Dynamique d’une population d’orignaux vivant dans une aire protégée, sans chasse ni prédateur apical

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Grand géant de nos forêts,

Dans les moments d'incertitudes et de doutes

Insuffle en moi ta confiance et ta sagesse.

Apprends-moi quand me faire discrète et quand m'exprimer.

Oh Prince de l'Eau, toi qui baignes dans les eaux de notre mère,

Toi qui y trouves refuge et substance,

Aide-moi à me relier à sa sagesse et sa force.

Comme toi je choisis de lancer mon cri, mon chant,

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Il y a un peu de toi dans chacun de nous…

Mariepierre Aubin (L'Ensauvageuse)

RÉSUMÉ

Les populations animales vivant à haute densité peuvent impacter négativement les écosystèmes (p. ex. en modifiant la structure de la végétation) et les sociétés humaines (p. ex. en augmentant la fréquence des accidents routiers). C'est le cas de l'orignal (*Alces alces americana*) dans certaines régions canadiennes, surtout dans des aires protégées sans prélèvement ni aménagement forestier. Peu d'études se sont intéressées aux populations d'orignaux vivant dans ce contexte, particulièrement en l'absence de leur prédateur principal (loup *Canis lupus*), avec pour conséquence un manque de connaissances et d'outils pour guider la gestion. Les objectifs de mon étude étaient 1) d'identifier les facteurs – et leurs interactions – qui régissent la dynamique des populations d'orignaux vivant dans de telles conditions, et pour ce faire, 2) de construire un modèle démographique. J'ai utilisé comme cas d'étude les variations d'abondance d'orignaux observées entre 1982 et 2020 au Parc national Forillon (Gaspésie, Québec). Mon hypothèse stipulait que la dynamique de cette population est principalement gouvernée par la compétition intraspécifique, le climat et le parasitisme par la tique d'hiver (*Dermacentor albipictus*), l'importance relative de ces facteurs pouvant varier avec le temps et la densité de la population. J'ai bâti un modèle de population structuré par l'âge et le sexe de façon à reproduire les fluctuations observées d'abondance, de rapport des sexes et de recrutement, et je l'ai paramétré à l'aide de la méthode de modélisation orientée par patrons (*lib. pattern-oriented modelling*). Mes résultats indiquent que la compétition intraspécifique a fortement influencé la survie, la reproduction et la dispersion des orignaux. Le climat hivernal était également un facteur important pour la survie des veaux, et entrait en interaction avec la charge de tiques et la densité. Contrairement à mon hypothèse, la prédation par l'ours (*Ursus americanus*) et le coyote (*Canis latrans*) a eu un effet marqué sur la survie des veaux, tandis que l'impact de la tique d'hiver était plus faible qu'attendu. Mes résultats ainsi que la plateforme analytique qui les supporte affinent notre connaissance de l'impact des facteurs environnementaux sur les populations de grands herbivores à haute densité, et constituent une base solide de réflexion et d'anticipation pour les gestionnaires.

Mots clés : dynamique des populations, orignal, gestion faunique, haute densité, modélisation, aire protégée, facteurs environnementaux, paramètres démographiques

ABSTRACT

Animal populations living at high density can negatively impact ecosystems (e.g. by modifying the vegetation structure) and humans (e.g. by making the traffic accidents more frequent). This is the case for moose (*Alces alces americana*) in some Canadian regions, especially in protected areas without hunting or harvesting. Few studies focused on moose populations living in this context, particularly in the absence of the main predator (wolf *Canis lupus*), causing a lack of information and tools to guide management. My study's objectives were to 1) identify the factors—and their interactions—that drive the dynamics of moose populations living in such conditions, and to do so, 2) build a demographic model. As a case study, I used the variations in moose abundance observed between 1982 and 2020 in Forillon National Park (Gaspésie, Quebec). My hypothesis stated that the dynamics of this population is mostly driven by intraspecific competition, climate and parasitism by winter tick (*Dermacentor albipictus*), with the relative importance of these factors varying with time and population density. I built an age- and sex-structured population model to reproduce the observed fluctuations in abundance, sex ratio and recruitment, and I parameterized it using the pattern-oriented modeling method. My results indicate that intraspecific competition strongly influenced moose survival, reproduction and dispersal. Winter climate was also a significant factor for calf survival and interacted with tick load and population density. Contrary to my hypothesis, predation by bears (*Ursus americanus*) and coyotes (*Canis latrans*) markedly affected calf survival, while the impact of the winter tick was weaker than expected. My results, along with the analytical platform supporting them, refine our knowledge of the impact of the environmental factors on high-density populations of large herbivores and provide managers with a solid basis for reflection and planning.

Keywords: population dynamics, moose, wildlife management, high density, modeling, protected area, environmental factors, demographic parameters

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ANOVA	Analysis of variance
a.s.l.	Above sea level
CI	Confidence interval
DBH	Diameter at breast height
GPS	Global Positioning System
ME	Metabolizable energy
MELCCFP	Ministère de l'Environnement, de la Lutte contre les changements climatiques, de la Faune et des Parcs
M : F	Males : Females
MRNF	Ministère des Ressources naturelles et des Forêts
N	Nitrogen
NAO	North Atlantic oscillation
NDD	Negative density dependence
PDD	Positive density dependence
POM	Pattern-oriented Modeling
US	United States
wt	Weight

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INTRODUCTION GÉNÉRALE

NOTION DE POPULATION

Une population est un groupe d'individus d'une espèce donnée, spatialement et/ou temporellement isolé d'autres individus de la même espèce (Dempster, 1975 ; Rockwood, 2006). Dès le début du 20e siècle, l'observation de ce niveau d'organisation, aussi bien chez les végétaux que chez les animaux, a soulevé trois questions principales : 1) Par quels mécanismes l'abondance d'une espèce dans un milieu donné est-elle déterminée ? 2) Qu'est-ce qui cause les variations spatiotemporelles de l'abondance et qu'est-ce qui gouverne leur amplitude ? 3) Si une espèce perdure dans un milieu, y a-t-il nécessairement régulation ou limitation de son abondance, et si oui, comment opère-t-elle ? (Solomon, 1970 ; Rockwood, 2006 ; Krebs, 2020). Ces questions demeurent les piliers de la recherche actuelle en dynamique des populations, et définissent l'importance de ces connaissances dans plusieurs domaines (p. ex. biologie de la conservation, gestion de la faune, écotoxicologie ; Alexander et al., 2012 ; Leopold, 2019 ; Krebs, 2020).

DYNAMIQUE DES POPULATIONS

La taille d'une population est déterminée au cours du temps par trois paramètres démographiques : la survie, le recrutement et la dispersion (Akçakaya et al., 1999 ; Ranta et al., 2005 ; Lawson et al., 2015). Ces paramètres n'ont généralement pas la même élasticité, c'est-à-dire que certains expliquent une plus grande part de la variation de la taille de la population que d'autres (Gaillard et al., 1998 ; Manlik et al., 2018). Par exemple, Koons et al. (2017) ont montré que le taux de survie des jeunes femelles contribuait 1,6 fois plus que celui des femelles adultes, et 3,7 fois plus que la fécondité, aux variations des taux de croissance des populations de petits fuligules (*Aythya affinis*) en Amérique du Nord entre 1957 et 2015.

Les paramètres démographiques sont susceptibles d'être influencés par des facteurs environnementaux comme la compétition, la prédation, les activités humaines, le climat, les maladies ou le parasitisme (Sibly & Hone, 2002 ; Vandermeer & Goldberg, 2013 ; voir Figure 1.1). Souvent, c'est une combinaison de plusieurs facteurs environnementaux qui s'avère à l'origine des changements d'effectifs observés (Nicholson, 1933 ; Saether, 1997 ; Olsson et al., 2019 ; Canales et al., 2020). Certains facteurs (p. ex. le climat) sont dits limitants : ils influencent la taille de la population indépendamment de sa densité et l'empêchent de dépasser un certain seuil, en induisant des pertes directes d'individus ou, indirectement, en abaissant la fécondité (Sinclair, 1989 ; Bergman et al., 2015). D'autres, comme la compétition, sont considérés comme régulateurs car ils permettent un retour à une densité dite « d'équilibre », en affectant la natalité et la mortalité différemment en fonction de la densité de la population (Sinclair, 1989 ; Bergman et al., 2015). Certains facteurs peuvent avoir un effet régulateur ou limitant selon la situation considérée (p. ex. prédation : Van Ballenberghe & Ballard, 1994 ; Marrotte et al., 2022).

Considérant l'importance que revêtent depuis longtemps les mammifères pour les populations humaines, par exemple par la chasse ou la domestication (Reeves & McCabe, 2007 ; Naughton & Canadian Museum of Nature, 2012 ; Weaver, 2020), la dynamique des populations de différentes espèces de mammifères a été particulièrement étudiée (Vaughan et al., 2000 ; Bonenfant et al., 2009 ; Andreassen et al., 2021). Dans la suite de cette introduction, je me concentrerai sur les grands herbivores, qui se retrouvent sur tous les continents et qui jouent un rôle clef au sein de plusieurs écosystèmes (Pringle et al., 2007 ; Vavra et al., 2007 ; Jia et al., 2018). Les mécanismes biologiques liant les facteurs environnementaux aux paramètres démographiques des populations de grands herbivores sont présentés ci-après.

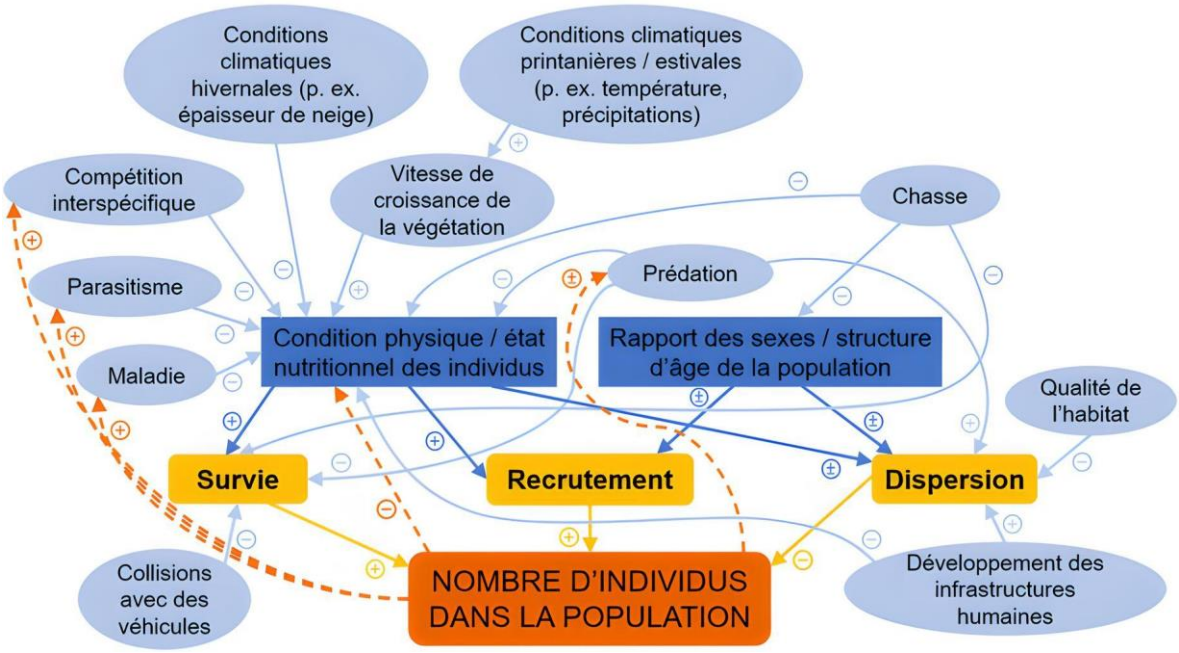

Figure 1.1 : Synthèse de l'influence des différents facteurs environnementaux (ovales bleu pâle) sur les paramètres démographiques (rectangles jaunes), qui déterminent le nombre d'individus d'une population de grands herbivores (dans une région à hiver froid). Les rectangles bleu foncé représentent des paramètres intermédiaires entre les facteurs environnementaux et les trois paramètres démographiques. Les flèches orange en pointillés signalent une rétroaction du nombre d'individus de la population (densité-dépendance). Le sens des interactions (positif ou négatif) est indiqué à côté des flèches, pour une augmentation/intensification de la bulle de départ de la flèche (p. ex. une augmentation de la survie a un effet positif sur le nombre d'individus dans la population). Un « ± » indique que le sens de l'interaction dépend de la valeur de départ ou du cas considéré (p. ex. une augmentation du nombre d'individus dans la population peut augmenter, diminuer ou ne rien changer au nombre d'individus prédatés selon le cas).

Survie

La probabilité d'un individu d'être encore en vie d'une année à l'autre (que je nommerai simplement « survie » par la suite) peut être affectée par différents facteurs au travers de mécanismes qui agissent à différentes échelles spatiotemporelles (Gaillard et al., 2000 ; Leopold, 2019). Parmi eux, la compétition intraspécifique, qui réduit la quantité de nourriture disponible *per capita*, a une incidence sur l'état nutritionnel de chaque individu (Monteith et al., 2014 ; Ayotte et al., 2020 ; Oates et al., 2021 ; voir Figure 1.1) et le rend

plus vulnérable aux effets des autres facteurs (p. ex. parasitisme : Vicente et al., 2007 ; Bourgoin et al., 2021). Par exemple, Kautz et al. (2020) ont observé une diminution de 4,3 % du risque de mortalité en fin d'hiver avec chaque kg de masse corporelle supplémentaire chez des femelles cerfs de Virginie (*Odocoileus virginianus*) au Michigan. L'état nutritionnel influence également la quantité de ressources qu'une femelle adulte peut allouer à la reproduction et aux soins parentaux (Therrien et al., 2007 ; Morano et al., 2013). Ainsi chez les ongulés, surtout chez les populations évoluant à de hautes densités, un mauvais état nutritionnel des femelles peut entraîner une diminution du poids des jeunes à la naissance (p. ex. caribou *Rangifer tarandus* : Adams, 2005 ; cerf mulet *Odocoileus hemionus* : Lomas & Bender, 2007 ; mouton de Soay *Ovis aries* : Kentie et al., 2020), et réduire leur probabilité de survie (p. ex. chevreuil *Capreolus capreolus* : Gaillard et al., 1997 ; cerf mulet : Monteith et al., 2014 ; gazelle d'Arabie *Gazella arabica* : Martin et al., 2022). La compétition interspécifique par exploitation, soit quand deux espèces utilisent la même ressource, est aussi connue pour réguler la taille des populations d'herbivores, via une réduction de la disponibilité de la ressource *per capita* (Belovsky, 1986 ; Macandza et al., 2012 ; Gamelon et al., 2020 ; voir Figure 1.1). De même, la compétition par interférence, qui peut prendre la forme d'agressions entre individus des deux espèces compétitrices, d'appropriation de territoire ou encore d'un blocage de l'accès aux ressources, peut également jouer un rôle régulateur puisque la condition physique des individus s'avère directement ou indirectement impactée (Ferretti et al., 2011 ; Sanchez-Pinzón & Domínguez, 2022). Toutefois, cette seconde forme de compétition interspécifique semble rare chez les ongulés (Ferretti & Mori, 2020).

La prédation (Bourbeau-Lemieux et al., 2011 ; Niedziałkowska et al., 2019) et la chasse (Fryxell et al., 1988 ; Bassi et al., 2020) diminuent également le taux de survie des proies en prélevant des individus dans la population. Dans certains cas, les réponses comportementales induites par le risque de prédation (p. ex. stratégies d'évitement dans le temps et dans l'espace) peuvent à elles seules réduire la survie (Gehr et al., 2018). De plus, les petits dont les mères ont été tuées ont généralement une probabilité plus faible d'atteindre l'âge adulte que les autres, ce qui occasionne une mortalité supplémentaire (p. ex. éléphant

d'Asie *Elephas maximus* : Perera et al., 2018 ; rhinocéros blanc *Ceratotherium simum* : Nhleko et al., 2022). Les collisions avec des véhicules sont aussi une cause non négligeable de mortalité pour certaines populations (p. ex. orignal *Alces alces* : Joyce & Mahoney, 2001 ; sanglier *Sus scrofa*, cerf élaphe *Cervus elaphus* et chevreuil : Torres et al., 2023). Le taux de survie d'une population est aussi affecté en cas de maladie (Smith et al., 2006 ; p. ex. pneumonie chez le mouflon canadien *Ovis canadensis* : Cassirer et al., 2018) ou de parasitisme (p. ex. tique d'hiver *Dermacentor albipictus* chez l'orignal : Musante et al., 2010 ; Ellingwood et al., 2020), notamment via une altération de la condition physique et une augmentation du stress alimentaire (voir Figure 1.1).

