresholds exist. These behavioural differences reflect variation in recreational intensity, landscape context, predator communities, and species-specific sensitivity to human disturbance, confirming that recreational disturbance does not act uniformly across large mammal species and underscoring the need for management strategies that explicitly account for species-specific responses rather than assuming consistent effects across large mammal communities (Fennell et al., 2023; Marion et al., 2024; Nix et al., 2018; Suraci et al., 2021).

From a management perspective, limiting trail density and maintaining disturbance-free areas may be especially critical to maintain populations of large, disturbance-sensitive herbivores such as moose. This is particularly important in smaller protected areas embedded within human-dominated landscapes (Cooke et al., 2023; Gaynor et al., 2025b). In such contexts, concentrating recreational use, implementing seasonal or temporary trail closures, or closing selected trail networks could help mitigate effective habitat loss (Dertien et al., 2021; Larson et al., 2016; Lesmerises et al., 2018; Polfus et al., 2011). The greater behavioural plasticity observed in white-tailed deer suggests a higher capacity to persist under recreational pressure, supporting the hypothesis that an increasing human footprint may favour smaller, more adaptable species over larger-bodied taxa (Suraci et al., 2021).

Future research should aim to disentangle the effects of different recreational activities (e.g. motorized vs. non-motorized, consumptive vs. non-consumptive), given that non-motorized activities do not universally elicit weaker responses and may generate strong avoidance in some systems (e.g. mountain biking; Naidoo & Burton, 2020), and to distinguish recreation-driven responses from those associated with hunting pressure in surrounding landscapes (Granados et al., 2023, 2024; Kays et al., 2016). Extending camera-trap deployments across full annual cycles would increase detection rates (Fennell et al., 2023; Hubbard et al., 2022; Procko et al., 2022, Smith et al., 2021; Wang et al., 2015) and allow explicit consideration of seasonal processes (e.g. Hubbard et al., 2022) alongside dynamic environmental covariates like vegetation productivity (NDVI; Granados et al.,

2023; Procko et al., 2022). Moreover, spatial and sensory dimensions of disturbance to identify human trail use or trail-density thresholds at which behavioural responses emerge should be explicitly integrated to provide actionable guidance for trail placement, zoning, and infrastructure planning in protected areas (Beaupré et al., 2025; Dertien et al., 2021). Integrating these elements will strengthen the evidence base needed to support adaptive management strategies that balance recreational access with the conservation of large mammals and the ecological functions they fulfill within protected areas.

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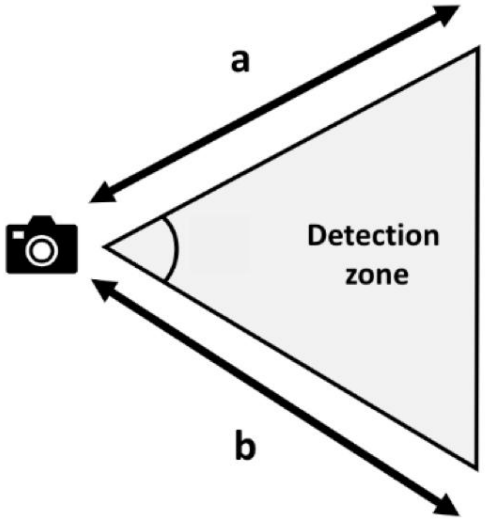
SUPPORTING INFORMATION



Appendix 1: Measurement of camera detection zones used to estimate sampling effort. Field personnel walked backward from the camera sensor along the left (a) and right (b) diagonals of the detection zone until the outermost detection was triggered, marking the corners of the effective detection area. Detection depth for each camera was calculated as the mean distance of diagonals *a* and *b* and incorporated into sampling effort. Camera effort was calculated as hours of operation per phase multiplied by mean detection depth.

Appendix 2: Covariates measured at 517 camera trap sites across the four national parks.

Variable	Description	Source
Anthropogenic		
Cumulative trail use (counts)	Sum of weekly hiker, biker and dog trail passages	Images processed using WildlifeNet2 from the Institut National d'Optique (INO)
Distance to trail (m)	Euclidean distance from a camera to the associated recreation trail	Linear features from SÉPAQ shapefiles
Environmental		
Mixed-wood forest (%)	Proportion of mixed-wood forest within a 25, 50 and 100-m radius, with a spatial resolution of 4 ha	Digital forest cover maps retrieved from the Ministère des Ressources naturelles et des Forêts (MRNF) (1:20,000)
Distance to nearest water body (m)	Euclidean distance to the nearest lake, river or permanent stream	The Geobase of the Quebec Hydrographic Network from the MRNF (1:20,000)
Topography		
Elevation at camera (m)	Elevation (spatial resolution: 1 m)	Digital terrain models from Light detection and Ranging (LiDAR) maps retrieved from MRNF (1:20,000)
TPI	Topographic position index	
Co-use/predation		
Predator presence	Sum of weekly bear and coyote detections	Camera traps
Deer presence	Weekly deer detections	Camera traps
Moose presence	Weekly moose detections	Camera traps

Appendix 3: Best performing radius (m) for each species–phase combination, selected from 25, 50, and 100 m during multi-scale analyses across 517 camera trap sites in four national parks.

Park	White-tailed deer				Moose				Black bear	
	TPI		% mixed-wood forest		TPI		% mixed-wood forest		TPI	% mixed-wood forest
	Day	Night	Day	Night	Day	Night	Day	Night		
MONP	100	50	25	25		25*		25*	–	–
GJNP	–	–	–	–	25	25	25	100	100*	25*
JCNP	50	50	25	25	–	–	–		–	–
MVNP	–	–	–	–	50	50	100	100	–	–

*Day and night were combined

Appendix 4: Significant distance-based Moran's eigenvector maps (dbMEM; PCNM eigenvectors) describing spatial structure within each park across species and diel phases. PCNMs with p-values (≤ 0.05) are marked with an (X) for each park–species–phase combination. Given the limited sample size (≈11 transects per park), when more than three significant PCNMs were detected, only a restricted subset (indicated in bold) was retained following model selection to avoid model overparameterization (see Methods – Response variable and covariate specifications).

PCNM	**MONP**			**GJNP**			**JCNP**		**MVNP**	
	White-tailed deer		Moose	Black bear	Moose		White-tailed deer		Moose	
	day	night	day + night	day + night	day	night	day	night	day	night
PCNM1	X	X					**X**		X	**X**
PCNM2					**X**	**X**		**X**	X	X
PCNM3	**X**								**X**	X
PCNM4	X	**X**								
PCNM5	X	X	**X**						X	
PCNM6	X								X	
PCNM7										
PCNM8										
PCNM9										
PCNM10	**X**									

Appendix 5: Sampling effort for wildlife detections and human trail use in each park during the study period (2022: May–August; 2023: June–September). Total sampling effort was quantified as camera-days, calculated as the mean number of days cameras were active within each park multiplied by the number of wildlife cameras deployed. Phase-specific effort (day and night) was quantified in camera-hours, calculated as the mean number of daytime or nighttime hours multiplied by the number of wildlife cameras. Because camera deployment durations were highly consistent within parks (see minimum–maximum ranges), these calculations provide a close approximation of total sampling effort.