Outre les facteurs qui précèdent, de nombreuses autres études ont mis en évidence un impact des conditions climatiques hivernales sur la survie des individus de certaines espèces (p. ex. chamois *Rupicapra rupicapra* : Rughetti et al., 2011 ; cerf de Virginie : Kautz et al., 2020 ; antilope d'Amérique *Antilocapra americana* : Eacker et al., 2023). En effet, lors des hivers les plus rudes, la réduction de l'accessibilité à la nourriture et l'augmentation des dépenses énergétiques pour la locomotion et/ou la thermorégulation induisent une diminution de la masse corporelle des animaux, en particulier des juvéniles (Saether et al., 1996 ; Crampe et al., 2002 ; Parker et al., 2009). Chez les herbivores, les conditions météorologiques printanières et estivales (c.-à-d. température, précipitation, ensoleillement) jouent également un certain rôle (p. ex. cerf élaphe : Loison & Langvatn, 1998 ; mouflon canadien : Douhard et al., 2018), parfois même plus important que celui des conditions hivernales (Simard et al., 2010). Par exemple, une étude de Pettorelli et al. (2007) a montré que la vitesse de croissance de la végétation était accrue en cas de températures élevées en avril et de fortes précipitations en mai. Les premiers stades phénologiques offrent un fourrage de plus haute qualité pour les herbivores, car c'est à ce moment que la teneur en protéines et la digestibilité sont à leurs valeurs les plus élevées, après quoi elles diminuent rapidement au cours de la croissance de la plante (Crawley, 1983 ; Hebblewhite et al., 2008 ; Middleton et al., 2018). Ainsi, dans l'étude de Pettorelli et al. (2007), l'accélération de la croissance de la végétation était associée à un ralentissement de la croissance des jeunes de l'année dans deux populations de mouflons canadiens et une population de chèvres des montagnes Rocheuses (*Oreamnos americanus*),

et à une diminution de la survie des jeunes à leur premier hiver chez le mouflon canadien et le bouquetin des Alpes (*Capra ibex*).

Recrutement

Le recrutement correspond à l'arrivée de nouveaux individus dans une population, par la naissance ou l'immigration (Nichols & Pollock, 1990 ; Nichols et al., 2000 ; Peery et al., 2006). Dans le cas des grands herbivores, cette notion est communément utilisée pour désigner le nombre de jeunes, issus des femelles de la population, qui ont survécu à leurs premiers mois de vie ou à leur première année (Gaillard et al., 1998 ; Owen-Smith & Mason, 2005 ; Proffitt et al., 2014), ou encore jusqu'à l'atteinte de leur maturité sexuelle (Bender, 2006 ; Gedir et al., 2018 ; Lamb et al., 2023). Cette valeur prend généralement la forme d'un taux de recrutement (nb de jeunes : 100 femelles adultes) qui peut être calculé à différents moments l'année selon l'espèce considérée (le plus souvent, à l'automne ou à la fin de l'hiver suivant la naissance ; p. ex. Bergerud & Elliott, 1998 ; DeCesare et al., 2012 ; Johnson et al., 2017 ; Desforges et al., 2021). Ce taux peut augmenter ou diminuer via un changement du numérateur, par exemple suite à une modification de la capacité des femelles à se reproduire (et donc du nombre de jeunes qui naissent), ou de la survie des jeunes au cours de leur première année, mais également par des variations au niveau du dénominateur, par exemple suite à une variation de la survie des femelles adultes.

Le taux de recrutement des populations d'herbivores est, lui aussi, susceptible de varier en réponse à la compétition intraspécifique qui, en affectant l'état nutritionnel des femelles, peut diminuer les taux de gestation et de gémellité (p. ex. saïga *Saiga tatarica*, mouton de Soay et cerf élaphe : Coulson et al., 2000 ; orignal : Boertje et al., 2019 ; voir Figure 1.1) et augmenter l'âge à primiparité (p. ex. gnou bleu *Connochaetes taurinus* : Mduma et al., 1999 ; cerf élaphe : Borowik & Jędrzejewska, 2018). La prédation a aussi un impact négatif sur le recrutement, principalement via une réduction du taux de survie des jeunes (p. ex. caribou et orignal : Hayes et al., 2003 ; wapiti *Cervus canadensis* : Lukacs et al., 2018). De plus, les coûts énergétiques associés aux réponses comportementales face au

risque de prédation (p. ex. vigilance, fuite, combat) sont susceptibles d'affecter négativement la reproduction et la croissance des espèces proies (Say-Sallaz et al., 2019 ; Dulude-de Broin et al., 2020). Le prélèvement par la chasse peut également modifier le rapport des sexes (mâles : femelles) et la structure d'âge d'une population (Langvatn & Loison, 1999 ; Kuzyk et al., 2018). Un rapport des sexes fortement biaisé en faveur des femelles et une proportion importante de jeunes mâles inexpérimentés sont susceptibles de retarder la conception et/ou la parturition (Milner et al., 2007). Or, les jeunes qui naissent plus tard ont généralement une masse plus faible (Holand et al., 2006, 2020) et/ou une saison de croissance plus courte (Feder et al., 2008), ce qui les rend plus vulnérables à la prédation (p. ex. cerf de Virginie : Michel et al., 2020) et aux conditions climatiques une fois l'hiver venu (p. ex. cerf mulet : Hurley et al., 2011) et peut donc diminuer le taux de recrutement (voir Figure 1.1). D'autre part, une très faible proportion de mâles dans la population a le potentiel de diminuer la fécondité des femelles (Solberg et al., 2002 ; Milner-Gulland et al., 2003), mais ce phénomène reste rare chez les ongulés (Mysterud et al., 2002).

Chez les herbivores, les conditions climatiques printanières et estivales peuvent également avoir un effet sur le recrutement (p. ex. cerf mulet : Johnson et al., 2017 ; mouflon de Dall *Ovis dalli* : Rattenbury et al., 2018 ; wapiti : Paterson et al., 2019). Par exemple, Monteith et al. (2015) ont mis en évidence un effet négatif des températures élevées et d'une faible quantité de précipitation au printemps et à l'été sur le taux de recrutement de l'orignal, suite à une diminution rapide de la qualité et de la digestibilité du fourrage (tel que décrit plus haut). Les conditions climatiques hivernales, notamment la profondeur de neige qui détermine l'accessibilité du fourrage, peuvent impacter négativement le recrutement en diminuant le taux de survie des jeunes mais aussi par le biais des effets à plus long terme sur la performance reproductive des femelles (p. ex. cerf élaphe : Proffitt et al., 2014 ; bœuf musqué *Ovibos moschatus* : Desforges et al., 2021 ; orignal : Holmes et al., 2021 ; voir Figure 1.1). Johnson et al. (2017) ont montré un lien entre la diminution du taux de recrutement d'une population de cerfs mulet et le développement résidentiel et énergétique dans le Colorado, probablement via une perte directe (changement d'utilisation de la terre et fragmentation du paysage) et indirecte (évitement des infrastructures) d'habitat. Finalement,

chez plusieurs ongulés, une forte charge parasitaire était liée à une dégradation de la condition physique des femelles et avait un effet délétère sur la fécondité (p. ex. caribou : Hugues et al., 2009 ; buffle d'Afrique *Syncerus caffer* : Budischak et al., 2018 ; orignal : Ellingwood et al., 2020).

Dispersion

La dispersion désigne le déplacement d'un jeune individu de son lieu de naissance vers celui où il se reproduira (dispersion natale), ou dans le cas d'un individu adulte, le déplacement d'un lieu de reproduction à un autre (dispersion de reproduction) (Greenwood, 1980 ; Ronce, 2007 ; Matthysen, 2012). Elle peut être décomposée en plusieurs étapes, soit l'émigration du site et/ou du groupe social d'origine, l'errance dans un territoire inconnu et enfin l'immigration dans un nouveau lieu de vie et/ou groupe social (Wolff, 1994 ; Ronce, 2007). Ce processus est à différencier de la migration, où les individus alternent régulièrement entre certains endroits (Matthysen, 2012), par exemple entre une aire (ou un site) d'hivernage et une aire d'estivage (Hjeljord, 2001), et dont je ne traiterai pas dans cette introduction. La dispersion natale et la dispersion de reproduction peuvent affecter la dynamique d'une population en retirant des individus, ce qui a un effet négatif direct sur sa taille, mais aussi un effet indirect car ces reproducteurs potentiels ne participeront plus au taux de croissance futur de la population. À ma connaissance, peu d'études se sont intéressées à la dispersion chez les ongulés au cours des 15 dernières années.

La dispersion natale est gouvernée par les interactions sociales entre individus : elle peut permettre l'évitement de la consanguinité (Roze & Rousset, 2009 ; p. ex. cheval *Equus caballus* : Linklater & Cameron, 2009 ; girafe *Giraffa camelopardalis* : Bond et al., 2021) et un meilleur succès reproducteur chez les jeunes mâles en diminuant la compétition avec les mâles plus âgés et dominants (p. ex. plusieurs espèces d'ongulés : Greenwood, 1980 ; Dobson, 1982 ; Hewison et al., 2021). En effet, chez les ongulés, les mâles sont souvent plus susceptibles de se disperser que les femelles (Dobson, 1982 ; Haanes et al., 2011 ; Bond et al., 2021 ; mais voir p. ex. Pérez-González & Carranza, 2009). La dispersion est aussi

nécessaire pour que les juvéniles issus d'une même portée, ou d'une même femelle s'étant reproduit plusieurs années consécutives, n'entrent pas en compétition les uns avec les autres (Bowler & Benton, 2005 ; p. ex. orignal : Ballard et al., 1991). La variabilité temporelle et spatiale des conditions environnementales (qualité des parcelles d'habitat, climat) influence également les patrons de dispersion (Bowler & Benton, 2005). Par exemple, Catchpole et al. (2004) ont identifié l'oscillation nord-atlantique (c.-à-d. *'North Atlantic Oscillation'*) hivernale comme faisant partie des variables permettant de prédire les variations du taux de dispersion chez les deux sexes du cerf élaphe.

Lorsqu'un jeune individu se sépare de sa mère et se disperse, il ne quitte généralement pas la population : il établit seulement son domaine vital un peu plus loin (Sweanor et al., 1992 ; Hjeljord, 2001 ; McFarlane et al., 2022). Toutefois, si la compétition pour les ressources alimentaires et/ou les partenaires est trop forte, l'individu peut parcourir une grande distance pour trouver une zone où la densité est plus faible (p. ex. cerf de Virginie : Nixon et al., 1991). Ce phénomène semble malgré tout relativement rare, puisque plusieurs études ont montré au contraire que la dispersion était retardée à de hautes densités, ce qui pourrait s'expliquer par une condition corporelle inadéquate pour supporter le coût énergétique de la dispersion (Wolff, 1994 ; Hjeljord, 2001 ; Baines et al., 2020). Dans la population de cerfs élaphes étudiée par Loe et al. (2009), les jeunes mâles se dispersaient moins loin lorsque la densité à leur lieu de naissance était faible, probablement afin de diminuer la compétition pour les ressources et favoriser leur croissance. Au contraire, McFarlane et al. (2022) ont observé la tendance inverse dans une population de caribous, avec une densité positivement corrélée à la qualité de l'habitat et négativement corrélée à la distance à la route, ce qui suggère que les jeunes mâles pourraient s'être retrouvés « piégés » au sein de parcelles restantes d'habitat convenable.

Outre la densité, puisque la dispersion chez les ongulés est généralement biaisée selon le sexe et l'âge (les mâles se dispersent plus que les femelles, et les jeunes individus davantage que les plus âgés : Greenwood, 1980 ; Dobson, 1982 ; Wolff, 1997), le taux de dispersion peut varier suivant les changements dans la structure d'âge et le rapport des sexes de la population (voir Figure 1.1). Par exemple, une étude de Long et al. (2008) sur le cerf

de Virginie a montré que les jeunes cerfs mâles se dispersaient davantage à l'automne qu'au printemps, suite à des changements dans la stratégie de gestion des deux populations étudiées ayant permis une diminution de la densité de femelles adultes et une augmentation de la densité de mâles adultes. Selon les auteurs, ces modifications de comportement reflètent une diminution du risque d'inceste (puisque la probabilité pour les jeunes mâles de se retrouver face à leur mère ou à leurs sœurs est réduite) et un accroissement du potentiel de compétition pour l'accouplement (car la densité de mâles adultes a augmenté ; Long et al. 2008).

La dispersion des adultes est moins fréquente que celle des juvéniles, mais peut néanmoins se produire en cas de forte compétition par exploitation et/ou interférence (Bowler & Benton, 2005 ; p. ex. bison d'Amérique *Bison bison* : Plumb et al., 2009 ; buffle d'Afrique : Spaan et al., 2019) ou pour des partenaires sexuels (p. ex. cerf élaphe : Clutton-Brock & Coulson, 2002) lorsque de fortes densités de population sont observées. D'autre part, un risque de prédation élevé peut résulter en une diminution de la dispersion de reproduction, car la fidélité interannuelle à un site de mise bas et/ou de reproduction où la distribution des ressources et des risques peut représenter un avantage (p. ex. caribou : Schaefer et al., 2000 ; Faille et al., 2010 ; Popp et al., 2011 ; relation non supportée par Schwenk, 2022) qui assure une meilleure survie individuelle (mais voir Lafontaine et al., 2017). Les perturbations anthropiques (p. ex. coupe forestière, développement de champs gaziers, de villes, d'oléoducs) peuvent modifier les patrons d'utilisation de l'espace des ongulés, voire même causer leur déplacement vers des zones moins perturbées mais où l'habitat est de moindre qualité (Davies et al., 2001 ; p. ex. cerf mulet : Northrup et al., 2016 ; caribou : Beauchesne et al., 2013 ; voir Figure 1.1).

GESTION DE LA FAUNE

La connaissance des mécanismes biologiques mentionnés ci-haut est essentielle dans le domaine de la gestion de la faune, aussi bien dans un objectif de conservation, d'exploitation que de contrôle de la surabondance (Leopold, 1933 ; Jean, 1998 ; Mills & Johnson, 2013). En effet, il est nécessaire de connaître les facteurs impliqués ainsi que leurs

modalités d'action sur les paramètres démographiques de la population considérée afin de déterminer 1) les facteurs et/ou paramètres les plus importants et 2) la meilleure stratégie à employer. Les modèles bâtis sur ces informations s'avèrent également utiles puisqu'ils peuvent permettre de tester au préalable différents scénarios de gestion, d'estimer leur efficacité et d'en prévoir les effets à plus ou moins long terme (Jean, 1998 ; McLane et al., 2011 ; Lacy, 2019 ; Niemuth et al., 2021).

Gestion des populations de grands herbivores : l'enjeu des hautes densités

Les populations de grands herbivores vivant à haute densité ont le potentiel, notamment via un broutement excessif de plusieurs espèces végétales, de modifier localement la structure et la composition des communautés végétales (Ramirez et al., 2018 ; p. ex. cerf mulet : Chollet et al., 2013 ; cerf sika *Cervus nippon* : Nishizawa et al., 2016), ce qui peut perturber le fonctionnement des écosystèmes et en altérer la biodiversité (p. ex. cerf de Virginie : Brousseau et al., 2013 ; plusieurs espèces de cervidés : Dolman et al., 2010 ; Crystal-Ornelas et al., 2021). Ces dégradations peuvent parfois être irréversibles (Côté et al., 2004 ; p. ex. orignal dans le parc national Terra-Nova et territoires adjacents : McLaren et al., 2009), et nécessiter des programmes de restauration des écosystèmes endommagés (p. ex. Charron & Hermanutz, 2017). Parmi les autres conséquences possibles, notons des dommages causés aux plants en champs agricoles ainsi qu'aux tiges d'arbres et d'arbustes en régénération en forêt, une propagation accrue des maladies infectieuses et une augmentation des risques de collisions avec des véhicules (Côté et al., 2004 ; Valente et al., 2020 ; Candaele et al., 2021). Ainsi, il apparaît essentiel d'effectuer un suivi de ces populations et d'élaborer des mesures de gestion adaptées (McLaren et al., 2004 ; Valente et al., 2020 ; Carpio et al., 2021).

Différents contextes peuvent permettre à une population de grands herbivores d'atteindre une haute densité : les principaux sont l'extirpation des grands prédateurs (p. ex. loup *Canis lupus*, cougar *Puma concolor* ; Potvin et al., 2003 ; Côté et al., 2004 ; Carpio et al., 2021), la réduction de la pression de chasse (via des réglementations plus protectrices

envers les femelles, une interdiction complète dans certaines aires protégées, ou pour des questions d'acceptabilité sociale ; Brown et al., 2000 ; Côté et al., 2004), la présence de nourriture de qualité en abondance dans les forêts aménagées et les champs cultivés (Fuller & Gill, 2001 ; Côté et al., 2004 ; Bobek et al., 2017) et des pratiques d'alimentation d'appoint (dans les zones de chasse ; Putman & Staines, 2004 ; Milner et al., 2014) et de diversion alimentaire (dans les zones sylvicoles et agricoles ; Peek et al., 2002 ; Ježek et al., 2016 ; González-Crespo et al., 2018). Par conséquent, les mesures de gestion diffèrent selon les contextes dans lesquels on trouve ces populations à haute densité (Carpio et al., 2021).