Park	**No. of cameras**		**Mean no. of days wildlife cameras were active (min - max)**	**Effort in camera-days**	**Daytime effort in camera-hours**	**Nighttime effort in camera-hours**
	Wildlife	Humans				
MONP	127	13	78.25 (74 – 83)	9,938	13,631	6,115
GJNP	92	10	68.41 (64 – 71)	8,688	13,538	5,856
JCNP	124	13	80.43 (71 – 89)	9,973	13,162	6,089
MVNP	89	9	71.74 (67 – 76)	6,385	9,218	4,842
Total	432	45	298.83 (64 – 89)	34,984	49,549	22,902

Appendix 6: Total species detections in each park for the entire study period (2022: May to August; 2023: June to September). Species detections with converging models are shown in bold.

Park	White-tailed deer			Moose			Black bear			Coyote		
	Day	Night	Total	Day	Night	Total	Day	Night	Total	Day	Night	Total
MONP	**1286**	**242**	1538	78	21	**99**	44	2	46	42	15	57
GJNP	16	1	17	**74**	**41**	115	65	8	**73**	0	0	0
JCNP	**199**	**88**	287	19	5	24	11	1	12	3	1	4
MVNP	41	7	48	**191**	**103**	294	41	4	45	0	0	0
Total	1542	338	1890	362	170	532	161	15	176	45	16	61

Appendix 7: Daytime white-tailed deer top-ranking mixed negative binomial models within $\Delta AIC_c < 2$ in MONP.

Covariates	Model 8		Model 6		Model 7	
	β	95% CI [Lower : Upper]	β	95% CI [Lower : upper]	β	95% CI [Lower : Upper]
Intercept	-7.20	[-7.40 : -6.86]	-7.06	[-7.41 : -6.71]	-7.06	[-7.41 : -6.71]
Elevation	0.25	[-0.04 : 0.54]	0.23	[-0.07 : 0.53]	0.22	[-0.08 : 0.52]
Distance to water	-0.29	[-0.52 : -0.07]	-0.30	[-0.52 : -0.07]	-0.29	[-0.52 : -0.06]
% mixed-wood forest	0.18	[0.07 : 0.29]	0.11	[-0.01 : 0.23]	0.13	[0.01 : 0.25]
TPI	0.24	[0.15 : 0.33]	0.24	[0.14 : 0.33]	0.24	[0.15 : 0.33]
Moose	0.09	[0.02 : 0.16]	0.08	[0.01 : 0.15]	0.08	[0.01 : 0.15]
Predators	0.10	[0.04 : 0.16]	–	–	–	–
Distance to trail	–	–	-0.12	[-0.22 : -0.02]	-0.12	[-0.22 : -0.02]
Distance to trail^2	–	–	-0.15	[-0.25 : -0.06]	-0.15	[-0.24 : -0.06]
Cumulative trail use	–	–	0.03	[-0.13 : 0.19]	-0.03	[-0.21 : 0.15]
Distance to trail^2 x trail use	–	–	–	–	0.06	[-0.04 : 0.16]
PCNM3	-0.36	[-0.65 : -0.07]	-0.30	[-0.60 : 0.00]	-0.30	[-0.60 : 0.00]
PCNM10	-0.18	[-0.29 : -0.07]	-0.24	[-0.36 : -0.12]	-0.23	[-0.35 : -0.11]
Model fit						
Pseudo R^2_m		0.043		0.046		0.045
Pseudo R^2_c		0.091		0.094		0.094

Appendix 8: Candidate models used to evaluate daytime detections rates of white-tailed deer using mixed negative binomial regression in MONP. The model number, covariates included in each model, the number of parameters (*k*) and the ΔAIC_c are presented. For all models, transect was included as a random factor and the effort was incorporated as an offset. A radius of 25 m for the % mixed-wood forest and 100 m for TPI were retained as radii and included in all models, along with PCNM 3 and PCNM 10.

Model #	Variables	*k*	ΔAIC_c
1	Elevation + distance to water + % mixed-wood forest + TPI + moose	10	8.91
2	Elevation + distance to water + % mixed-wood forest + TPI + moose + distance to trail	11	6.94
3	Elevation + distance to water + % mixed-wood forest + TPI + moose + distance to trail^2	12	7.63
4	Elevation + distance to water + % mixed-wood forest + TPI + moose + distance to trail + cumulative trail use	12	8.87
5	Elevation + distance to water + % mixed-wood forest + TPI + moose + cumulative trail use x distance to trail	13	10.9
6	Elevation + distance to water + % mixed-wood forest + TPI + moose + cumulative trail use + distance to trail^2	13	0.14
7	Elevation + distance to water + % mixed-wood forest + TPI + moose + cumulative trail use x distance to trail^2	14	0.75
8	Elevation + distance to water + % mixed-wood forest + TPI + moose + predators	11	0.00

Appendix 9: Daytime white-tailed deer top-ranking mixed negative binomial models within $\Delta AIC_c < 2$ in JCNP.

Covariates	Model 7		Model 3	
	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]
Intercept	-12.27	[-22.66 : -1.89]	-12.23	[-21.74 : -2.72]
Elevation	-1.47	[-2.79 : -0.16]	-1.54	[-2.90 : -0.17]
Distance to water	1.46	[0.70 : 2.23]	1.51	[0.74 : 2.28]
% mixed-wood forest	-0.08	[-0.50 : 0.33]	-0.15	[-0.55 : 0.26]
TPI	-0.18	[-0.43 : 0.08]	-0.18	[-0.44 : 0.07]
Distance to trail	-0.03	[-0.28 : 0.21]	-0.02	[-0.26 : 0.23]
Distance to trail^2	-0.25	[-0.48 : -0.02]	-0.27	[-0.50 : -0.05]
Cumulative trail use	0.07	[-0.23 : 0.37]	–	–
Distance to trail^2 x trail use	-0.23	[-0.47 : 0.00]	–	–
PCNM1	-4.65	[-20.78 : 11.49]	-4.54	[-19.32 : 10.23]
Model fit				
Pseudo R^2_m		0.78		0.77
Pseudo R^2_c		0.81		0.81

Appendix 10: Nighttime white-tailed deer top-ranking mixed negative binomial model within $\Delta AIC_c < 2$ in MONP.

Covariates	Model 7		
	β	95% CI [Lower : Upper]	
Intercept	-8.13		[-8.53 : -7.74]
Elevation	0.14		[-0.26 : 0.54]
Distance to water	-0.33		[-0.77 : 0.12]
% mixed-wood forest	0.28		[0.06 : 0.50]
TPI	0.29		[0.11 : 0.46]
Distance to trail	-0.61		[-0.83 : -0.38]
Distance to trail^2	-0.13		[-0.33 : 0.07]
Cumulative trail use	-0.41		[-0.75 : -0.06]
Distance to trail^2 x trail use	0.24		[0.04 : 0.43]
PCNM4	-0.29		[-0.63 : 0.04]
Model fit			
Pseudo R^2_m			0.097
Pseudo R^2_c			0.130

Appendix 11: Nighttime white-tailed deer top-ranking mixed negative binomial models within $\Delta AIC_c < 2$ in JCNP.

Covariates	Model 3		Model 6		Model 7	
	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]
Intercept	-10.08	[-11.02 : -9.15]	-10.04	[-10.93 : -9.14]	-10.03	[-10.89 : -9.18]
Elevation	-2.36	[-3.38 : -1.34]	-2.45	[-3.43 : -1.46]	-2.43	[-3.41 : -1.45]
Distance to water	1.64	[0.88 : 2.41]	1.69	[0.98 : 2.40]	1.63	[0.98 : 2.28]
% mixed-wood forest	-0.43	[-1.04 : 0.17]	-0.40	[-1.00 : 0.21]	-0.28	[-0.91 : 0.35]
TPI	-0.38	[-0.79 : 0.03]	-0.39	[-0.80 : 0.02]	-0.36	[-0.77 : 0.05]
Distance to trail	-0.29	[-0.69 : 0.11]	-0.31	[-0.72 : 0.09]	-0.33	[-0.74 : 0.07]
Distance to trail^2	-0.66	[-1.08 : -0.23]	-0.66	[-1.08 : -0.24]	-0.61	[-1.03 : -0.19]
Cumulative trail use	–	–	-0.15	[-0.52 : 0.22]	-0.03	[-0.44 : 0.38]
Distance to trail^2 x trail use	–	–	–	–	-0.28	[-0.74 : 0.19]
PCNM2	0.92	[-0.87 : 2.71]	0.97	[-0.84 : 2.77]	0.96	[-0.90 : 2.83]
Model fit						
Pseudo R^2_m		0.35		0.36		0.35
Pseudo R^2_c		0.40		0.40		0.38

Appendix 12: Daytime moose top-ranking mixed negative binomial models within $\Delta AIC_c < 2$ in GJNP.

Covariates	Model 2		Model 3		Model 7		Model 4	
	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]
Intercept	-10.14	[-10.62 : -9.66]	-10.03	[-10.58 : -9.47]	-10.04	[-10.63 : -9.45]	-10.11	[-10.59 : -9.63]
Elevation	0.46	[-0.17 : 1.09]	0.45	[-0.17 : 1.08]	0.48	[-0.27 : 1.23]	0.37	[-0.32 : 1.07]
Distance to water	0.67	[0.36 : 0.97]	0.65	[0.34 : 0.96]	0.70	[0.37 : 1.04]	0.70	[0.37 : 1.04]
% mixed-wood forest	0.23	[-0.15 : 0.61]	0.27	[-0.12 : 0.65]	0.37	[-0.08 : 0.82]	0.28	[-0.13 : 0.69]
TPI	-0.52	[-1.00 : -0.03]	-0.53	[-1.02 : -0.04]	-0.54	[-1.02 : -0.06]	-0.52	[-1.00 : -0.04]
Distance to trail	0.55	[0.15 : 0.95]	0.64	[0.17 : 1.10]	0.63	[0.17 : 1.09]	0.54	[0.14 : 0.94]
Distance to trail^2	–	–	-0.15	[-0.53 : 0.22]	-0.20	[-0.59 : 0.19]	–	–
Cumulative trail use	–	–	–	–	0.13	[-0.36 : 0.63]	-0.10	[-0.49 : 0.29]
Distance to trail^2 x trail use	–	–	–	–	-0.42	[-0.95 : 0.11]	–	–
PCNM2	0.59	[0.20 : 0.99]	0.62	[0.22 : 1.02]	0.64	[0.23 : 1.05]	0.58	[0.19 : 0.97]
Model fit								
Pseudo R^2_m		0.16		0.17		0.18		0.14
Pseudo R^2_c		0.16		0.17		0.18		0.14

Appendix 13: Daytime moose top-ranking mixed negative binomial models within $\Delta AIC_c < 2$ in MVNP.