Les aires protégées constituent une situation propice à la croissance des populations de grands herbivores, principalement du fait que la chasse y est interdite ou très réduite, mais aussi souvent par l'absence de grands prédateurs (Carpio et al., 2021). Dans ces lieux, les stratégies généralement privilégiées pour diminuer l'abondance des grands herbivores sont l'abattage (van Beeck Calkoen et al., 2020), malgré une acceptabilité sociale mitigée (Martínez-Jauregui et al., 2020), et le contrôle de la fertilité (Massei et al., 2014). Les modèles sont fréquemment employés pour simuler les effets de ces différentes méthodes et déterminer leurs modalités d'application en accord avec l'objectif visé en termes de niveau d'abondance (p. ex. cerf de Virginie : Raiho et al., 2015 ; cerf axis *Axis axis* et daim européen *Dama dama* : Gogan et al., 2001 ; cerf élaphe : Bradford & Hobbs, 2008 ; sanglier : Croft et al., 2020 ; orignal : Franklin et al., 2020 ; âne commun *Equus asinus* : Gedir et al., 2021).

Cas de l'orignal

Ongulé de la famille des cervidés, l'orignal est largement distribué dans les écosystèmes tempérés d'Amérique du Nord, d'Europe centrale et d'Asie (Timmermann & Rodgers, 2017 ; Jensen et al., 2018, 2020). En Amérique du Nord, on le retrouve dans les forêts boréales (p. ex. St-Pierre et al., 2022) ou mixtes (p. ex. Lenarz et al., 2011), les plaines inondables (p. ex. Seaton et al., 2011), les deltas et les vallées fluviales (p. ex. O'Donoghue et al., 2013), les toundras subalpines (p. ex. Anderson et al., 2018), ainsi que dans certaines forêts pluviales tempérées côtières (Darimont et al., 2005). Les orignaux se nourrissent

principalement de feuilles d'arbres et d'arbustes en été, et de ramilles en hiver (Timmermann & McNicol, 1988 ; Christopherson et al., 2019 ; Spitzer et al., 2020). Les milieux les plus propices en termes d'abondance et de qualité du fourrage semblent être les milieux forestiers en régénération, par exemple entre 10 et 30 ans après le passage d'un feu (Schwartz & Franzmann, 1989 ; Maier et al., 2005 ; Fredriksson et al., 2023), d'une épidémie d'insectes (Smith et al., 2010 ; Franklin & Harper, 2016) ou d'une coupe forestière (Matchett, 1985 ; Mumma et al., 2021). Les espèces feuillues, comme les érables (*Acer spp.*), les bouleaux (*Betula spp.*) et le sorbier (*Sorbus americana*), sont préférées (Belovsky, 1981 ; Crête, 1989 ; Peterson et al., 2020), mais les ramilles de sapin (*Abies balsamea*) sont également consommées quand les ressources viennent à manquer, particulièrement en hiver et dans des populations à haute densité (Desgagnés et al., 2022). Dans les habitats alluviaux et les toundras, l'orignal se nourrit de différentes communautés d'arbustes riverains dont la taille dépasse l'épaisseur de neige au sol en hiver, comme le saule (*Salix spp.*) et l'aulne (*Alnus spp.*) (Zhou et al., 2017 ; Cooley et al., 2019).

L'habitat de l'orignal comprend aussi des zones où la canopée est plus fermée, comme des peuplements de résineux ou de hautes communautés d'arbustes (Peek, 2007 ; Wattles & DeStefano, 2013 ; Oyster et al., 2018). Ces zones sont utilisées aussi bien l'été (contre la chaleur) que l'hiver pour se protéger du froid, du vent et se déplacer dans une neige moins profonde (Dussault et al., 2005 ; Alston et al., 2020 ; Burkholder et al., 2022). Elles assurent également un couvert favorisant une faible détectabilité par les prédateurs et les chasseurs (Timmermann & McNicol, 1988 ; Dussault et al., 2005 ; Ofstad et al., 2020). Enfin, les orignaux sélectionnent les points d'eau (étangs, lacs), où ils consomment des plantes aquatiques riches en minéraux, et où ils peuvent se baigner afin de faciliter leur thermorégulation les jours de forte chaleur (Timmermann & McNicol, 1988 ; Tendeng et al., 2016 ; Tischler et al., 2019).

L'orignal est une espèce gibier très importante dans toute son aire de répartition, où il suscite un grand intérêt économique et a une importance culturelle établie (Timmermann & Rodgers, 2005 ; Lefort & Massé, 2015 ; Popp et al., 2019). Comme les autres cervidés, l'orignal est aussi une espèce impliquée dans la déprédation, étant susceptible de causer des

dommages aux champs cultivés et aux forêts aménagées, et régulièrement impliquée dans des accidents routiers (Joyce & Mahoney, 2001 ; Wallgren et al., 2013 ; Laforge et al., 2016 ; Laliberté & St-Laurent, 2020). Des cas de surbroutement, ayant induit des modifications à long terme dans l'écosystème, ont également été rapportés (p. ex. parc national de l'île Royale : Gorkiewicz, 2006 ; Rotter & Rebertus, 2015). Les densités estimées sont généralement comprises entre 0,1 et 1 orignal/km² (Jensen et al., 2018, 2020). Toutefois, dans certaines conditions, elles peuvent excéder ces niveaux : par exemple, dans la réserve faunique de Matane (Québec), où le loup a disparu depuis un siècle, où le taux d'exploitation par la chasse est faible et où le milieu est productif, une densité moyenne d'orignaux de 4,8/km² a été observée, avec un maximum de 19,3/km² dans l'un des ravages (Lamoureux et al., 2007). Dans le parc national du Gros Morne (Terre-Neuve), où le loup est aussi absent et où, à l'époque, la chasse était interdite, la zone de plus forte densité en mars 1998 hébergeait 14,1 orignaux/km² (McLaren et al., 2000). Cependant, au cours de la dernière décennie, une tendance au déclin des populations d'orignaux a été constatée dans plusieurs juridictions d'Amérique du Nord (p. ex. Alberta, Ontario, Saskatchewan, Manitoba, Terre-Neuve, New Hampshire, Idaho, Territoires du Nord-Ouest : Timmermann & Rodgers, 2017 ; Arsenault et al., 2019 ; Ross & Mason, 2020). Dans d'autres, au contraire, une augmentation des densités et une expansion de l'aire de répartition ont été rapportées (p. ex. Québec, Nouveau-Brunswick, Maine, Alaska : Tape et al., 2016 ; Timmermann & Rodgers, 2017).

De nombreux modèles de dynamique des populations existent pour l'orignal, parmi lesquels la plupart peuvent permettre de projeter le niveau d'abondance dans le futur. La majorité a été développée pour des systèmes où le prédateur principal de l'orignal, le loup, était présent (p. ex. Zarnoch & Turner, 1974 ; Ballard et al., 1986 ; Messier, 1994 ; Rempel, 2011 ; Carroll, 2013 ; Rempel et al., 2021 ; Kalén et al., 2022) et/ou dans lesquels la chasse sportive ou de subsistance était pratiquée (p. ex. Boer & Keppie, 1988 ; Cederlund & Sand, 1991 ; Lehtonen, 1998 ; Pugesek, 2003 ; Doak et al., 2016 ; Ruprecht, 2016 ; Kuzyk et al., 2018), parfois dans le contexte d'une forêt aménagée (p. ex. Puttock et al., 1996 ; Franklin et al., 2020 ; Hessami, 2022). Ainsi, parmi les nombreux modèles disponibles, peu sont adaptés

au contexte d'une population d'orignaux vivant dans une aire protégée et en l'absence du prédateur principal.

OBJECTIFS ET RÉSUMÉ DES RÉSULTATS

Mon étude visait 1) à identifier les facteurs – et leurs interactions – qui régissent la dynamique d'une population d'orignaux vivant à haute densité dans un milieu protégé, sans prélèvement ni aménagement forestier, et où le prédateur apical (le loup) est absent depuis plus de 150 ans, pour ensuite 2) développer un modèle de dynamique des populations adapté à un tel système, utile à des fins de gestion.

Pour répondre à mes objectifs, j'ai effectué une revue de littérature afin d'identifier les facteurs les plus pertinents – et leurs interactions les plus probables – pouvant opérer au sein de la population d'orignaux du Parc national Forillon, notre cas d'étude. Sur cette base, j'ai construit un modèle de dynamique de population permettant de reproduire le plus efficacement possible les changements de taille de la population observés entre 1982 et 2020. Avec l'aide de mes coauteurs, j'ai donc utilisé la méthode de modélisation orientée par patrons (*Pattern-oriented Modeling* ; Grimm et al., 1996, 2005 ; Gallagher et al., 2021) pour construire le modèle et en calibrer les paramètres. Cette méthode s'appuie sur le principe que les patrons (c.-à-d. des structures non aléatoires dans les données de terrain ; Grimm et al., 1996) observés à différents niveaux d'organisation (p. ex. individus, populations) contiennent de l'information à propos des autres niveaux. Lors de la construction ou de la paramétrisation d'un modèle, plusieurs patrons peuvent donc être combinés pour « filtrer » les structures de modèle ou les combinaisons de valeurs des paramètres qui ne permettent pas leur émergence simultanée dans le système (Grimm et al., 2005). Pour ma part, j'ai utilisé comme patrons les séries temporelles d'abondance, de rapport des sexes et de taux de recrutement recueillies entre 1982 et 2020 dans le parc lors d'inventaires aériens. Ainsi, le modèle a constitué un outil de choix pour tester et estimer l'influence des différents facteurs retenus sur la dynamique de la population.

Les résultats des simulations qui ont le mieux reproduit la réalité de l'évolution des trois patrons (abondance, rapport des sexes et taux de recrutement) indiquent que les effets de densité-dépendance ont joué un rôle majeur à partir des années 2000 en impactant la survie de toutes les classes d'âge, ainsi que le recrutement et la dispersion. En effet, nos résultats suggèrent que la population s'est retrouvée au-dessus de la capacité de support du milieu pendant plusieurs années (2014, 2015 et 2017). Le climat hivernal était également un facteur important pour le taux de survie des veaux, et les résultats mettent en lumière des interactions avec la charge de tiques et la densité. Les scénarios sélectionnés par notre modèle ont mis en évidence un délai dans les effets du climat hivernal, successivement sur les taux de mise bas et de gémellité des femelles orignaux et sur le taux de survie des veaux à l'hiver. La prédation exercée par l'ours noir et le coyote a eu un effet marqué sur le taux de survie des veaux, malgré leur statut de prédateurs opportunistes, avec des taux de prédation annuels compris entre 25 et 65 %. La charge de tiques estimée était relativement faible pour toute la durée de la simulation, avec pour seul impact une réduction de la survie des veaux comprise entre 0 et 13 % selon la période de temps. L'émigration et l'immigration expliquaient quant à elles la plus grande part de la variation du rapport des sexes de la population, avec plusieurs mâles quittant le parc et plusieurs femelles y entrant sur une base annuelle.

CHAPITRE 1
QUAND LE LOUP N'EST PAS LÀ : MODÉLISATION DE LA DYNAMIQUE D'UNE POPULATION D'ORIGNAUX DANS UNE AIRE PROTÉGÉE

RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

Les populations à haute densité peuvent menacer l'intégrité écologique des écosystèmes via des effets en cascade. Quand de telles situations requièrent des mesures de gestion, celles-ci doivent être guidées par une connaissance suffisante des mécanismes biologiques en jeu. Les modèles de simulation sont des outils puissants pour acquérir ce type de connaissance. L'orignal (*Alces alces americana*) est une espèce qui est récemment devenue surabondante dans certaines régions du nord-est de l'Amérique, au point de parfois nécessiter des mesures de gestion particulières. De nombreux modèles de dynamique des populations existent pour l'orignal, toutefois peu sont adaptés aux populations retrouvées à haute densité, dans une aire protégée (sans chasse ni exploitation forestière) et où le prédateur principal de l'orignal (le loup gris *Canis lupus*) est absent, comme celle qui occupe le Parc national Forillon (Québec, Canada). Les objectifs de cette étude étaient donc 1) d'identifier les facteurs – et leurs interactions – qui régissent la dynamique des populations d'orignaux vivant de telles conditions, et 2) de développer un modèle démographique adapté, utile à des fins de gestion. Ce modèle de population, structuré par l'âge et le sexe, a été paramétré en utilisant la stratégie de modélisation orientée par patrons (*lib.* POM). Nos résultats ont montré la présence d'un fort impact négatif de la densité de la population sur la survie, la reproduction et la dispersion. La prédation par les ours noirs (*Ursus americanus*) et les coyotes (*Canis latrans*) a induit une mortalité substantielle des veaux chaque année. Contrairement à d'autres zones du nord-est de l'Amérique du Nord, la tique d'hiver (*Dermacentor albipictus*) avait seulement un faible effet sur la survie des veaux, sauf lorsque la densité d'orignaux s'est approchée de la capacité support. Les variations du rapport des

sexes de la population étaient principalement expliquées par une dispersion biaisée par le sexe. Notre modèle apporte de nouvelles connaissances sur la dynamique des populations d'ongulés à haute densité et peut être utilisé pour prévoir l'évolution d'une population sous différents scénarios de gestion.

Cet article, intitulé « *While the wolf is away: modeling the dynamics of a moose population in a protected area* », a été rédigé en collaboration avec mon directeur Martin-Hugues St-Laurent, professeur à l'UQAR, mon codirecteur Pierre Etcheverry, biologiste pour Parcs Canada, et Sarah Bauduin, biologiste à l'Office Français de la Biodiversité. Il sera soumis pour publication au printemps 2025 à la revue scientifique avec comité de lecture *Ecological Modelling*. Ma contribution en tant que première auteure comprend le développement du modèle, la réalisation des simulations, la compilation des résultats ainsi la rédaction et la révision de l'article. Mon directeur et mon codirecteur ont fourni l'idée originale, orienté et encadré le projet, effectué les démarches pour assurer un financement, et ont activement participé à la rédaction et la révision de l'article. Sarah Bauduin a contribué au raffinement de la méthodologie en me faisant profiter de son expertise concernant le POM, et a également participé à la révision de l'article. Des résultats préliminaires de ce projet ont fait l'objet de présentations orales au 15^{e} colloque annuel du Centre d'Étude de la Forêt, au 47^{e} congrès annuel de la Société Québécoise pour l'Étude Biologique du Comportement, ainsi qu'aux 9^{e} et 10^{e} réunions du comité-conseil du partenariat de recherche sur les relations tique-orignal-climat.

WHILE THE WOLF IS AWAY: MODELING THE DYNAMICS OF A MOOSE POPULATION IN A PROTECTED AREA

ABSTRACT

Populations at high density can threaten the ecological integrity of ecosystems through cascading effects. When such situations need to be managed, the associated practices must be guided by sufficient knowledge of the biological mechanisms at play. Simulation models are powerful tools for acquiring such knowledge. Moose (*Alces alces americana*) is a species that recently became overabundant in some areas of eastern North America, to the point of sometimes requiring specific management measures. While numerous models exist for moose population dynamics, few of them are adapted to populations that live at high density like the one in Forillon National Park (Quebec, Canada), which is a protected area (no hunting or harvesting), and where the moose's apical predator (grey wolf *Canis lupus*) is absent. Thus, this study's objectives were 1) to identify the factors—and their interactions—that drive the dynamics of moose populations living in a system with such conditions, and 2) to build a demographic model adapted to this system and useful for management purposes. This sex- and age-structured population model was parameterized using the pattern-oriented modeling (POM) strategy. We found that the moose population exhibited strong negative density dependence in survival, reproduction and dispersal. Predation by alternative predators, black bears (*Ursus americanus*) and coyotes (*Canis latrans*), caused substantial calf mortality each year. Contrary to other areas in northeastern North America, winter tick only had a slight effect on calf survival, except when moose density approached carrying capacity. The variations in the population's sex ratio were mainly explained by a sex-biased dispersal. Our model provides new insights concerning the dynamics of high-density ungulate populations and can be used to forecast a population's future under different management scenarios.

INTRODUCTION

Year-to-year fluctuations of abundance are common in wild-ranging animal populations. A variety of intrinsic and extrinsic factors (hereafter called "dynamics-driving factors"; e.g. competition, predation, human activities, climate, disease) are likely to affect the vital rates (i.e. survival, recruitment and dispersal) that influence a population's size over time (Nicholson, 1933; Turchin, 2003; Rushing et al., 2017). How these factors can limit vital rates is a constant subject of research in population ecology, since their interactions are not yet fully understood (Sutherland et al., 2013; Krebs, 2020).