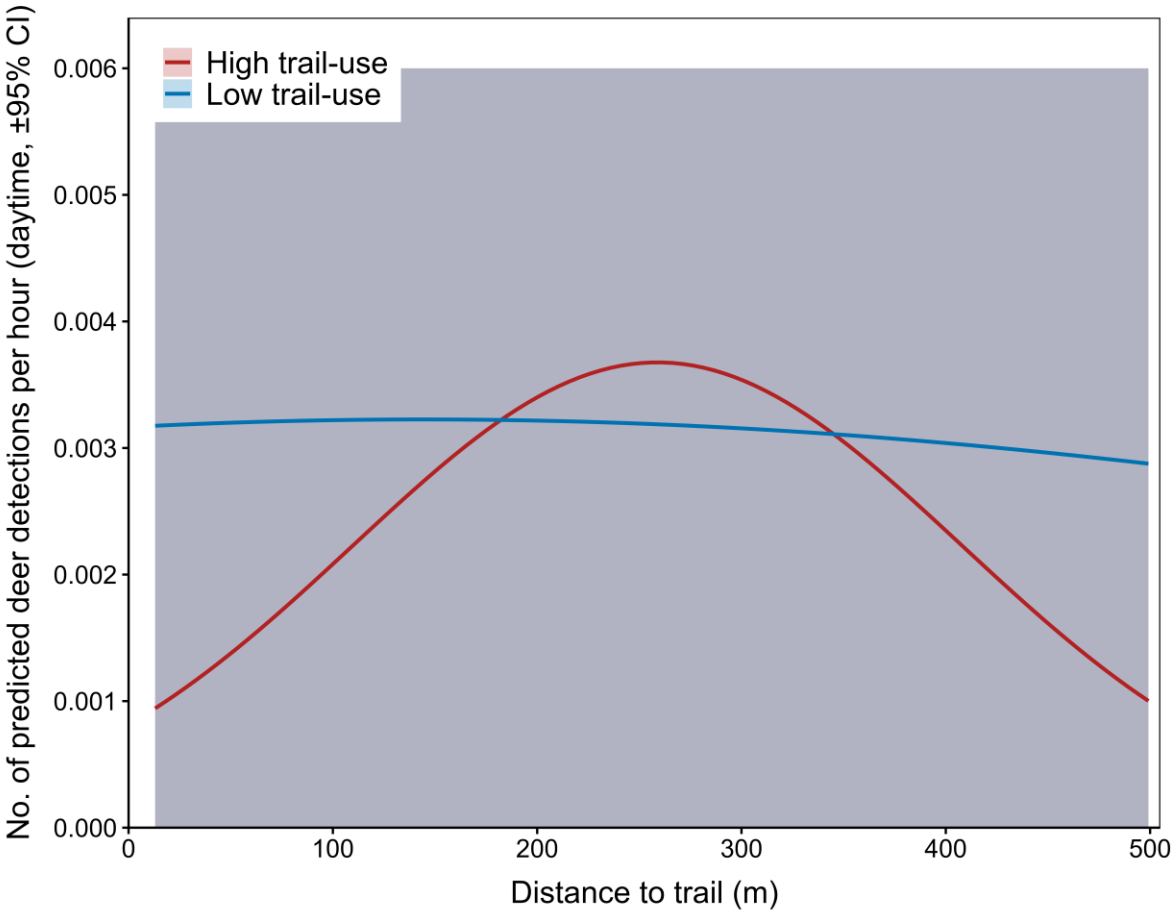
Covariates	Model 4		Model 5		Model 2		Model 6	
	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]
Intercept	-9.06	[-9.41 : -8.71]	-9.03	[-9.38 : -8.69]	-9.09	[-9.57 : -8.61]	-9.00	[-9.41 : -8.58]
Elevation	-0.98	[-1.27 : -0.69]	-0.98	[-1.27 : -0.69]	-1.24	[-1.63 : -0.85]	-0.98	[-1.27 : -0.69]
Distance to water	-0.21	[-0.45 : 0.04]	-0.18	[-0.43 : 0.06]	-0.28	[-0.60 : 0.04]	-0.20	[-0.45 : 0.05]
% mixed-wood forest	-0.09	[-0.45 : 0.27]	-0.10	[-0.45 : 0.25]	-0.04	[-0.40 : 0.33]	-0.09	[-0.45 : 0.27]
TPI	-0.13	[-0.43 : 0.17]	-0.14	[-0.44 : 0.16]	-0.14	[-0.45 : 0.17]	-0.14	[-0.45 : 0.16]
Deer	-0.08	[-0.25 : 0.08]	-0.08	[-0.24 : 0.09]	-0.09	[-0.26 : 0.07]	-0.09	[-0.26 : 0.08]
Distance to trail	0.49	[0.26 : 0.73]	0.43	[0.17 : 0.68]	0.48	[0.24 : 0.71]	0.52	[0.26 : 0.77]
Distance to trail^2 (log)	–	–	–	–	–	–	-0.07	[-0.32 : 0.18]
Cumulative trail use	0.44	[0.04 : 0.84]	0.38	[-0.02 : 0.78]	–	–	0.44	[0.05 : 0.84]
Distance to trail x (log) trail use	–	–	0.16	[-0.06 : 0.38]	–	–	–	–
PCNM3	0.67	[0.26 : 1.08]	0.61	[0.19 : 1.02]	0.49	[0.04 : 0.94]	0.68	[0.27 : 1.09]
Model fit								
Pseudo R^2_m		0.24		0.23		0.24		0.25
Pseudo R^2_c		0.24		0.23		0.25		0.25

Appendix 14: Nighttime moose top-ranking mixed negative binomial models within $\Delta AIC_c < 2$ in MVNP.

Covariates	Model 3		Model 6	
	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]
Intercept	-8.40	[-8.88 : -7.93]	-8.42	[-8.90 : -7.94]
Elevation	-1.07	[-1.42 : -0.72]	-1.18	[-1.65 : -0.71]
Distance to water	0.07	[-0.24 : 0.38]	0.09	[-0.23 : 0.41]
% mixed-wood forest	-0.23	[-0.63 : 0.16]	-0.23	[-0.62 : 0.17]
TPI	-0.36	[-0.72 : 0.01]	-0.36	[-0.72 : 0.01]
Distance to trail	0.41	[0.10 : 0.73]	0.41	[0.09 : 0.73]
Distance to trail^2	-0.35	[-0.69 : -0.01]	-0.34	[-0.69 : 0.00]
Cumulative trail use	–	–	-0.13	[-0.49 : 0.24]
PCNM1	0.58	[0.18 : 0.98]	0.64	[0.20 : 1.08]
Model fit				
Pseudo R^2_m		0.20		0.21
Pseudo R^2_c		0.20		0.21

Appendix 15. Candidate models used to evaluate daytime detections rates of white-tailed deer using mixed negative binomial regression in JCNP. The model number, covariates included in each model, the number of parameters (k) and the ΔAIC_c are presented. For all models, transect was included as a random factor and the effort was incorporated as an offset. A radius of 25 m for the % mixed-wood forest and 50 m for TPI were retained as radii and included in all models, along with PCNM 1.

Model #	Variables	k	ΔAIC_c
1	Elevation + distance to water + % mixed-wood forest + TPI	8	2.31
2	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail	9	4.29
3	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail^2	10	0.59
4	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail + cumulative trail use	10	5.92
5	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail	11	3.70
6	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use + distance to trail^2	11	2.11
7	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail^2	12	0.00



Appendix 16: Predicted daytime detection rates of white-trailed deer as a function of the interaction between quadratic distance to trail (m) and daytime cumulative trail use (visitors per week) in Jacques-Cartier National Park, Quebec, Canada. The response variable represents weekly predicted detections per camera-hour. The blue line shows predictions at minimum daytime trail use (n = 0 visitors per week), and the red line shows predictions at maximum daytime trail use (n = 6204 visitors per week). 95% confidence intervals for both curves are present as shaded grey areas; in this case, confidence intervals are overlapping.

Appendix 17. Candidate models used to evaluate nighttime detections rates of white-tailed deer using mixed negative binomial regression in MONP. The model number, covariates included in each model, the number of parameters (k) and the ΔAIC_c are presented. For all models, transect was included as a random factor and the effort was incorporated as an offset. A radius of 25 m for the % mixed-wood forest and 50 m for TPI were retained as radii and included in all models, along with PCNM 4.

Model #	Variables	k	ΔAIC_c
1	Elevation + distance to water + % mixed-wood forest + TPI	8	33.30
2	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail	9	3.24
3	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail^2	10	3.05
4	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail + cumulative trail use	10	3.83
5	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail	11	5.48
6	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use + distance to trail^2	11	3.70
7	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail^2	12	0.00

Appendix 18. Candidate models used to evaluate nighttime detections rates of white-tailed deer using mixed negative binomial regression in JCNP. The model number, covariates included in each model, the number of parameters (k) and the ΔAIC_c are presented. For all models, transect was included as a random factor and the effort was incorporated as an offset. A radius of 25 m for the % mixed-wood forest and 50 m for TPI were retained as radii and included in all models, along with PCNM 2.

Model #	Variables	k	ΔAIC_c
1	Elevation + distance to water + % mixed-wood forest + TPI	8	10.85
2	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail	9	9.33
3	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail^2	10	0.00
4	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail + cumulative trail use	10	11.02
5	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail	11	12.50
6	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use + distance to trail^2	11	1.38
7	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail^2	12	1.78

Appendix 19. Candidate models used to evaluate daytime detections rates of moose using mixed negative binomial regression in GJNP. The model number, covariates included in each model, the number of parameters (k) and the ΔAIC_c are presented. For all models, transect was included as a random factor and the effort was incorporated as an offset. A radius of 25 m for the % mixed-wood forest and 25 m for TPI were retained as radii and included in all models, along with PCNM 2.