Population size can sometimes reach a more or less stable equilibrium around the carrying capacity, which is the maximum number of individuals that can be sustained by an ecosystem for a given species (Pearl and Reed, 1920; Macnab, 1985). However, the combined effect of several dynamics-driving factors may occasionally cause the decline of a population (e.g. woodland caribou *Rangifer tarandus caribou*: Wittmer et al., 2005; wild salmons *Oncorhynchus spp.*: Miller et al., 2014), whereas the relaxation of one or more of these factors can trigger a population growth toward higher densities (e.g. eastern grey kangaroo *Macropus giganteus*: Banks et al., 2000; moose *Alces alces*: Dziki-Michalska et al., 2019).

High-density animal populations are of particular concern for population ecologists, as they have the potential to cause a variety of problems, such as the transmission of diseases to humans (raccoon *Procyon lotor*: Majeau et al., 2023), the extirpation of prey populations (red fox *Vulpes vulpes*: Kinnear et al., 2002) and a change in the vegetation structure (sika deer *Cervus nippon*: Nishizawa et al., 2016). Via cascading effects, they can irreversibly alter the community structure and result in a completely different ecosystem (Côté et al., 2004; Dexter et al., 2013). Thus, government agencies and land managers may want to control certain populations to preserve the ecosystem's ecological integrity (Mills et al., 2020; Valente et al., 2020). To be effective, such interventions must be based on a sufficient understanding—and empirical evidence—of the mechanisms that drive the dynamics of the focal populations (Leopold, 1933; Jean, 1998; Mills and Johnson, 2013). Gathering relevant

data and building such knowledge can require extensive field sampling and surveys as well as important investments in time and money (Noyes et al., 2000; Environmental Protection Authority, 2020). Hence, wildlife and land-use managers and policy-makers sometimes rely on simulation models to overcome these difficulties (Jean, 1998; McLane et al., 2011; Niemuth et al., 2021).

Models are synthetical and quantitative tools that are especially helpful in population ecology (Akçakaya et al., 1999; McLane et al., 2011). They are precious allies to understand and explain the causal mechanisms of population dynamics, but also to forecast a population's future (Jean, 1998; White, 2000). Sex- or age-structured models are among the most frequently used, since they fit with the life-history traits of many animal species (Jensen, 2000; Mignatti et al., 2012; Winker et al., 2020). Through their separate treatment of different classes of individuals, these models help to assess the relative importance of demographic drivers in shaping population dynamics and to adapt management practices.

Moose is a very important game species of great economic and cultural interest throughout its distribution range (Timmermann and Rodgers, 2005; Lefort and Massé, 2015). While a decline in moose populations is currently observed in some areas of North America (e.g. Alberta, Idaho, New Hampshire, Ontario, Newfoundland: Timmermann and Rodgers, 2017; Manitoba, Saskatchewan: Arsenault et al., 2019), in other places, densities have been reported to increase over the last decade (Alaska, Maine, New Brunswick: Timmermann and Rodgers, 2017; Quebec: Lefort and Massé, 2015; Desgagnés et al., 2022), potentially causing lasting damage to the forest areas moose inhabit (Rotter and Rebertus, 2015; De Vriendt et al., 2021). Therefore, it appears essential to closely monitor high-density moose populations and identify the factors at play (McLaren et al., 2004; Valente et al., 2020).

Messier (1991) analyzed the contribution of food competition, wolf predation (*Canis lupus*) and snow accumulation to the interannual variation of moose abundance on Isle Royale (northeastern US). His results suggest that moose population cyclicity in this area is led by food competition (triggering a population decline at high densities) and wolf predation (being regulatory at low densities and antiregulatory at high densities). Indeed, an impressive

increase in moose abundance was observed after a wolf population decline on this island between 1980 and 1996, followed by a massive moose population crash due to starvation (Peterson, 1999). In other sectors where predation was low, the moose populations kept growing for several years despite high harvest densities or low pregnancy and twinning rates resulting from negative density dependence (White et al., 2006; Boertje et al., 2009). In Poland, the "top-down control" exerted by wolves on a moose population was surpassed by the interplay of a ban on culling, the proximity of preferred habitats, and a sex ratio severely skewed toward females, which promoted reproductive success (Dziki-Michalska et al., 2019). In the Matane Wildlife Reserve (eastern Canada), where wolf has been extirpated for more than 150 years, the moose population maintained its growth rate even at a density of 3 moose/km^2 by reducing the twinning ovulation rate, thus ensuring a higher probability to reproduce from year to year (Gingras et al., 2014).

Among the studies conducted on high-density moose populations, very few took place in the absence of the two main causes of mortality: grey wolf, the apical predator of moose, and hunting (but see McLaren et al., 2000). Consequently, we have no tool to model the population dynamics of this cervid species under such circumstances, but some interesting results obtained for another ungulate species can be used as a starting point. For instance, Hebblewhite et al. (2002) reported that elk (*Cervus elaphus*) population growth was driven by density and human-caused mortality (highway and railway) in Banff National Park in quasi absence of wolf predation. Lubow et al. (2002) modeled the size of an elk subpopulation of the Rocky Mountain National Park in winter between 1965 and 2001 and projected it until 2020. They noticed that the vital rates were not significantly influenced by winter temperature or by summer temperature or precipitation but showed important evidence of density dependence.

In this study, we aimed at improving our understanding of the dynamics of high-density moose populations living in a protected area where no sport harvest or logging is allowed, and where the main predator has been absent for more than 150 years. To do so, we built a sex- and age-structured population model to identify the factors—and their interactions—that drive the dynamics of a high-density moose population living in a protected area with

such conditions. We hypothesized that in this system, climate, intraspecific competition and parasitism would explain most of the fluctuations in moose population size, and that their relative influence would vary over time and according to the density of the population.

METHODS

Study area

Our study area covers the Forillon National Park, located at the tip of the Gaspé Peninsula in Quebec (Canada), and some adjacent areas (Figure 2.1a). Delimited by the Gulf of St. Lawrence, the Gaspé Bay and Highway 197, the 245 km^2 study area can be considered as geographically closed by these natural barriers (water bodies) coupled with the recent urban development along Highway 197 constraining animal emigration and immigration (Pettigrew et al., 2021). Logging is forbidden in the park since its creation in 1970, and hunting can only occur on the adjacent private and public lands since then. Highway 132 passes in the Forillon National Park along the coast, and the park territory supports several hiking and cross-country skiing trails.

Elevation ranges from 0 to 560 m a.s.l., and the landscape is a complex mosaic of valleys, ravines, mountains, streams and a few lakes (Lafleur, 1972). The study area experiences a humid continental climate with several days of strong winds and fog (Robitaille and Saucier, 1998). From 1982 to 2020, temperatures ranged between -35.5 °C and +36.0 °C, the mean annual precipitation reached up to 752 mm of rain and the mean annual snowfall was of 375 cm between mid-November and late April (maximum snow depth of 244 cm) (Environment and Climate Change Canada, 2021). The forested area is representative of the balsam fir (*Abies balsamea*) – yellow birch (*Betula alleghaniensis*) bioclimatic domain and covers most (95%) of the park. Some old, abandoned fields complete land covers (Comeau et al., 2006; Brandt, 2009). Tree cover in the valleys primarily consists of yellow birch and maple (*Acer spp.*), while lowlands are occupied by balsam fir and yellow birch, along with northern white cedar (*Thuja occidentalis*) in wet areas. Highlands are dominated by balsam fir, white birch (*B. papyrifera*) and white spruce (*Picea glauca*) (Majcen, 1974). A large part

(~70%) of the coniferous stands within the park limits was affected by a spruce budworm (*Choristoneura fumiferana*) outbreak between 1975 and 1992 (Boulanger and Arseneault, 2004), converting an area (< 4% of the park's surface) into early seral stands (Del Degan et al., 1995). A similar outbreak is under way since 2016.

Moose density in the Forillon National Park increased substantially over the last decades, from 0.2/km^2 in 1973 to 3.5/km^2 in 2017 (Figure 2.1b; Sigouin, 2018). Potential incidental predators include black bears (*Ursus americanus*) and coyotes (*Canis latrans*), while the grey wolf was extirpated from the Gaspé Peninsula at the beginning of the 20th century (Georges, 1976). White-tailed deer (*Odocoileus virginianus*) is the only other large herbivorous mammal found in the area, but densities are very low (Lebel and De Bellefeuille, 2021). The winter tick (*Dermacentor albipictus*) is also present and may increase moose mortality, especially for calves (at least slightly).

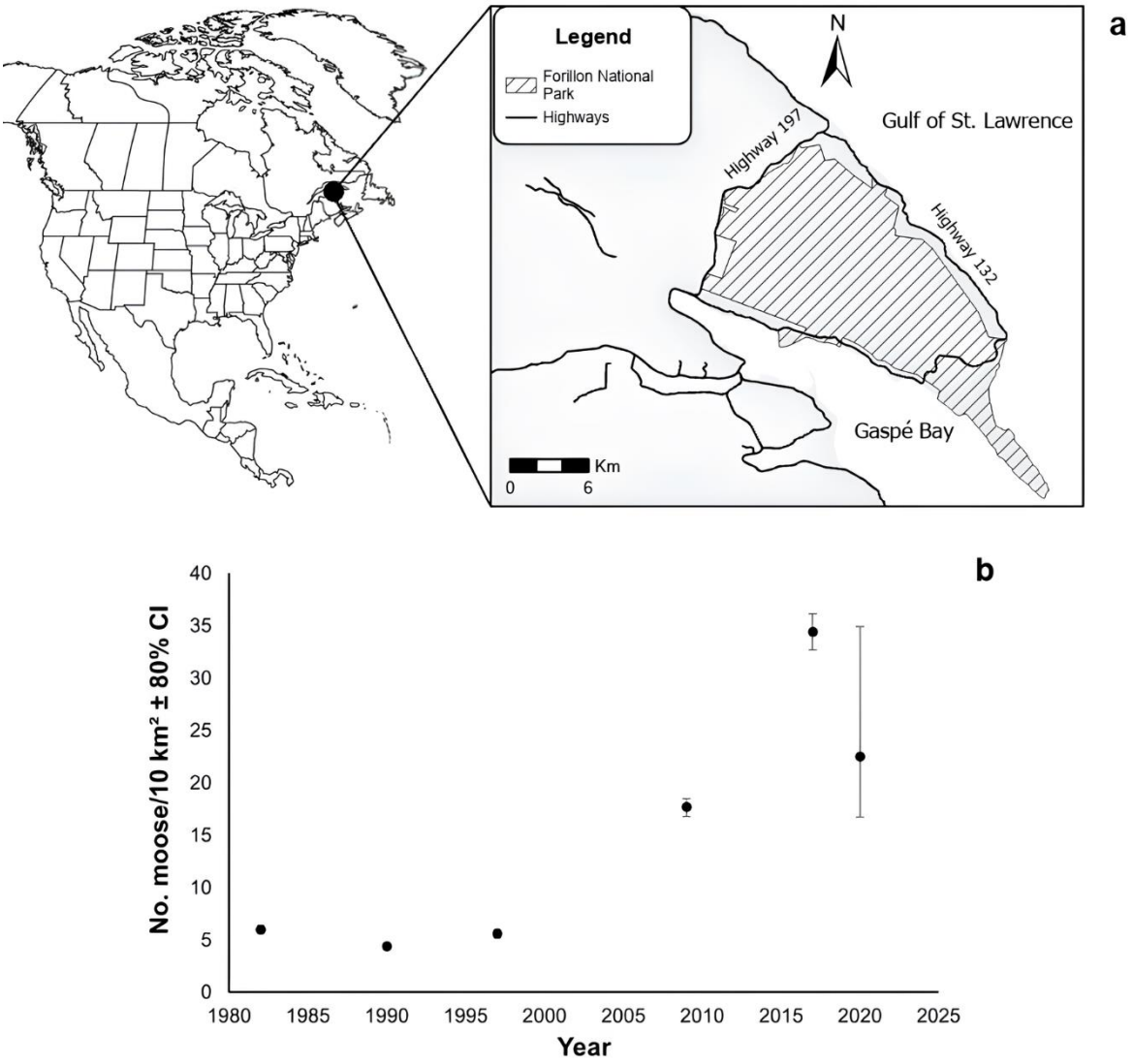

Figure 2.1: a) Location of the study area in the province of Quebec, Canada (left), and area covered by the Forillon National Park, with adjacent paved roads in thin lines (right). b) Variation of moose density (no. of moose/10 km^2) in the park between 1982 and 2020, as estimated using aerial surveys conducted in late winter.

Description of our population dynamics model

We used a sex- and age-structured population model to simulate changes in moose population size in the park from 1982 to 2020 (Figure 2.1b), with a yearly time step. Our model is divided into different individual modules, each one simulating the effect of one of

the dynamics-driving factors using the datasets described below. A flowchart summarizing the interactions between the different modules for one time step is provided (Figure 2.2). Analyses, model construction and simulations were all performed in R 4.2.1 (R Core Team, 2022).

Sparse data were a challenge and definitely influenced our choice of methodology. For instance, integrated population models (IPMs) are a well-suited tool for conservation ecology but require several datasets (usually including capture-recapture or mark-recovery data) to be parameterized (Schaub and Abadi, 2011), which were not available in our situation. Having little information about population vital rates (e.g. survival, productivity) could have been overcome by using *N*-mixture models (Royle, 2004; Madsen and Royle, 2023) to parameterize a projection matrix (Caswell, 2001), but the *N*-mixture models may not provide accurate estimates of vital rates in the presence of density dependence or environmental stochasticity (Bellier et al., 2016), which are two important features of our study area. We thus chose to rely on pattern-oriented modeling (POM), a method that we believe was better adapted to our dataset and objectives, since it allowed us to update the vital rates annually (involving, for example, harvest data, road mortality and snow depth) and build a more explicit model regarding some biological mechanisms.

The POM method relies on the principle that patterns (defined as non-random structures in the data; Grimm et al., 1996) observed at higher levels of organisation (e.g. communities, populations) hold information about lower levels (e.g. individuals), and vice versa (Grimm and Railsback, 2012; Gallagher et al., 2021). POM can be used either for model design or parameter calibration, using multiple patterns as filters to reject any model structure or set of parameter values that prevents their simultaneous emergence in the system (Grimm et al., 2005; Kramer-Schadt et al., 2007). Thus, the POM procedure allows researchers to obtain "structurally realistic" models and overcome data scarcity (Grimm et al., 2005; Gallagher et al., 2021). However, POM can only identify the most appropriate model structure (or parameter value) among the possibilities provided by the modeller, which may not be the perfect optimum. In addition, the chosen patterns must match the model's purpose,

i.e. they must be discriminatory criteria for model structure or respond under the parameters to be calibrated (Gallagher et al., 2021).

Various types of information (e.g. single value, distribution) and elements (e.g. distances, genetic data, carbon stocks) can be used as patterns (Gallagher et al., 2021). We used three different patterns: the time series of abundance, sex ratio (M : F) and recruitment rate of our moose population; all of them were obtained via aerial surveys conducted between 1982 and 2020 (see Appendix 2.1 for details about the aforementioned time series and the methods used to collect them). We divided our period of modeling into 5 subperiods (bounded by the years in which the inventories were carried out: 1982–89, 1990–96, 1997–2008, 2009–16 and 2017–19) in order to allow the value and elasticity (i.e. the magnitude of the effect of a change in this value on the population dynamics; Gaillard et al., 1998) of the parameters to vary over time.

The dynamics of a large herbivore population are largely dependent on its population structure, since vital rates of individuals are proven to vary with age and sex (Gaillard et al., 1998, 2000; Marescot et al., 2015). We thus decided to model our moose population as the sum of five groups of individuals: 1) calves (males and females < 1 year of age), 2) yearling (between 1 and 2 years old) females, 3) yearling males, 4) adult (> 2 years old) females and 5) adult males. The vital rates of each group are impacted to a different extent by all the dynamics-driving factors included in the model throughout a simulation (Figure 2.2). We presumed an even sex ratio at birth (Lenarz et al., 2010; Severud et al., 2019; Lee et al., 2020). We assumed that yearling females do not twin, and we set 0.5 as their maximum parturition rate for all the simulations (Schwartz and Hundertmark, 1993; Testa, 2001; Markussen et al., 2018), although parturition rates as high as 0.74 have been documented for yearling females in some low-density populations (Boertje et al., 2007). We also set 0.7 as the maximum twinning rate (calculated based on cows with calves; review by Ruprecht et al., 2016; Boertje et al., 2019).