Model #	Variables	k	ΔAIC_c
1	Elevation + distance to water + % mixed-wood forest + TPI	8	5.33
2	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail	9	0.00
3	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail^2	10	1.37
4	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail + cumulative trail use	10	1.80
5	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail	11	3.54
6	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use + distance to trail^2	11	3.04
7	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail^2	12	1.55
8	Elevation + distance to water + % mixed-wood forest + TPI + bear	9	6.79

Appendix 20. Candidate models used to evaluate daytime detections rates of moose using mixed negative binomial regression in MVNP. The model number, covariates included in each model, the number of parameters (*k*) and the ΔAIC_c are presented. For all models, transect was included as a random factor and the effort was incorporated as an offset. A radius of 100 m for the % mixed-wood forest and 50 m for TPI were retained as radii and included in all models, along with PCNM 3.

Model #	Variables	*k*	ΔAIC_c
1	Elevation + distance to water + % mixed-wood forest + TPI + deer	9	14.05
2	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail + deer	10	0.94
3	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail^2 + deer	11	2.69
4	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail + cumulative trail use (log-transformed) + deer	11	0.00
5	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use (log-transformed) x distance to trail + deer	12	0.05
6	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use (log-transformed) + distance to trail^2 + deer	12	1.75
7	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use (log-transformed) x distance to trail^2 + deer	13	3.81
8	Elevation + distance to water + % mixed-wood forest + TPI + deer + bear	10	14.07

Appendix 21. Candidate models used to evaluate nighttime detections rates of moose using mixed negative binomial regression in MVNP. The model number, covariates included in each model, the number of parameters (*k*) and the ΔAIC_c are presented. For all models, transect was included as a random factor and the effort was incorporated as an offset. A radius of 100 m for the % mixed-wood forest and 50 m for TPI were retained as radii and included in all models, along with PCNM 1.

Model #	Variables	k	ΔAIC_c
1	Elevation + distance to water + % mixed-wood forest + TPI	8	4.65
2	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail	9	2.07
3	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail^2	10	0.00
4	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail + cumulative trail use	10	3.47
5	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail	11	5.52
6	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use + distance to trail^2	11	1.57
7	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail^2	12	3.58

Appendix 22. Candidate models used to evaluate nighttime detections rates of moose using mixed negative binomial regression in GJNP. The model number, covariates included in each model, the number of parameters (k) and the ΔAIC_c are presented. For all models, transect was included as a random factor and the effort was incorporated as an offset. A radius of 100 m for the % mixed-wood forest and 25 m for TPI were retained as radii and included in all models, along with PCNM 2.

Model #	Variables	k	ΔAIC_c
1	Elevation + distance to water + % mixed-wood forest + TPI	8	0.00
2	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail	9	1.17
3	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail^2	10	3.21
4	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail + cumulative trail use	10	3.20
5	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail	11	4.32
6	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use + distance to trail^2	11	5.25
7	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use x distance to trail^2	12	7.30

Appendix 23: Nighttime moose top-ranking mixed negative binomial models within $\Delta AIC_c < 2$ in GJNP.

Covariates	Model 1		Model 2	
	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]
Intercept	-9.83	[-10.58 : -9.09]	-9.85	[-10.57 : -9.12]
Elevation	0.83	[-0.37 : 2.04]	0.83	[-0.35 : 2.02]
Distance to water	0.29	[-0.13 : 0.70]	0.31	[-0.10 : 0.72]
% mixed-wood forest	-0.29	[-1.16 : 0.59]	-0.22	[-1.07 : 0.62]
TPI	-0.31	[-0.93 : 0.32]	-0.43	[-1.12 : 0.26]
Distance to trail	–	–	-0.24	[-0.75 : 0.27]
PCNM2	0.75	[0.23 : 1.28]	0.80	[0.26 : 1.34]
Model fit				
Pseudo R^2_m		0.18		0.19
Pseudo R^2_c		0.18		0.19

Appendix 24. Candidate models used to evaluate the probability of day-night moose detections using mixed logistic regression in MONP. The model number, covariates included in each model, the number of parameters (*k*) and the ΔAIC_c are presented. For all models, transect was included as a random factor and the effort (log-transformed) was incorporated as a fixed effect. A radius of 25 m for the % mixed-wood forest and 25 m for TPI were retained as radii and included in all models, along with PCNM 5.

Model #	Variables	*k*	ΔAIC_c
1	Elevation + distance to water + % mixed-wood forest + TPI + deer + effort (log-transformed)	9	12.38
2	Elevation + distance to water + % mixed-wood forest + TPI + deer + distance to trail + effort (log-transformed)	10	8.29
3	Elevation + distance to water + % mixed-wood forest + TPI + deer + distance to trail^2 + effort (log-transformed)	11	10.30
4	Elevation + distance to water + % mixed-wood forest + TPI + deer + distance to trail + cumulative trail use + effort (log-transformed)	11	7.86
5	Elevation + distance to water + % mixed-wood forest + TPI + deer + cumulative trail use x distance to trail + effort (log-transformed)	12	0.00
6	Elevation + distance to water + % mixed-wood forest + TPI + deer + cumulative trail use + distance to trail^2 + effort (log-transformed)	12	9.87
7	Elevation + distance to water + % mixed-wood forest + TPI + deer + cumulative trail use x distance to trail ^{2} + effort (log-transformed)	13	6.66
8	Elevation + distance to water + % mixed-wood forest + TPI + deer + predators + effort (log-transformed)	10	11.50

Appendix 25: Moose day-night top-ranking mixed logistic model in MONP.

Covariates	Model 5	
	β	95% CI [Lower : Upper]
Intercept	-6.16	[-10.62 : -1.69]
Elevation	0.38	[-0.03 : 0.79]
Distance to water	0.19	[-0.28 : 0.67]
% mixed-wood forest	0.43	[0.07 : 0.79]
TPI	-0.05	[-0.33 : 0.22]
Deer	0.29	[0.05 : 0.52]
Distance to trail	0.63	[0.23 : 1.02]
Cumulative trail use	-0.71	[-1.35 : -0.08]
Distance to trail x trail use	0.63	[0.19 : 1.07]
PCNM5	-0.36	[-0.65 : -0.07]
log(Effort)	-0.18	[-0.29 : -0.07]
Model fit		
Pseudo R^2_m		0.32
Pseudo R^2_c		0.35

Appendix 26. Candidate models used to evaluate day-night detections rates of bear using mixed negative binomial regression in GJNP. The model number, covariates included in each model, the number of parameters (k) and the ΔAIC_c are presented. For all models, transect was included as a random factor and the effort was incorporated as an offset. A radius of 25 m for the % mixed-wood forest and 100 m for TPI were retained as radii and included in all models, but no PCNM was included.

Model #	Variables	k	ΔAIC_c
1	Elevation + distance to water + % mixed-wood forest + TPI	7	0.12
2	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail	8	1.62
3	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail^2	9	3.07
4	Elevation + distance to water + % mixed-wood forest + TPI + distance to trail + cumulative trail use (log-transformed)	9	0.67
5	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use (log-transformed) x distance to trail	10	0.38
6	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use (log-transformed) + distance to trail^2	10	2.29
7	Elevation + distance to water + % mixed-wood forest + TPI + cumulative trail use (log-transformed) x distance to trail^2	11	3.51
9	Elevation + distance to water + % mixed-wood forest + TPI + moose	8	0.00

Appendix 27: American black bear day-night top-ranking mixed negative binomial models within $\Delta AIC_c < 2$ in GJNP. No PCNM axes were significant, hence their exclusion.

Covariates	**Model 9**		**Model 1**		**Model 5**		**Model 4**		**Model 2**	
	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]	β	95% CI [Lower : Upper]
Intercept	-10.08	[-10.57 : -9.59]	-10.06	[-10.56 : -9.57]	-10.07	[-10.53 : -9.60]	-10.03	[-10.48 : -9.58]	-10.06	[-10.55 : -9.57]
Elevation	-0.52	[-0.95 : -0.09]	-0.55	[-0.98 : -0.12]	-0.62	[-1.04 : -0.19]	-0.63	[-1.05 : -0.21]	-0.54	[-0.97 : -0.12]
Distance to water	0.13	[-0.34 : 0.59]	0.10	[-0.38 : 0.57]	0.26	[-0.23 : 0.75]	0.25	[-0.24 : 0.73]	0.08	[-0.39 : 0.55]
% mixed-wood forest	0.19	[-0.23 : 0.61]	0.15	[-0.27 : 0.57]	0.28	[-0.15 : 0.71]	0.23	[-0.19 : 0.65]	0.14	[-0.27 : 0.56]
TPI	-0.42	[-0.73 : -0.11]	-0.42	[-0.73 : -0.11]	-0.47	[-0.82 : -0.12]	-0.41	[-0.76 : -0.07]	-0.36	[-0.71 : 0.00]
Moose	-0.41	[-1.07 : 0.25]	–	–	–	–	–	–	–	–
Distance to trail	–	–	–	–	0.09	[-0.24 : 0.42]	0.09	[-0.24 : 0.42]	0.12	[-0.21 : 0.46]
(log) cumulative trail use	–	–	–	–	-0.33	[-0.76 : 0.10]	-0.38	[-0.80 : 0.04]	–	–
Distance to trail x (log) trail use	–	–	–	–	-0.24	[-0.55 : 0.07]	–	–		–
Model fit										
Pseudo R^2_m		0.057		0.041		0.059		0.050		0.042
Pseudo R^2_c		0.081		0.068		0.080		0.069		0.066

CONCLUSION GÉNÉRALE

RETOUR SUR LE CONTEXTE DE L'ÉTUDE

Les perturbations anthropiques constituent l'un des principaux moteurs d'altération des paysages. Elles influencent directement le comportement des animaux, leur répartition dans l'espace et la dynamique de leurs populations (Crooks et al., 2017 ; Dirzo et al., 2014 ; Geffroy et al., 2015 ; Miller et al., 2022 ; Sih, 2013). Parmi ces perturbations anthropiques, la pratique d'activités récréatives dans les milieux naturels protégés occupe une place particulière : bien qu'elles soient souvent perçues comme peu perturbatrices comparativement à l'exploitation forestière, l'urbanisation ou la chasse, elles représentent une source croissante de dérangement pour la faune, comme en témoigne l'augmentation documentée de 32,5 % des jours-visites entre 2000 et 2009 aux États-Unis seulement (Guimarães et al., 2025 ; Larson et al., 2016 ; Muhly et al., 2011). Cette tendance se reflète également au Québec, où la fréquentation des parcs du réseau de la Sépaq a augmenté de 25,3 % entre 2017 et 2024 (Institut de la statistique du Québec, 2025). Les parcs nationaux, qui ont pour mission à la fois de conserver la biodiversité et de rendre la nature accessible au public, se trouvent ainsi confrontés à un dilemme entre conservation et mise en valeur des territoires. Dans ce contexte, il apparaît essentiel de mieux caractériser la réponse des grands mammifères aux activités récréatives, au-delà de leur simple présence ou absence dans un parc, en considérant également les ajustements fins de leur utilisation de l'espace et du temps.

Plusieurs études ont montré que les prédateurs, tels que le loup gris (*Canis lupus*) et le coyote (*C. latrans*), tendent à éviter les milieux situés à proximité des sentiers récréatifs, en raison d'une perception accrue du risque associé à la présence humaine (Ciuti et al., 2012 ; Frid et Dill, 2002 ; Patten et Burger, 2018 ; Smith et al., 2022). Ce comportement peut, à son tour, favoriser l'utilisation de ces mêmes secteurs par des herbivores comme le cerf mulet (*Odocoileus hemionus*) ou l'orignal (*Alces alces*), qui peuvent y trouver un refuge partiel

contre la prédation (Beaupré et al., 2025 ; Berger, 2007 ; Muhly et al., 2011 ; Shannon et al., 2014). Parallèlement, la présence humaine peut induire des modifications des patrons d'activité, notamment une augmentation de l'activité nocturne chez des espèces habituellement diurnes ou crépusculaires, telles que l'ours noir (*Ursus americanus*), afin d'éviter les périodes de forte fréquentation humaine (Gaynor et al., 2018 ; Nix et al., 2018 ; Zeller et al., 2019). Enfin, l'exposition répétée à l'humain sans conséquences négatives immédiates peut favoriser des processus d'habituation, réduisant la méfiance des individus et modifiant leur comportement spatial (Hansen et Aanes, 2015 ; Smith et al., 2005).

C'est dans ce cadre conceptuel que s'inscrivait mon projet, dont l'objectif principal était d'évaluer les impacts des activités récréatives sur la répartition spatiotemporelle des grands mammifères dans quatre parcs nationaux du Québec (Mont-Orford, Grands-Jardins, Jacques-Cartier et Monts-Valins). Plus précisément, il visait à quantifier la relation entre l'occurrence de plusieurs espèces clés de la grande faune du Québec méridional (cerf de Virginie *Odocoileus virginianus*, orignal, caribou forestier *Rangifer tarandus caribou*, loup gris, coyote et ours noir) et l'utilisation des sentiers récréatifs par les randonneurs. Pour répondre à cet objectif, 517 caméras automatisées ont été déployées en été en 2022 et 2023 dans quatre parcs selon un plan d'échantillonnage aléatoire stratifié couvrant un gradient de fréquentation humaine et de distance aux sentiers (jusqu'à 500 m). Mon dispositif permettait donc de quantifier l'intensité d'utilisation des sentiers par les activités humaines (randonnée, randonnée avec chiens en laisse, vélo de montagne et de route) et le taux photographique des espèces de grande faune à proximité des sentiers, pour ensuite relier le tout à diverses covariables environnementales (p. ex. couverture de forêt, élévation, position topographique, occurrence de compétiteurs) et temporelles (phases de la journée) pour modéliser la réponse spatiale des grands mammifères au dérangement anthropique.