The aerial surveys did not discriminate yearlings from adults in their counts; we thus needed to approximate the number of yearlings present in the population at the beginning of

each time period. Since a simulation begins on March 1st (i.e. the approximate date of the aerial surveys; Figure 2.2), the number of yearlings present in the population on March 1st of year *t* can be calculated by multiplying the number of calves (9 months old) in the population on March 1st of year *t-1* by the 9–12 months survival rate, the yearling emigration rate and the rate of yearling mortality from hunting, also accounting for some immigration, and assuming no mortality of yearlings due to predation (see section *Predation*). We relied on the assumption that the number of calves in the population at the beginning of a given time period was similar to that of the year before. In addition, preliminary results suggested a mean 9–12 months survival rate of 0.70. Yearling emigration rate is variable, but can reach 0.30 (Ballard et al., 1991); we assumed an intermediate value of 0.15, as it is partly offset by immigration. At this early stage of our research, we hypothesized that the hunting mortality for yearlings was negligible, as our study population lives in a protected area. Thus, the number of yearlings present in the population at the beginning of each time period was set at 60% (0.70 multiplied by 0.85, that is 1-0.15) of the number of calves, respecting the sex ratio observed during the associated survey; we performed a sensitivity analysis to verify that this choice did not meaningfully impact the population trajectory.

The relations between the dynamics-driving factors and the vital rates were modeled using several equations (see Appendix 2.2). When using non-linear convex or linear functions, the vital rates related to climate (see below) decreased too sharply, and the simulated population crashed. Thus, we used non-linear concave functions (with logarithmic-style curves), which were the most efficient to reproduce our patterns. Such a relationship between dynamics-driving factors (e.g. snow depth, winter tick engorgement) and vital rates (e.g. annual adult survival, weaning success, juvenile winter survival) was previously documented in several ungulate populations (elk: Garrott et al., 2003; Brodie et al., 2013; moose: Keech et al., 2011; DeBow et al., 2021; Alpine ibex *Capra ibex ibex*: Mignatti et al., 2012; Sitka black-tailed deer *Odocoileus hemionus sitkensis*: Gilbert et al., 2020).

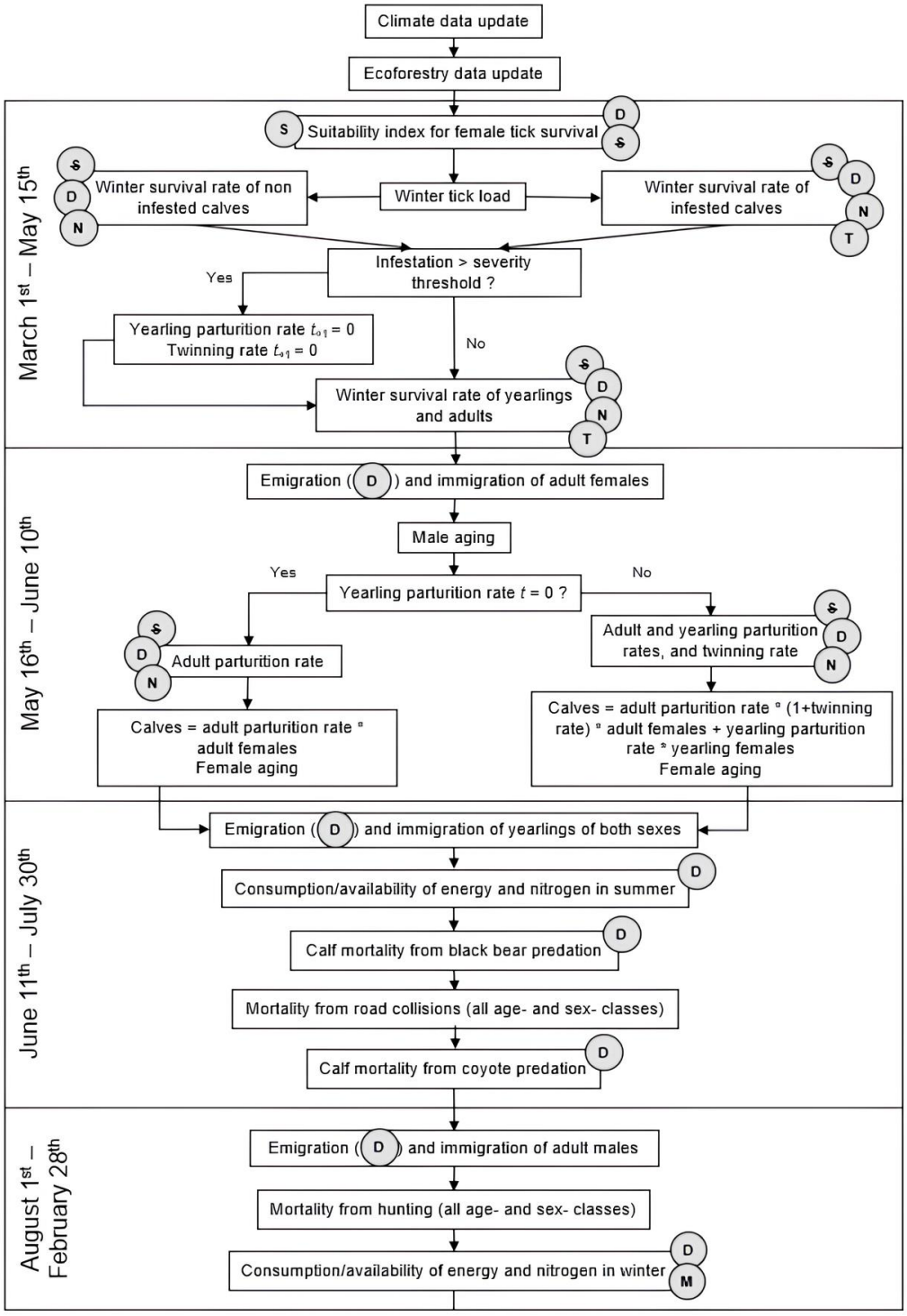

Figure 2.2: Flowchart of the model for a yearly time step. The grey circles specify the influence of the population size (D: density) or some dynamics-driving factors (S: date of first snow; ~~S~~: date of snowmelt; N: NIVA index; T: winter tick load; M: mean winter snow depth).

Climate

Climate data were downloaded from the ERA5-Land Hourly dataset on Google Earth Engine, a reanalysis obtained using satellite imagery (Munõz Sabater, 2019). We selected snow depth (cm) as our unique climate variable and averaged our hourly values to obtain daily means for our study area. Many studies reported the importance of winter severity, especially snow depth, on the dynamics of ungulates. It has been shown that during very snowy winters, moose energy expenditures associated to movement were higher and food was more difficult to find, as it is often partially buried under snow, thereby lowering moose body mass (Visscher et al., 2006; Melin et al., 2023). These cascading effects lead to a reduced productivity and survival (Bishop and Rausch, 1974; Milner et al., 2013), sometimes with a time lag of 1 to 3 years (Crête and Courtois, 1997; Parker et al., 2009). The NIVA index is one of the indices frequently used to illustrate the cumulative effect of an important snow cover on wildlife over time (Potvin and Breton, 1992; Finstad, 2008; Simard et al., 2010). We used its first component to represent the relative variation in the harshness of winter conditions for moose: hereafter, NIVA will refer to the sum of daily snow depth from first snow to snowmelt (in days-cm).

Moreover, moose accumulate fat reserves during summer when the food is abundant and of high quality, and then use them to survive winter (Schwartz and Renecker, 2007; Parker et al., 2009; Shively et al., 2019). These body reserves get gradually depleted, and moose spend a long time in a negative energy balance until green-up (Schwartz and Renecker, 2007; Parker et al., 2009; Ellingwood et al., 2019). A lasting state of negative energy balance can cause weight loss, which can increase perinatal mortality (Keech et al., 2000; Milner et al., 2013) and even decrease winter and spring survival of adults (DelGiudice et al., 2011). In light of the above, we modeled the parturition rates (of yearlings and adults), the twinning rate and the late winter-early spring survival rate (later called "winter survival rate") of calves, 1-year-olds and adults as functions of NIVA and the date of snowmelt (timing of green-up; Brown, 2011; Kautz et al., 2020; see Appendix 2.2 for more details). We tested for a 1-year delay in the effect of NIVA on these 5 vital rates using several

scenarios. We hypothesized that the winter survival rate of calves infested by winter tick is lower than or equal to that of non-infested calves (see section *Winter tick*).

Available energy and nitrogen for moose in the habitat

Carrying capacity is a widely used concept in the literature, although caution is required (Chapman and Byron, 2018). It seems particularly relevant in our study area, given that the wolf's absence means that it does not exert a "top-down" control over the moose population, and because timber harvesting and moose sport hunting are prohibited in the park. Moreover, negative browsing effects of the recent high moose densities on the park's forest are now observed (Sigouin and Samson, 2022), suggesting that a shortage of food resources may have occurred in the last few years.

Metabolizable energy is among the most limiting factors for wild ungulates (Dumont et al., 2005; Parker et al., 2009; Welch et al., 2015) and of primary importance for their performance (Illius and Gordon, 1999; Parker et al., 2009). An increasing number of studies also suggest that proteins (nitrogen) can be significantly limiting for large herbivores (Cain et al., 2017; Barboza et al., 2018; Shively et al., 2019). We therefore incorporated the concept of carrying capacity in our model by comparing the total available metabolizable energy (ME) and nitrogen (N) within the park to the total annual ME and N requirements of the moose population.

Using ArcGIS Pro 2.9 (ESRI, 2021), we used the digital ecoforestry maps of the 2^{d}, 3rd, 4th and 5th decennial forest inventory programs published by the Ministère des Ressources naturelles et des Forêts du Québec (MRNF) to classify forest stands in our study area as open (conifer canopy closure < 50%) and closed habitats (conifer canopy closure > 50%) following Crête (1989). This author evaluated the annual forage production (in kg/ha) between 0.5 and 3 m in height for the 2 types of habitat in winter (November–May) and summer (June–October) in a sector adjacent to our study area. We did not use annual updates of the ecoforestry maps, but instead had one value for each type of habitat per inventory: we consider this an acceptable approximation since the forest in our study area is not disturbed

by logging, and no fire occurred in the park during the study period. The most precise map that we could access for the 2nd forest inventory program was composed of 16 ha tessels, compared to a smaller spatial resolution of 4 ha for the 3rd, 4th and 5th inventories. We classified our forest stands the same way as for the other inventories (open and closed habitats), except that the information of the dominance of coniferous or deciduous species within mixedwood stands was not available in the digital file. We thus used the same proportion as in the 3rd inventory, considering that a major modification of the landscape in the time interval between two inventories (~10 years) is unlikely in the absence of disturbance like logging or fire.

Other forest inventories conducted by park managers (in 1995, 2006 and 2015) suggested that apart from balsam fir, the mean number of twigs/ha did not change over time for the main tree species consumed by moose (see Appendix 2.3). This may be explained by the absence of disturbance other than spruce budworm, which severely damaged only < 4% of the park's forest (Del Degan et al., 1995). As for balsam fir, 11.1% (11/99) of the plots surveyed in 2015 showed a very high number of twigs/ha (> 3,000) while the overall median value of the 99 plots was stable between 1995 and 2015 (~400 twigs/ha). The very rich plots were located mostly within old (> 50 years old), dense stands that were partially impacted by the spruce budworm in 1983–1984, triggering the regeneration of a dense balsam fir cohort. Such a post-outbreak regeneration pattern for balsam fir has been documented in other studies conducted in Quebec (Morin, 1994; Bouchard et al., 2005; Chagnon et al., 2022). We accounted for this sharp but localized increase of food resources by making the annual forage production of balsam fir dependent on the time elapsed since the last spruce budworm outbreak. We delayed the starting point of the regeneration of balsam fir by 2–3 years (in 1986) because the triggering of the growth of a new cohort due to the canopy opening usually occurs a few (up to 5) years after the defoliation/mortality of mature trees (Blais, 1981; Bouchard et al., 2006; Virgin and MacLean, 2017). We extracted the data for the 11 concerned vegetation plots and distinguished the amount of forage produced by saplings vs. trees. We then calculated the mean production of twigs/ha for saplings in 1995, 2006 and 2015, to which we fitted an exponential curve. We transposed this exponential growth curve

to the annual forage production of balsam fir in kg/ha for 11% of the forest while respecting the proportions.

As suggested by Crête (1989), balsam fir was not considered to be completely available when calculating the amount of resources in winter, as this species is a great source of nitrogen but is difficult to digest due to the presence of secondary metabolites such as condensed tannins (Robbins et al., 1987b; Windels and Hewitt, 2011). Instead, we hypothesized that moose would first consume all the twigs of deciduous species (Crête, 1989; Månsson, 2007; Peterson et al., 2020) and then rely on the less palatable balsam fir by the end of winter (Crête and Courtois, 1997; Desgagnés et al., 2022; Spitzer et al., 2023). Hence, we used the POM method to estimate the proportion of balsam fir to be added with the other variables in the calculation.

We removed the forage with a height ranging from 0.5 m to the mean value of daily snow depth for the winter period (Hanley et al., 2012). Moreover, we excluded the part of the forage that moose calves cannot reach, as they are smaller than adults, making the forage between 1.5 m and 3 m in height available only for yearlings and adults. We modeled the requirements of calves so that they rely on forage 14 weeks out of 20 in summer, because although they suckle until late August, they already feed mainly on forage by mid-July (Gasaway and Coady, 1974; Schwartz, 2007).

We used data collected on 70 moose harvested by sport hunters at the Seigneurie Nicolas-Riou outfitter (Quebec; 48°14’00’’ N, 68°45’00’’ O; 320 km away from Forillon National Park) to build equations relating moose age (for males and females separately) to body weight. Considering that this harvested population has quite a young age structure for males (the oldest in this dataset was 5.5 years old), and that male moose usually reach their maximum body weight at 5.5-6.5 years of age (Sand et al., 1995; Jensen et al., 2013), we hypothesized that the weight of males older than 5.5 would be around the same value. As done elsewhere (Wallin et al., 1996), we fitted a non-linear model to the weight data for both sexes (males: n=33, R^2=0.85, P-value=6.979e^{-16}; females: n=37, R^2=0.88, P-value=2.200e^{-16}). We converted field-dressed weights into whole weights using the

regression equation calculated by Jensen et al. (2013) (n=154; R^2=0.93). Having no information regarding the age structure of our population in Forillon, we estimated the mean age of adult males and females via POM. Hoy et al. (2020) studied the moose populations of Isle Royale and Yellowstone National Parks between 1959 and 2015 and found that the mean age of adults (> 1 year old) varied from 4 to 10 years old from year to year. However, wolf predation in Isle Royale and Yellowstone likely influenced the age structure of these moose populations, since wolves tend to select calves and individuals older than 9 years (Lake et al., 2013; Mech and Nelson, 2013). Therefore, moose in Forillon presumably live older than in the aforementioned study areas, so we set a range of 5 to 12 years old for the mean age of adults of both sexes in the POM.

The values used to approximate the total available ME (kcal) and N (g) within the study area and the total ME and N requirements of the population for both winter and summer of each year considered in our model are listed in Table 2.1. We performed a sensitivity analysis on these values, i.e. we increased and decreased each one by 5% while keeping the others constant, to verify that a slight modification did not meaningfully impact the results of the model simulations. The most sensitive values were estimated via POM. We chose ME and N requirements that allow body maintenance, gestation and lactation, antler growth, calf growth and a 30% body mass gain in summer (Schwartz et al., 1988; Reese and Robbins, 1994; Moen and Pastor, 1998).

The energetic balance (see section *Climate*) can become negative in winter when moose density is high because individuals deplete the available winter forage more quickly (Boertje et al., 2007; Paragi et al., 2015). We incorporated an effect of density on the different vital rates, respecting the sequence described by Eberhardt (1977, 2002) and Gaillard et al. (1998): the survival rate of calves is the first to be impacted when density increases, followed by the age at first reproduction, parturition rate of adult females and then survival rates of adults. Consequently, when the ratio between the total population requirements in the limiting nutrient and its availability in the habitat exceeded a given threshold in winter, the survival rate of calves (infected or not by winter tick) decreased. We set this first threshold at 0.5, as was done elsewhere (Rempel et al., 2021). Similarly, when this ratio reached a second

threshold (between 0.5 and 0.8, estimated with POM), the parturition rate of yearling females was set to 0 and the twinning rate was reduced (decrease estimated via POM, with a maximum of 0.25 as did Rempel et al., 2021). When the ratio of population requirements/availability of the limiting nutrient exceeded a third threshold value (between the second threshold and 0.9, estimated with POM), the parturition rate of adult females was reduced (decrease estimated in the same way as for the twinning rate). Finally, when the ratio exceeded a fourth threshold value (between the third threshold and 1, estimated with POM), the yearling and adult survival rates decreased (maximum decrease of 0.2: Rempel et al., 2021).

Table 2.1: Values used to calculate the total available metabolizable energy (kcal) and nitrogen (g) and the total metabolizable energy and nitrogen requirements of the population within the study area in winter and in summer for each year covered by the model. wt= weight.

Description	**Value[1]**	**Unit**	**References**
Availability			
Annual production of leaves between 0.5 and 3 m in height in open habitat (summer forage)[2]	167	kg-dry wt[3]/ha	Crête, 1989
Annual production of leaves between 0.5 and 3 m in height in closed habitat (summer forage)[2]	44	kg-dry wt/ha	Crête, 1989
Annual production of deciduous twigs between 0.5 and 3 m in height in open habitat (winter forage)[2]	28	kg-dry wt/ha	Crête, 1989
Annual production of deciduous twigs between 0.5 and 3 m in height in closed habitat (winter forage)[2]	8	kg-dry wt/ha	Crête, 1989
Annual production of balsam fir twigs between 0.5 and 3 m in height in open habitat[2]	387	kg-dry wt/ha	Crête, 1989
Annual production of balsam fir twigs between 0.5 and 3 m in height in closed habitat[2]	185	kg-dry wt/ha	Crête, 1989
Mean digestible energy content of summer forage	*POM*	kcal/g-dry wt	Rea and Gillingham, 2001; Barboza et al., 2018; Schrempp et al., 2019; Peterson et al., 2020
Mean digestible energy content of winter forage	*POM*	kcal/g-dry wt	
Digestible energy content of balsam fir	*POM*	kcal/g-dry wt	
Efficiency of energy metabolism	78	%	Robbins, 1993
Mean crude protein content of summer forage[4]	*POM*	g/100g-dry wt	Crête and Jordan, 1982; Crête, 1989; Rea and Gillingham, 2001; Schrempp et al., 2019; Peterson et al., 2020
Mean crude protein content of winter forage[4]	*POM*	g/100g-dry wt	
Crude protein content of balsam fir in summer[4]	*POM*	g/100g-dry wt	
Crude protein content of balsam fir in winter[4]	*POM*	g/100g-dry wt	
Efficiency of protein metabolism	82	%	Robbins, 1993

Kjeldahl nitrogen conversion factor	6.25		
Requirements			
Required intake of metabolizable energy in summer[5]	345	kcal/kg body $wt^{0.75}$/day	Moen and Pastor, 1998
Required intake of metabolizable energy for yearlings and adults in winter (body maintenance)	144	kcal/kg body $wt^{0.75}$/day	Schwartz et al., 1988; Pekins, 2020
Required intake of metabolizable energy for calves in winter (growth)	181	kcal/kg body $wt^{0.75}$/day	Tarr and Pekins, 2002; Pekins, 2020
Additional requirement of metabolizable energy for gestation in winter[6]	101.6	kcal/singleton/day	Robbins and Moen, 1975
	83.6	kcal/twin/day	
Required intake of N for body maintenance[7]	0.254	g/kg body $wt^{0.75}$/day	Schwartz et al., 1987; Schwartz and Renecker, 2007
Required intake of N for protein deposition (30% mass gain in summer)	17.3	g/male/day	Moen and Pastor, 1998
	13.0	g/female/day	
Required intake of N for gestation[6]	508	g/singleton	Robbins and Moen, 1975
	418	g/twin	
Required intake of N for lactation[8]	3,800	g/singleton	Reese and Robbins, 1994; Schwartz and Renecker, 2007
	3,173	g/twin	
Required intake of N for antler growth[9]	780	g/adult male	Moen and Pastor, 1998
	120	g/yearling male	

[1] The values noted as '*POM*' were estimated with pattern-oriented modeling.

[2] Habitats with conifer canopy closure < 50% are open; habitats with conifer canopy closure > 50% are closed.

[3] The mass values were standardized by removing the water content and expressed in kg or g of dry weight (dry-wt).

[4] Converted in digestible protein using the equation of Robbins et al. (1987a).

[5] Calculated to meet a 30% gain in body mass throughout the summer, and energy requirements for late gestation, lactation and antler growth.

[6] Calculated with a mean birth mass of 17 kg for singletons and 14 kg for twins (Schwartz and Hundertmark, 1993; DelGiudice and Severud, 2016; McDonough et al., 2022).

[7] This value was tripled for weaned calves because of their rapid growth rate (Ullrey et al., 1967; Schwartz and Renecker, 2007).

[8] Calculated for 120 days of suckling (using Fig. 1 and Fig. 2 in Reese and Robbins, 1994).

[9] Calculated for a mean of 13 kg antlers for adult males and 2 kg antlers for yearling males (Bubenik, 2007).

Winter tick

Moose is the main host of the winter tick, which seems to become more and more abundant with the changing climate and frequently causes widespread mortality of calves in North America since 2000 (Samuel, 2004; Jones et al., 2017, 2019). The Gaspé Peninsula is no exception, despite its relatively cold climate less suitable to tick development, as 96% of the moose sampled south of the St. Lawrence River in autumn 2012–2014 were hosting ticks (Ministère des Forêts, de la Faune et des Parcs, 2016). The lifecycle of winter ticks has five stages: 1) drop-off of adult females from host in March-April, 2) egg laying and hatching before June, 3) larvae quiescence in the ground litter during summer, 4) questing from mid-September to the offset of winter, and 5) growth on the host (Samuel, 2004). We did not have accurate data to predict annual tick load of moose (i.e., the number of winter ticks per individual), so we relied on a literature review and decided to focus on two key periods of the tick's lifecycle that are largely influenced by climate: drop-off and questing. We did not account for the risk of desiccation of quiescent larvae during dry summers (Addison et al., 2016; Dunfey-Ball, 2017) because our study area experiences a humid climate with much more summer rainfall compared to other studies, such as those conducted in the northeastern United States (Jones et al., 2017, 2019; Healy et al., 2020). Spring and fall temperatures were also reported to significantly influence tick load (Aalangdong, 1994; Dunfey-Ball, 2017). Wilton and Garner (1993) and Samuel (2007) mentioned that warmer temperatures in March and April can increase the survival of adult female ticks when they drop from moose and thus contribute to the occurrence of die-offs. In our study area, the daily mean temperature was -5.6 °C in March and 0.3 °C in April from 1982 to 2020, compared to 4.3 °C in April in the Edmonton region (Samuel, 2007). Besides, daily mean temperature in Forillon never exceeded -1.5 °C in March and 3.0 °C in April, the latter being the threshold value identified by Wilton and Garner (1993) above which tick-induced hair damage and loss for moose was more severe. Therefore, we did not consider the effect of spring temperatures on tick load.

Whether or not the ground is still covered by snow when adult tick females drop from their host is significant because they may die before laying eggs (Drew and Samuel, 1986). We thus computed the date of snowmelt for each year and built a suitability index

for female tick survival. We did the same for the date of first snow, since it terminates the questing period (Samuel, 2004); if this date was posterior to the date of first prolonged cold (the last of 3 consecutive days with mean temperature < 0 °C), which reduces the activity of questing larvae, the latter was computed instead (Samuel, 2007; Holmes et al., 2018). We also considered moose density as a factor influencing tick load because the more hosts available, the more parasites survive and reproduce (Samuel, 2004, 2007; Dunfey-Ball, 2017). In order to test whether one of these 3 factors (date of snowmelt, date of first snow/cold or host density) had a prominent effect on the final tick load, we added multipliers (estimated via POM) to each of them to allow a variation in their respective weight in the calculation of the suitability index for female tick survival between the simulations.

The prevalence (i.e., the percentage of moose infested by winter ticks) was estimated with the POM method. Pouchet (2023) found that 40±30% of the moose in Gaspésie were hosting ticks. We thus tested a range of 10 to 70% (i.e. 40±30% following Pouchet, 2023) of prevalence with POM. However, the results of this recent study may not be representative of the reality in the ’80s, so we reduced the lower bound from 10% to 0% for all our time periods except the most recent (2017–2019).

For a given year *t* in the model, the tick load faced by moose in spring is determined based on the three criteria cited above. The possible mean tick load in our model ranged from 0 to 45,000 ticks per moose, which corresponds to values observed in the wild (Musante et al., 2007; Jones et al., 2019). However, the type of equation linking the annual tick load to our female tick survival index was uncertain. We tested three types of equation: linear, logarithmic or exponential, with parameters estimated with POM. The linear and logarithmic equations led to mean tick loads (i.e. no. of ticks/moose) ranging from 0 to 18,000, and from 0 to 35,000, respectively, for the 1990–1996 period. The same trend was observed for the 1997–2008 period, with respective ranges of 0–30,000 and 0–37,000. In comparison, tick load on calf hides collected between 2014 and 2016 in New Hampshire (where climate is much more favorable to winter tick survival and reproduction) ranged from 19,000 to 95,000, with a mean of 47,000 (Jones et al., 2019). From 1977 to 1991, Samuel (2004, 2007) documented a mean tick load < 10,000 ticks/moose when moose density was under 1 moose/km² in Elk Island National Park

(Alberta), which is almost at the same latitude as Forillon National Park. Furthermore, using the linear or logarithmic equation would have led to mean tick loads > 35,000 for multiple years between 2009 and 2016 for a non-negligible proportion of simulations, which would have greatly reduced winter calf survival, and hampered adult reproduction and survival. This is obviously not the case considering the rapid increase in moose abundance, which roughly doubled during this time period. Preliminary results rather suggested that successful simulations for 2009–2016 were consistently associated with relatively low mean tick loads (< 20,000). A recent study also showed that both winter tick load and winter tick prevalence in our study area are among the lowest in Quebec (Pouchet, 2023). Thus, we selected the exponential-type equation as the best fitting in our situation, and we did not test the two other forms for the three remaining time periods.

Tick bites can impair moose health in three main ways: first, tick-induced self-grooming lowers the appetite and the time allocated to feeding and thus decreases energy reserves (Samuel, 2004). Second, hair damage and loss due to grooming result in a higher energy cost for maintaining body temperature (Samuel, 2004). Finally, moose can experience anemia due to blood loss from ticks and must spend supplementary energy to replace it (Samuel, 2004; Musante et al., 2007). All these processes can trigger or worsen a state of negative energy balance in winter (Ellingwood et al., 2019; Rosenblatt et al., 2021), which can affect moose survival rate. Since grooming, hair damage and blood loss are proportional to tick load (Mooring and Samuel, 1998; Samuel, 2004), we calculated the winter survival rate of infested calves based on tick load, NIVA and the date of snowmelt (see above). We assumed adult and yearling moose are unlikely to die from the effects of ticks due to higher body weight and blood volume (Samuel, 2007; Musante et al., 2007; Jones et al., 2019), except in circumstances of high tick load during several consecutive years (DeBow et al., 2021; Harris et al., 2021). A year t was marked as "year of severe infestation" if the tick load was higher than 35,000 ticks per individual (Healy et al., 2020). In such cases, the parturition rate of yearling females and the twinning rate were automatically set to 0 for the year t_{+1} (in accordance with results obtained by Musante et al., 2007, 2010; Jones et al., 2017, 2019). Moreover, we implemented a function that added mortality for yearlings and adults if this tick load threshold was

exceeded for two successive years or more (estimated with the POM method, with a maximum mortality rate of 0.15 as it was seen in DeBow et al., 2021).

Predation

Black bears and coyotes are the only potential predators of moose in the Forillon National Park. It has been shown that black bears are a threat to moose calves, mainly during their 4 to 6 first weeks of life (Zager and Beecham, 2006; Ballard and Van Ballenberghe, 2007). Several studies reported black bear predation on yearling and adult ungulates, but these cases are rare (Ballard, 1992; Svoboda et al., 2011). We assumed no mortality due to predation among adult and yearling moose in our study area. Black bear density in the park was probably under 2.0 bears/10 km^2 during the '80s (Ministère de l'Environnement, de la Lutte contre les Changements climatiques, de la Faune et des Parcs du Québec [MELCCFP], *unpublished data*). It was then estimated to range between 2.3 and 4.7 bears/10 km^2 by the end of the 1990s (Leblanc and Huot, 2000), an estimation confirmed in 2015 (Pettigrew et al., 2021). The results of the most recent survey (2020) suggest that the bear density is now between 4 and 7 bears/10 km^2 (Gaudet-Boulay and Sigouin, *in prep*). In our model, we thus made the bear density vary between 1.0 and 2.0 bears/10 km^2 from 1982 to 1990 using a normal distribution (mean = 1.5, SD = 0.2), between 2.3 and 4.7 bears/10 km^2 from 1991 to 2017 (mean = 3.5, SD = 0.55) and between 4.0 and 7.0 bears/10 km^2 from 2018 to 2020 (mean = 5.4, SD = 0.6). The length of the period when calves are vulnerable to black bear predation (between 30 and 90 days according to authors: Ballard et al., 1980; Zager and Beecham, 2006; Ballard and Van Ballenberghe, 2007) was estimated via POM. Similarly, the proportion of adult bears (> 2 years old) in the population (between 0.60 and 0.85: Hellgren and Vaughan, 1989; Bales et al., 2005; Hébert et al., 2009), the age class that can predate moose, was estimated with POM. Indeed, a sensitivity analysis showed that the elasticity of these two parameters was not negligible. The kill rate of bears on moose calves was also estimated via POM, and we made it vary annually in proportion to the ratio between moose density and bear density (i.e. moose : bear density ratio) because the higher the moose numbers with respect to bears, the higher the probability of encounter.

The coyote, on the other hand, usually kills moose calves that are up to 6 months old (Wolfe, 1974; Crête and Desrosiers, 1995; but see Benson and Patterson, 2013). The coyote colonized the Gaspé Peninsula during the '70s (Georges, 1976), and its density was estimated between 0.7 and 0.8 coyotes/10 km^2 in the park before 2000 (Fortin, 1995), but recent harvest data suggest that it has increased since then (MELCCFP, *unpublished data*). However, the populations of white-tailed deer, the main prey of coyote, have been collapsing since 2015 in Gaspésie (MELCCFP, *unpublished data*). We thus hypothesized that the coyote density in our study area declined slightly in response to this collapse. As we did for black bears, we used normal distributions to make the coyote population in the park vary in size, ranging from 0.7 to 0.8 coyotes/10 km^2 for the 1982–2000 period (mean = 0.75, SD = 0.02), from 0.8 to 1.0 coyotes/10 km^2 for 2001–2015 (mean = 0.90, SD = 0.06) and from 0.7 to 0.8 coyotes/10 km^2 for 2016–2020 (mean = 0.75, SD = 0.02). The kill rate of coyotes on moose calves was estimated using POM but was allowed to vary annually in proportion to the moose : coyote density ratio.

As we parameterized our model, we noted that the values of kill rates that we found in the literature very frequently yielded high predation rates on calves for both bears and coyotes, which reduced the ability of our model to reproduce the patterns observed in the field. Thus, we implemented maximum values for predation rates in the model to allow lower values of predation rates to be explored as well, by forcing the model to select from a lower range of values. For each time period, we tested several values for this maximum, with 5% intervals (e.g. for 1997–2008, we tested maximum predation rates of calves of 25%, 30%, 35% and 40%). For each time period, we stopped testing higher or lower values when the percentage of simulations reproducing our patterns markedly decreased, or the deviation between simulated and observed patterns markedly increased (see below). For a given maximum predation rate, the model was free to explore all the values below this limit, including all the possible decimals.

Dispersal

Although moose movement across the park boundaries might be constrained by the peninsular situation of the park and the presence of Highway 197 (and its urban development), emigration and immigration are still possible. Indeed, moose are regularly

seen crossing Highway 197 in both directions, and this is confirmed by the movements of 21 GPS-collared females, tracked since 2020 (P. Etcheverry, *unpublished data*). We thus allowed individuals from all our groups (excluding calves) to enter or leave the park once a year in proportions estimated using POM, with a higher probability of dispersal for yearling individuals (Ballard et al., 1991; Labonté et al., 1998; Dodge et al., 2004). We tested two alternative hypotheses for this emigration process: 1) in the case of a positive density dependence (PDD), emigration would be low but greater than zero at low densities (relative to carrying capacity), essentially because competition for food resources would be weak and leaving the natal range would offer only a subtle advantage, and would thereafter increase at higher densities due to a more intense competition for both food resources or mates (literature review by Hundertmark, 2007; Rempel et al., 2021); 2) according to a negative density dependence (NDD) scenario, the emigration rate would decrease at high densities because of aggressive behaviour in older males, a low gain from dispersal since all areas are occupied or because of a poor body condition that hinders travel (Hjeljord, 2001).

Regarding immigration rates, we hypothesized that they would display no particular pattern and vary randomly between years, as the outsiders do not know the environmental characteristics (e.g. density, habitat quality, etc.) in the park before entering it (Akçakaya et al., 1999). Therefore, we used normal distributions with mean and standard deviation estimated using the POM method.