RETOUR SUR LES PRINCIPAUX RÉSULTATS

Mes résultats mettent en évidence que les sentiers récréatifs, et la fréquentation humaine qui leur est associée, influencent de manière significative l'utilisation de l'espace

par les grands mammifères, mais de façon variable selon les espèces et le contexte écologique. Chez l'orignal, le taux de détection diminuait fortement à proximité des sentiers, traduisant une réduction marquée de l'utilisation des zones associées aux infrastructures récréatives, conformément aux résultats rapportés dans d'autres études (Neumann et al., 2011; Rogala et al., 2011; Suraci et al., 2021). Cette réponse était particulièrement prononcée dans le parc soumis à la plus forte pression récréative (Mont-Orford), où la probabilité de détection demeurait quasi nulle à moins de 300–400 m des sentiers, suggérant une sensibilité élevée à la présence humaine. Malgré de potentiels indices d'un effet de type « bouclier humain » (*lib. human shield*, *sensu* Berger 2007) et certaines variations selon la période d'activité, l'orignal montrait globalement une réduction marquée d'utilisation des zones situées à proximité des sentiers, surtout lorsque l'intensité de la fréquentation humaine était élevée. Ces résultats suggèrent que chez ce cervidé de grande taille, à la vulnérabilité et à la productivité plus faibles que le cerf de Virginie, l'activité récréative induirait une perte d'habitat fonctionnel associée à une réduction de l'utilisation de l'espace à proximité des sentiers, plutôt qu'un simple réajustement contextuel de l'utilisation de l'espace (Granados et al., 2023 ; Neumann et al., 2010 ; Polfus et al., 2011).

Le cerf de Virginie présentait quant à lui une grande plasticité comportementale, utilisant préférentiellement des secteurs situés à des distance intermédiaire aux sentiers et modulant son occupation de l'espace en fonction des phases du jour. Dans les secteurs soumis à une forte fréquentation humaine diurne, l'utilisation réduite des zones à proximité des sentiers se prolongeait la nuit, révélant un effet de report de la perturbation humaine. Ces réponses sont cohérentes avec les traits d'histoire de vie du cerf de Virginie, une proie de plus petite taille et plus vulnérable à la prédation que l'orignal. Dans ce contexte, la proximité des sentiers récréatifs pourrait constituer un refuge partiel contre les prédateurs locaux, tels que le coyote et l'ours noir, favorisant une utilisation flexible de l'espace selon l'intensité et le moment des perturbations humaines. Un tel patron est conforme au concept de paysage du risque contextuel, dans lequel la valeur relative d'un habitat dépend non seulement de sa structure physique, mais aussi de l'intensité et de la distribution spatiotemporelle des pressions anthropiques, qui interagissent avec les risques naturels, tel que la prédation, en

accentuant ou en atténuant l'utilisation de certains habitats selon le niveau de risque perçu (Laundré et al., 2010 ; Marion et al., 2024 ; Oriol-Cotterill et al., 2015).

Au-delà de la simple distance aux sentiers, mes analyses montrent que l'intensité de la fréquentation humaine constitue un déterminant majeur des réponses de grands mammifères. En intégrant simultanément la distance aux sentiers et les niveaux de fréquentation humaine dans nos modèles, j'ai pu observer que la perturbation ne peut être comprise adéquatement à partir de la seule dimension spatiale, mais qu'elle résulte plutôt de l'interaction entre la configuration des infrastructures et la pression d'utilisation. Ce résultat est conforme à ceux de Beaupré et al. (2025), selon lesquels les effets du dérangement ne dépendent pas uniquement de la distance aux infrastructures, mais aussi de l'intensité d'utilisation humaine (Marion et al., 2024 ; Zeller et al., 2024). De plus, dans plusieurs cas, mes résultats mettent en évidence des relations non linéaires de type quadratique, ce qui suggère des changements marqués des réponses comportementales à mesure que la pression récréative augmente, en cohérence avec le concept de seuils d'influence proposé par Dertien et al. (2021). Ces dynamiques suggèrent une transition progressive des réponses comportementales avec l'augmentation de la pression récréative, allant d'un ajustement au dérangement vers une utilisation de plus en plus restreinte de l'espace, pouvant se traduire par une relocalisation et, conséquemment, à une perte fonctionnelle d'habitat.

RETOMBÉES THÉORIQUES DE L'ÉTUDE

Sur le plan théorique, mon mémoire contribue à dépasser une lecture souvent unidimensionnelle des effets des activités récréatives sur la faune. Bien que l'influence des infrastructures linéaires et des activités humaines sur la faune aient été largement documentée, la plupart des travaux antérieurs se concentrent soit sur des gradients spatiaux (distance aux routes ou aux sentiers ; Dertien et al., 2021 ; Rowland et al., 2000), soit sur des modifications globales des rythmes d'activité (Tucker et al., 2018), notamment l'augmentation de la nocturnalité (Gaynor et al., 2018 ; Nix et al., 2018; Procko et al. 2022). En combinant une résolution spatiale fine, une partition temporelle explicite (phases de jour)

et un gradient de pression humaine mesuré de façon indépendante dans quatre aires d'étude, mon étude propose un cadre d'analyse dans lequel les effets de la perturbation varient selon la localisation spatiale et le moment de la journée, plutôt que comme un effet additif de variables isolées. Plus précisément, mes résultats soutiennent notamment l'hypothèse que les perturbations récréatives ont des effets reportés sur le comportement entre les différentes périodes d'activité, c.-à-d. que la pression humaine exercée à un moment de la journée influence l'utilisation de l'espace des proies à d'autres moments. Ces résultats suggèrent ainsi que les réponses de la faune aux activités récréatives peuvent persister au-delà des périodes d'exposition directe aux humains, en modulant à la fois l'utilisation de l'espace et les dynamiques spatiotemporelles des espèces, ce qui souligne la pertinence de considérer les effets différés potentiels des perturbations anthropiques sur la faune. Cette perspective élargit les approches centrées sur les seuls déplacements d'activité vers la nuit et suggère que les réponses de la grande faune à la fréquentation humaine s'inscrivent dans une dynamique de paysage du risque contextuel, dépendant à la fois de la structure des habitats et de la distribution spatio-temporelle des usages récréatifs (Gaynor et al., 2019 ; Laundré et al., 2010 ; Oriol-Cotterill et al., 2015).