Hunting and road accidents

The number of moose harvested by sport hunters is normally known with precision, as reporting big game harvest is a legal requirement in the province of Quebec. Annual harvesting data were taken from the Wildlife Incident Management System of the park for the period 1982–2019. We accounted for all mortalities that occurred within 5 km of the park (Chamberland and Sigouin, 2017). We also subtracted from the population the individuals that were killed by vehicle collision on Highways 132 and 197 (see Appendix 2.4). For hunting and road mortalities, our datasets did not differentiate adult individuals (> 2 years old) from yearlings. Since they are separated in our model, we removed individuals from each category in proportion to their presence in the population (e.g. if in

year *t* 7 males > 1 year old died from hunting, and yearling males accounted for 1/7 of the male segment of the population, then 1 yearling male and 6 adult males died).

Model parameterization

In order to account for stochasticity in the model, we chose to do multiple replicates for each tested parameter set (Rangel et al., 2007; Desforges et al., 2021). This allowed us to avoid selecting a set of parameter values that "accidentally" reproduces the observed patterns as a result of stochasticity. For a given parameter set, we did several tests, increasing the number of replicates until the mean values for our three patterns stopped varying. A total of 100 replicates was the minimum required to stabilize the means of sex ratio and recruitment rate for the periods 1982–1989 and 1990–1996. This number increased to 120 replicates for the periods 1997–2008 and 2017–2019, and 140 replicates for 2009–2016 due to more stochasticity. Based on the above, and to be safe, we chose to generate respectively 120, 140 and 160 replicates for each simulation. Unfortunately, the mean for the moose abundance pattern could not be perfectly stabilized for the last three time periods and kept varying (< 8 individuals) between replicates, even when we increased the number of replicates to over 300. This did not impact the results (see Appendix 2.5).

We had a total of 83 parameters to estimate with the POM strategy (see Appendix 2.2, which presents a comprehensive list of these parameters with their respective ranges, all determined based on careful literature reviews, along with the associated equations in the different modules). However, according to Grimm and Railsback (2012), the models calibrated using the POM method usually include 10 to 20 parameters to be estimated. These should be restricted to the ones for which the value is particularly uncertain or to which the model is very sensitive. Besides, as far as we know, no published study used POM to estimate more than 17 parameter values (Topping et al., 2012). We thus managed to reduce the number of variables from 83 to 20 following the process described below (see Figure 2.3 for a visual support). The results without fixed parameter values are available in Appendix 2.6 for comparison.

We ran 100,000 simulations sampling a different value for each parameter to calibrate by POM for each subperiod and each scenario of our population model to cover a large part of the possible combinations for the parameter values (see Table 2.2 for a summary of the tested scenarios). At the beginning of each simulation, parameter values were independently sampled from uniform distributions (this only concerns the parameters estimated with POM). A simulation was selected if the 95% confidence intervals (CI) around the simulated values (means of the replicates) were included in the 80% CI around the observed values (aerial surveys) for the three patterns simultaneously. For each scenario, we calculated the success rate as the percentage of tested parameter sets that were retained. We plotted these values and searched for a clear breakpoint between the "high" and "low" success rates. We selected the scenarios for which the success rates were above this break (step B in Figure 2.3).

For each tested parameter set, the deviation between simulated and observed values was calculated as follows:

$$\text{Deviation} = |obs_{POP} - sim_{POP}|/CI80_{POP} + |obs_{sex\_ratio} - sim_{sex\_ratio}|/CI80_{sex\_ratio} + |obs_{recruitment} - sim_{recruitment}|/CI80_{recruitment} \quad \text{(eq. 1)}$$

where obs_{POP}, obs_{sex_ratio} and $obs_{recruitment}$ are respectively the moose abundance, sex ratio and recruitment rate derived from the aerial surveys; sim_{POP}, sim_{sex_ratio} and $sim_{recruitment}$ are the same values obtained from the model (means of the replicates), and $CI80_{POP}$, $CI80_{sex\_ratio}$ and $CI80_{recruitment}$ are respectively the 80% confidence intervals around obs_{POP}, obs_{sex_ratio} and $obs_{recruitment}$. The deviation ranged from 0 to 3.

For each selected scenario, we ran the number of simulations required to obtain at least 5,000 successful parameter sets, which was necessary to have stable means for all the parameters. We selected the parameter set for which the deviation between simulated and observed values was smallest (step D in Figure 2.3). We then performed sensitivity analyses: for each selected scenario and each period of time, we fixed all the parameter values to those of the parameter set with the least deviation and tested the sensitivity of the results (the simulated values of our three patterns) to variations in these values. We did that by increasing and decreasing by 5% every value estimated via POM one at a time (as seen in Smythe et al., 2019; Desforges et al., 2021). Please note that, for instance, a

5% increase of the value of one of the parameters involved in the calculation of the adult female parturition rate does not necessarily translate in a 5% increase of the adult female parturition rate itself. Following Grimm and Railsback (2012), the results of these sensitivity analyses (available in Appendix 2.7) were used to define which of our 83 parameters could be fixed for each period of time. When making this choice, we made a trade-off between the sensitivity and several other criteria, namely the necessity to leave at least one unfixed parameter value in each module to allow flexibility and the possible shift of the mean value of a parameter with respect to the mean of its range (another way to measure its sensitivity if not detected by the sensitivity analysis).

Once we knew which parameters could be fixed, we calculated their mean values with all the successful parameter sets (step F in Figure 2.3). We rounded them to three significant digits, which was the highest level of precision that we could obtain (even using 25,000 parameter sets did not improve precision). We consider this level of precision suitable in regard of the amplitude of the parameter ranges. Indeed, the last significant digit was always well below the ±5% tested in the sensitivity analysis. Moreover, most of the fixed parameters had a mean value really close, if not equal, to the mean of their range, indicating that the model could manage to reproduce the patterns whatever the values of these parameters. A summary of the fixed parameters and their values for each subperiod of time is presented in Appendix 2.8.

For the 20 remaining parameters, we performed a second step of POM, running as many simulations as needed to minimize the deviation between simulated and observed patterns for each time period (step G in Figure 2.3). The corresponding numbers of "successful" parameter sets were above 7,500 (i.e. the closeness between simulated and observed values was only slightly, or not at all, improved when having over 10,000 successful parameter sets; Appendix 2.5). Our final results are the ones associated with the parameter sets leading to the smallest deviation for each time period.

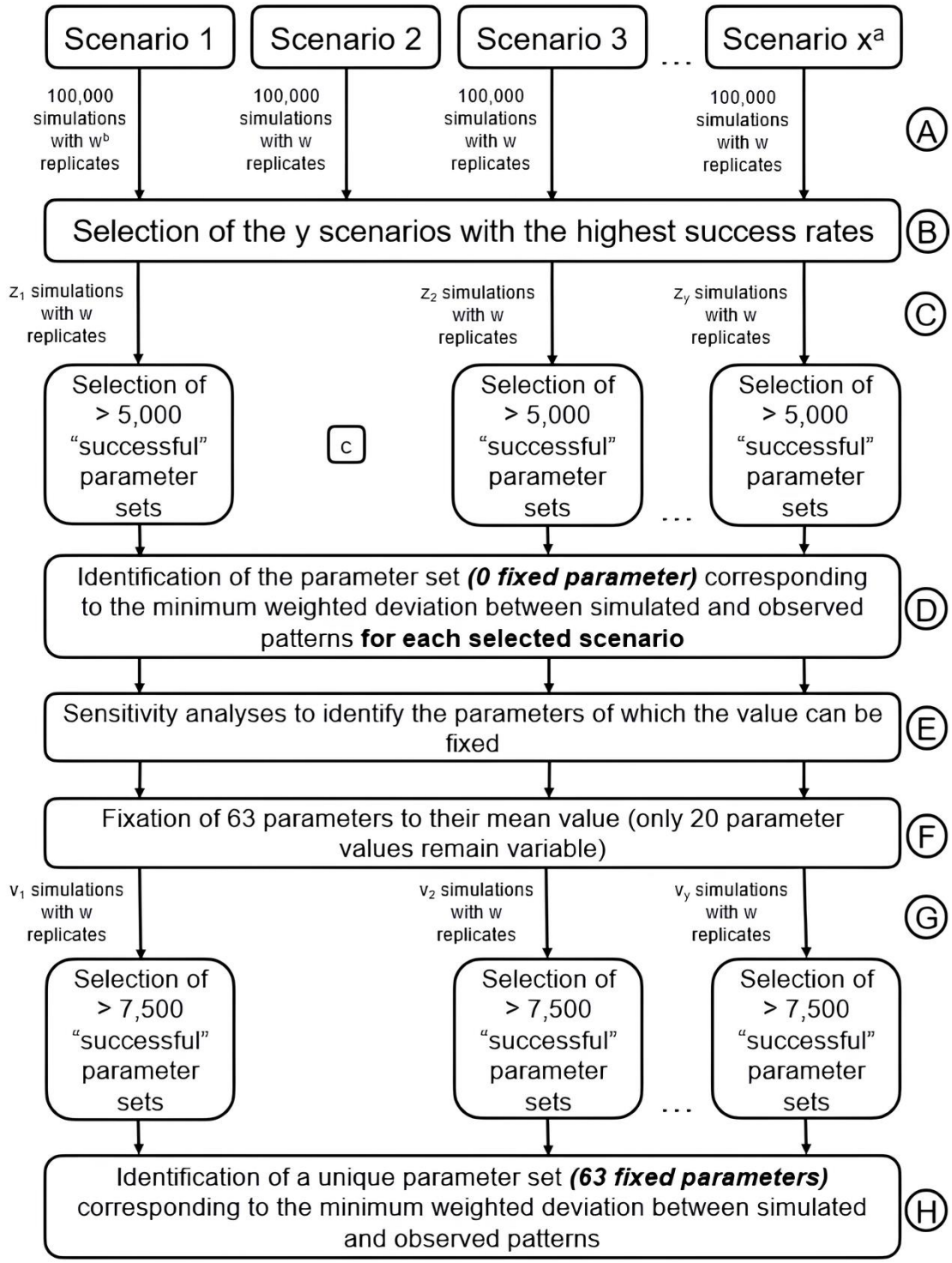

Figure 2.3: Summary of the steps involved in the parameterization of the model. This sequence is conducted for each of our five time periods. z and v represent different numbers of simulations. [a] x=8 for 1982–1989 and 1990–1996, and x=16 for 1997–2008, 2009–2016, and 2017–2019. [b] w=120 for 1982–1989 and 1990–1996, w=140 for 1997–2008 and 2017–2019, and w=160 for 2009–2016. [c] The "missing box" under scenario 2 illustrates that this scenario was not selected (i.e. it had a low success rate compared to the others) and thus did not undergo the next steps of parameterization.

Table 2.2: Summary of the tested scenarios for each period of time. y.= yearling; a.= adult; PDD= positive density dependence in dispersal; NDD= negative density dependence in dispersal. Blank cells represent scenarios that were tested but not selected, while shaded cells represent the selected scenarios. The "**X**" identifies for each time period the scenario which led to the minimum weighted deviation between estimated and observed patterns. For the first two periods, the two dispersal scenarios were merged into one: indeed, moose density remained relatively low and stable between 1982 and 1996, so the two patterns of emigration yielded similar figures.

	Time period							
Scenario of delay of winter effects on the vital rates	**1982–89**	**1990–96**	**1997–2008**		**2009–16**		**2017–19**	
	Dispersal scenario							
	-	**-**	**PDD**	**NDD**	**PDD**	**NDD**	**PDD**	**NDD**
1. No delay for all								
2. Delay: reproduction	**X**							
3. Delay: y. and a. survival			**X**					
4. Delay: y. and a. survival, and reproduction		**X**				**X**		
5. Delay: calf survival							**X**	
6. Delay: calf survival, and reproduction								
7. Delay: calf survival, and y. and a. survival								
8. Delay for all								

RESULTS

We ran several million simulations using pattern-oriented modeling to reproduce the variations in moose abundance, sex ratio and recruitment rate for 5 periods of time between 1982 and 2020. These patterns were reproduced with great precision (Figures 2.4 to 2.6), and between 2 and 5 scenarios were selected for each time period (Table 2.2). The percentage of simulations for the selected scenarios that successfully reproduced the observed patterns of moose density, sex ratio and recruitment rate (hereafter "success rate") varied between 4.2 and 9.0% for 1982–1989, 14.0 and 15.0% for 1990–1996, 2.1 and 2.9% for 1997–2008, 1.5 and 3.3% for 2009–2016, and 30.6 and 32.9% for 2017–2019. The minimum weighted absolute deviations between the mean values of observed and simulated patterns reached 0.30, 0.05, 0.02, 0.05 and 0.03, respectively, for these same periods.

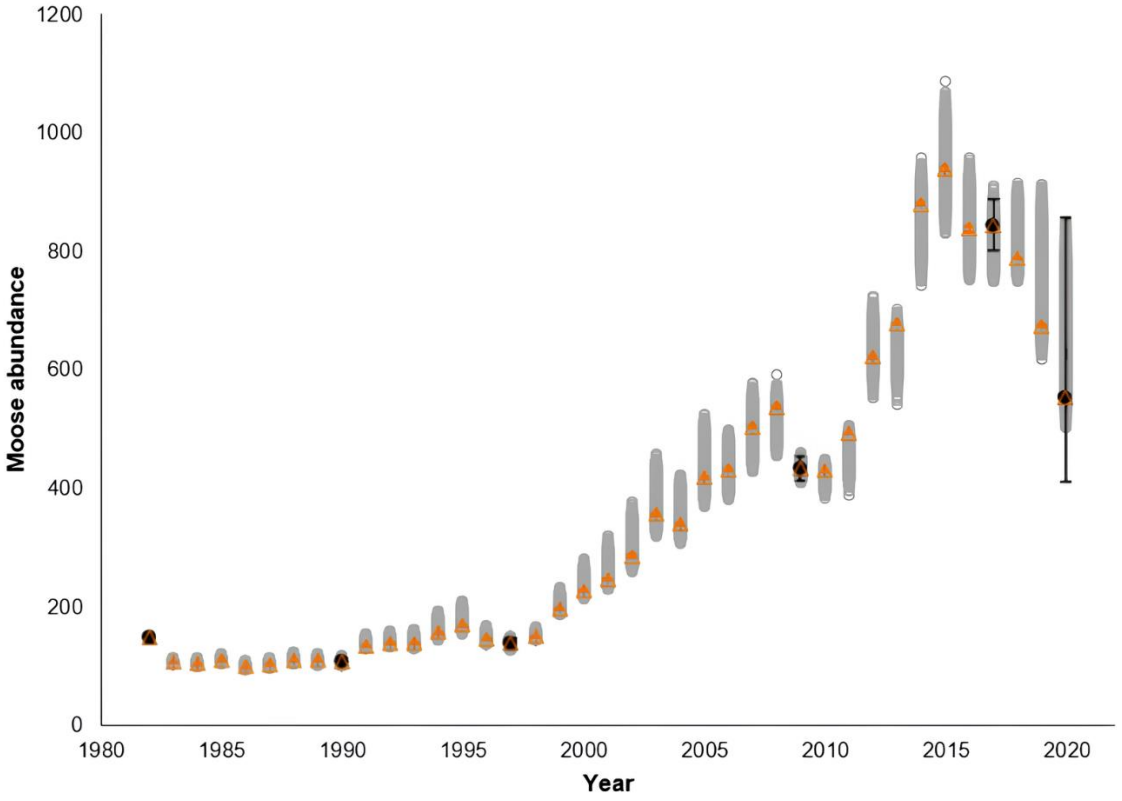

Figure 2.4: Variation of moose abundance in the Forillon National Park between 1982 and 2020. Black circles are the data derived from aerial surveys (error bars represent the 80% CI). Orange triangles are the modelled values derived from the results of the simulation with the smallest deviation between simulated and observed patterns for each period of time (error bars represent the 95% CI). Grey circles are the modelled values derived from the results of all the successful simulations for each period of time (from the same scenario as the simulation with the smallest deviation).