À une échelle plus large, mon étude appuie l'hypothèse selon laquelle l'intensification de l'empreinte humaine ne modifie pas uniquement l'utilisation de l'espace à court terme, mais peut également agir comme un filtre écologique, favorisant les espèces les plus tolérantes aux perturbations au détriment de celles présentant des exigences spatiales élevées ou une faible flexibilité comportementale (Gamelon et al., 2014 ; Suraci et al., 2021). Ce mécanisme est susceptible, à long terme, de contribuer à des changements dans la composition des communautés, avec des effets potentiels sur les interactions trophiques et la dynamique des écosystèmes (Gaynor et al., 2019 ; Suraci et al., 2016).

Enfin, mes résultats s'inscrivent dans une extension récente du cadre conceptuel du « bouclier humain » (*lib. human shield*, *sensu* Berger 2007). Bien que ce mécanisme ait été principalement formulé dans le contexte des interactions prédateur-proie, Gaynor et al. (2025) soulignent qu'il peut également s'appliquer à des relations antagonistes ou

compétitives, y compris intraspécifiques. Dans notre système, la comparaison entre les réponses du cerf de Virginie et de l'orignal suggère que l'activité récréative peut modifier indirectement les interactions entre espèces en conférant un avantage aux taxons les plus tolérants à la perturbation. Cette modulation anthropique du paysage du risque pourrait ainsi avoir des répercussions à l'échelle des communautés, en accentuant les différences de réponse entre espèces flexibles et espèces sensibles à la fréquentation humaine.

RETOMBÉES APPLIQUÉES DE L'ÉTUDE

Les résultats de mon étude ont des retombées directes pour la gestion des aires protégées et l'aménagement du territoire. En exploitant des modèles non linéaires pour analyser les relations entre la distribution spatiale des grands mammifères, la distance aux sentiers et leur intensité de fréquentation par les randonneurs, j'ai mis en évidence des zones où la pression récréative pouvait entraîner une perte fonctionnelle d'habitat pour certaines espèces, offrant ainsi une base pour l'identification de capacités de charge récréative et de seuils de perturbation (Procko et al., 2022). Ces informations peuvent guider la conception de stratégies de zonage, la limitation de l'accès à certaines sections de sentiers ou la réorganisation du réseau pour maintenir des noyaux d'habitats à faible perturbation. Par exemple, certaines périodes biologiquement sensibles, telles que la mise bas chez l'orignal, pourraient faire l'objet de fermetures temporaires ou de restrictions ciblées sur certains sentiers (Brown et al., 2012 ; Courtois et Crête, 1988 ; Rogala et al., 2011).

L'approche multi-sites adoptée dans mon projet permet d'évaluer la constance ou la variabilité des réponses fauniques en fonction du contexte écologique et anthropique, ce qui renforce la robustesse des recommandations. Elle ouvre également la possibilité de comparer l'utilisation de l'espace à proximité des sentiers avec celle de zones plus éloignées, non influencées par les infrastructures récréatives, afin de mieux quantifier l'étendue et l'intensité des impacts humains. Enfin, en ciblant la majorité des espèces de grands mammifères et en échantillonnant un large gradient de fréquentation, mon étude fournit une base empirique solide pour évaluer les compromis entre accessibilité au public et conservation de la

biodiversité à l'échelle du réseau de parcs, tout en orientant les décisions de gestion vers une approche spatiale et temporelle nuancée des perturbations humaines.

LIMITES ET PERSPECTIVES

Comme dans toute étude, certaines limites doivent toutefois être prises en compte dans l'interprétation de mes résultats et ouvrent des perspectives pour de futurs travaux. Tout d'abord, la durée relativement courte des déploiements de caméras a restreint l'analyse de processus saisonniers tels que l'élevage des jeunes ou l'exposition aux conditions hivernales, qui influencent l'utilisation de l'espace chez plusieurs espèces (Hubbard et al., 2022 ; Lesmerises et al., 2017). Des inventaires couvrant un cycle annuel complet permettraient d'intégrer explicitement la dimension saisonnière et d'examiner l'interaction entre perturbation récréative et contraintes environnementales, et même d'augmenter les taux de détections des espèces moins abondantes (p. ex. caribou, ours, loup, coyote) pour lesquelles nous n'avons pas pu réaliser d'analyses statistiques. Ces suivis prolongés offriraient également l'opportunité d'inclure des covariables environnementales dynamiques, telles que la productivité de la végétation (NDVI), reconnue comme un déterminant majeur de la distribution des grands mammifères (Fennell et al., 2023 ; Granados et al., 2023 ; Procko et al., 2022).

De plus, étendre mon dispositif à une échelle spatiale plus grande permettrait l'intégration de facteurs paysagers externes tels que la distance aux limites des parcs, la composition de l'habitat retrouvé dans les zones périphériques des parcs, la densité routière, les activités de coupe forestière ou de chasse, et améliorerait l'inférence en informant sur la manière avec laquelle le contexte régional module les réponses observées à l'intérieur des aires protégées (Nickel et al., 2020 ; Procko et al., 2022 ; Smith et al., 2021). De telles perspectives sont d'autant plus cruciales que plusieurs parcs étudiés sont ceinturés de paysages fragmentés ou fortement anthropisés, incluant des matrices agricoles, des secteurs sous aménagement forestier et des territoires soumis à la chasse. Dans un tel contexte, la protection de massifs d'habitat à faible perturbation à l'intérieur des limites des parcs apparaît

comme un levier essentiel pour maintenir des populations viables de grands mammifères (Granados et al., 2023 ; Polfus et al., 2011 ; Smith et al., 2022).

Néanmoins, mes résultats consolident une base de connaissances déjà solides permettant des évaluations futures plus intégrées des projets de développement de sentiers récréatifs, combinant données fauniques, pressions anthropiques multiples et indicateurs de qualité de l'habitat. Malgré ses limites, mon étude fournit des éléments robustes quant aux déterminants de la répartition des grands mammifères dans des environnements soumis à la récréation et souligne l'importance d'approches spatiotemporelles fines pour comprendre les mécanismes sous-jacents aux réponses observées.

CONCLUSION

Mon étude indique clairement que les sentiers récréatifs et l'activité humaine associée contribuent à structurer l'utilisation de l'espace par les ongulés dans divers paysages protégés. En mettant en évidence à la fois des patrons comportementaux récurrents et des réponses propres à certaines espèces, ce projet souligne l'importance de considérer la dimension spatiotemporelle des perturbations anthropiques dans la gestion des aires protégées. L'ampleur de mon dispositif d'échantillonnage et des analyses spatiotemporelles suggère que la fréquentation humaine peut entraîner une perte fonctionnelle d'habitat pour certaines espèces, soulignant l'importance de préserver des secteurs à faible perturbation à l'intérieur des aires protégées (Ciuti et al., 2012 ; Cooke et al., 2023 ; Polfus et al., 2011 ; Smith et al., 2021). Au-delà de la simple caractérisation des effets du dérangement découlant des sentiers récréatifs, mon projet de maîtrise offre une base scientifique pour orienter des stratégies de gestion adaptative conciliant usage récréatif et conservation de la biodiversité.

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