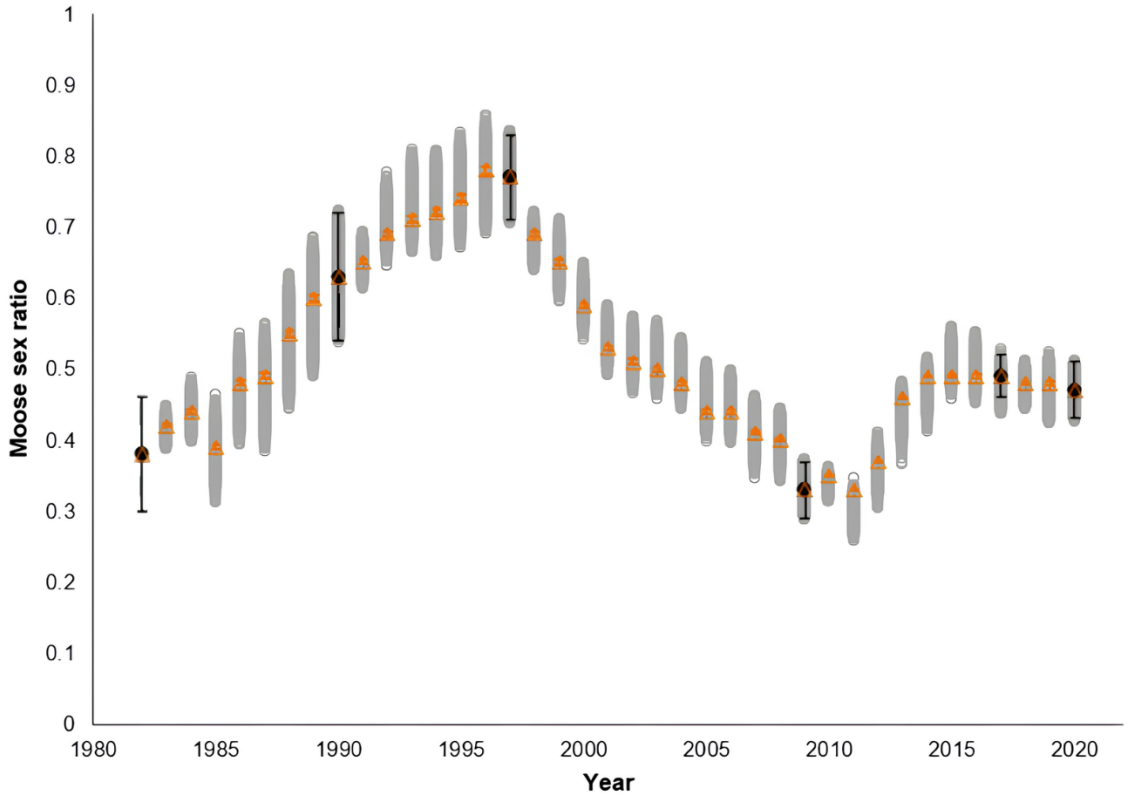

Figure 2.5: Variation of moose sex ratio in the Forillon National Park between 1982 and 2020. Black circles are the data derived from aerial surveys (error bars represent the 80% CI). Orange triangles are the modelled values derived from the results of the simulation with the smallest deviation between simulated and observed patterns for each period of time (error bars represent the 95% CI). Grey circles are the modelled values derived from the results of all the successful simulations for each period of time (from the same scenario as the simulation with the smallest deviation).

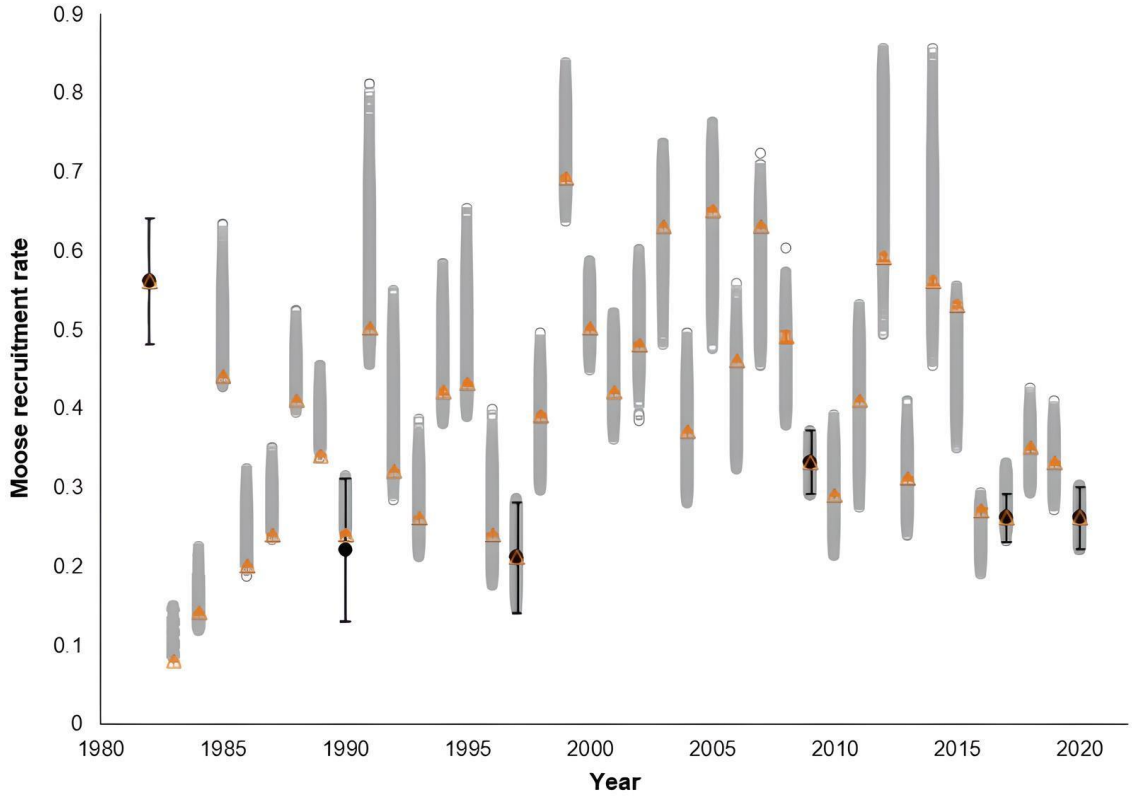

Figure 2.6: Variation of moose recruitment rate in the Forillon National Park between 1982 and 2020. Black circles are the data derived from aerial surveys (error bars represent the 80% CI). Orange triangles are the modelled values derived from the results of the simulation with the smallest deviation between simulated and observed patterns for each period of time (error bars represent the 95% CI). Grey circles are the modelled values derived from the results of all the successful simulations for each period of time (from the same scenario as the simulation with the smallest deviation).

The impact of moose density on population dynamics

According to the selected simulations, winter calf survival rate was variable from one time period to another and highly affected by density (Table 2.3). Overall, winter survival rates of yearlings and adults were stable from 1982 to 2016, but decreased sharply between 2017 and 2019 (Table 2.3). The reproductive rates were mostly stable between 1982 and 2008 (Table 2.3). The parturition rate of yearling and adult females, along with the twinning rate, markedly decreased as moose density increased. Indeed, the moose abundance became progressively closer to the carrying capacity of the park over time, and then strayed from it

during the last time period. According to the best simulation for the 2009–2016 period, the moose carrying capacity was estimated to be 3.2/km² (Table 2.3), and was exceeded in 2014, 2015 and 2017. The ratio of moose nutritional requirements/availability in summer stayed under 0.50 during all the time periods. When comparing the requirements/availability ratios for energy (ME) and nitrogen (N), energy was the less abundant nutritional resource in summer, as the ratio was about twice as high as for nitrogen. However, during winter, nitrogen was slightly more limiting from 1982 to 2008 (with mean differences in the requirements/availability ratio ranging from 0.00 to 0.10). Then, energy became slightly more limiting (mean differences of 0.02 in the requirements/availability ratio in 2009–2016, and 0.08 in 2017–2019).

Predation, winter weather and parasitism influence moose abundance

Overall, our model suggests that the proportion of calves killed annually by black bears and coyotes decreased through time, and the summer survival rate of calves increased (Table 2.3). The combined kill rate was lowest in 1990–1996, and highest in 2009–2016. The calf survival rate also appeared to be sensitive to winter severity and length (Appendix 2.9). The most successful scenarios for the periods 1982–1989, 1990–1996 and 2009–2016 all include a 1-year delay in the effects of cumulative snow depth (NIVA) and date of snowmelt on the reproductive performance of females (Table 2.2). On the contrary, for the periods 1997–2008 and 2017–2019, the scenarios with no delay in the effects of winter on reproductive rates were more successful. The winter survival rate was only slightly different between calves infested or not by the winter tick, except for the periods 1990–1996 and 2009–2016 (Table 2.3). The winter tick prevalence was highly variable (Table 2.3). Mean winter tick load increased with time (except for a decrease in 1990–1996 and 2009–2016), but never exceeded the threshold of severe infestation (35,000 ticks/moose). Winter tick did not affect the survival rates of yearlings and adults or the reproductive rates (Table 2.3).

Hunting mortality and dispersal are sex-biased

Hunting mortality increased with time for all sex and age classes (Table 2.3). The survival rates during autumn (i.e. hunting season) were lower and decreased more for males than for females and calves. The number of moose entering the park each year increased with time (Table 2.3). They were mainly female, with more yearlings than adults. Overall, the number of moose leaving the park each year also increased with time, except for a decrease in 2009–2016. Indeed, the scenarios with positive density dependence in dispersal were more supported than those with negative density dependence in dispersal, except for the period 2009–2016 (Table 2.2). Males were proportionately more numerous to emigrate than females, and yearling males accounted for the higher number of emigrants.

Table 2.3: Mean values of the vital rates and some environmental parameters from the selected simulation for each subperiod. The selected simulation is the one for which the weighted deviation between the observed and simulated values of our three patterns is smallest. The 95% confidence intervals are shown in parentheses. For each vital rate in the "winter/spring survival" and "reproduction" sections, the first line indicates the "gross value"; the line "*after winter tick*" indicates the value of the vital rate after considering the effect of winter tick; and the line "*after density dependence*" indicates the "final value" after taking into account the effect of winter tick AND the effect of moose density. A "-" indicates that the value is identical to that of the line above.

	Time period				
	1982–1989	**1990–1996**	**1997–2008**	**2009–2016**	**2017–2019**
Survival					
Winter/spring (*end of hunting season – May 31st*)					
Calves not infested by winter tick	0.76 (0.01)	0.62 (0.01)	0.63 (0.01)	0.79 (0.01)	0.69 (0.02)
after density dependence	-	-	0.59 (0.01)	0.72 (0.01)	0.59 (0.02)
Calves infested by winter tick	0.77 (0.01)	0.54 (0.01)	0.64 (0.01)	0.68 (0.01)	0.66 (0.01)
after density dependence	-	-	0.59 (0.01)	0.59 (0.01)	0.55 (0.01)
Yearling females	0.99 (0.00)	0.96 (0.00)	0.96 (0.00)	0.95 (0.00)	0.91 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	0.95 (0.00)	0.92 (0.00)	0.84 (0.00)
Yearling males	0.98 (0.00)	0.97 (0.00)	0.96 (0.00)	0.95 (0.00)	0.91 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	-	0.92 (0.00)	0.84 (0.00)
Adult females	0.93 (0.00)	0.95 (0.00)	0.96 (0.00)	0.97 (0.00)	0.90 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	-	0.95 (0.00)	0.81 (0.00)
Adult males	0.97 (0.00)	0.96 (0.00)	0.95 (0.00)	0.95 (0.00)	0.91 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	0.94 (0.00)	0.92 (0.00)	0.84 (0.00)
Summer (*June 1st – start of hunting season*)					
Proportion of calves killed by predators	0.65 (0.00)	0.55 (0.00)	0.30 (0.00)	0.35 (0.00)	0.25 (0.00)
Combined kill rate (calves/predator/year)	0.67 (0.02)	0.42 (0.01)	0.47 (0.01)	1.04 (0.02)	0.44 (0.02)
Total summer survival of calves (*predation + vehicle collisions*)	0.33 (0.00)	0.45 (0.00)	0.69 (0.00)	0.64 (0.00)	0.74 (0.00)

Yearling females (*vehicle collisions*)	1.00 (0.00)	1.00 (0.00)	0.99 (0.00)	0.99 (0.00)	1.00 (0.00)
Yearling males (*vehicle collisions*)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
Adult females (*vehicle collisions*)	1.00 (0.00)	0.99 (0.00)	0.98 (0.00)	0.99 (0.00)	0.99 (0.00)
Adult males (*vehicle collisions*)	1.00 (0.00)	1.00 (0.00)	0.99 (0.00)	0.99 (0.00)	1.00 (0.00)
Autumn (*hunting season*)					
Calves	0.98 (0.00)	0.98 (0.00)	0.98 (0.00)	0.95 (0.00)	0.95 (0.00)
Yearling females	1.00 (0.00)	1.00 (0.00)	0.99 (0.00)	0.98 (0.00)	0.97 (0.00)
Yearling males	0.99 (0.00)	1.00 (0.00)	0.92 (0.00)	0.91 (0.00)	0.86 (0.00)
Adult females	0.98 (0.00)	0.98 (0.00)	0.99 (0.00)	0.98 (0.00)	0.96 (0.00)
Adult males	0.94 (0.00)	0.96 (0.00)	0.92 (0.00)	0.91 (0.00)	0.86 (0.00)
Annual					
Calves not infested by winter tick	0.26 (0.00)	0.26 (0.01)	0.46 (0.01)	0.50 (0.00)	0.40 (0.00)
Calves infested by winter tick	0.26 (0.00)	0.24 (0.01)	0.46 (0.01)	0.43 (0.00)	0.40 (0.00)
Yearling females	1.00 (0.00)	0.96 (0.00)	0.93 (0.00)	0.90 (0.00)	0.81 (0.00)
Yearling males	0.99 (0.00)	0.96 (0.00)	0.89 (0.00)	0.83 (0.00)	0.71 (0.00)
Adult females	0.92 (0.00)	0.92 (0.00)	0.94 (0.00)	0.93 (0.00)	0.78 (0.00)
Adult males	0.93 (0.00)	0.92 (0.00)	0.87 (0.00)	0.83 (0.00)	0.72 (0.00)
Reproduction					
Parturition rate of yearling females	0.19 (0.01)	0.18 (0.01)	0.17 (0.01)	0.15 (0.01)	0.00 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	0.16 (0.01)	0.00 (0.00)	-
Parturition rate of adult females	0.74 (0.01)	0.75 (0.01)	0.80 (0.00)	0.77 (0.01)	0.60 (0.01)
after density dependence	-	-	0.79 (0.00)	0.69 (0.00)	0.53 (0.01)
Twinning rate	0.22 (0.01)	0.20 (0.01)	0.22 (0.01)	0.29 (0.01)	0.01 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	0.21 (0.01)	0.20 (0.01)	0.00 (0.00)
Immigration					
Yearling females (no. individuals/year)	0.50 (0.03)	1.04 (0.04)	4.62 (0.07)	6.89 (0.10)	7.19 (0.15)
Yearling males (no. individuals/year)	0.29 (0.03)	0.95 (0.04)	0.96 (0.03)	1.74 (0.03)	2.99 (0.05)
Adult females (no. individuals/year)	0.12 (0.02)	0.74 (0.04)	3.65 (0.05)	5.14 (0.10)	5.77 (0.14)

Adult males (no. individuals/year)	0.20 (0.03)	1.18 (0.04)	0.47 (0.03)	0.97 (0.03)	2.03 (0.06)
Proportion of yearling female immigrants[1]	0.10 (0.01)	0.15 (0.01)	0.24 (0.01)	0.14 (0.00)	0.19 (0.01)
Proportion of yearling male immigrants[1]	0.05 (0.01)	0.16 (0.01)	0.08 (0.00)	0.04 (0.00)	0.09 (0.00)
Proportion of adult female immigrants[1]	0.00 (0.00)	0.01 (0.00)	0.03 (0.00)	0.02 (0.00)	0.02 (0.00)
Proportion of adult male immigrants[1]	0.01 (0.00)	0.03 (0.00)	0.01 (0.00)	0.01 (0.00)	0.01 (0.00)
Emigration					
Yearling females (no. individuals/year)	1.41 (0.03)	0.71 (0.03)	2.04 (0.08)	0.00 (0.00)	5.56 (0.22)
Yearling males (no. individuals/year)	1.63 (0.03)	1.57 (0.03)	6.52 (0.25)	0.39 (0.04)	6.13 (0.24)
Adult females (no. individuals/year)	3.00 (0.00)	1.09 (0.02)	0.96 (0.04)	1.00 (0.07)	4.63 (0.11)
Adult males (no. individuals/year)	2.13 (0.02)	1.01 (0.01)	2.19 (0.05)	0.40 (0.04)	4.05 (0.09)
Proportion of yearling female emigrants	0.23 (0.00)	0.09 (0.00)	0.08 (0.00)	0.00 (0.00)	0.14 (0.00)
Proportion of yearling male emigrants	0.27 (0.00)	0.24 (0.00)	0.24 (0.00)	0.02 (0.00)	0.16 (0.00)
Proportion of adult female emigrants	0.06 (0.00)	0.02 (0.00)	0.01 (0.00)	0.00 (0.00)	0.01 (0.00)
Proportion of adult male emigrants	0.08 (0.00)	0.02 (0.00)	0.03 (0.00)	0.00 (0.00)	0.02 (0.00)
Environmental parameters					
Carrying capacity					
Distance to carrying capacity (requirements/availability ratio) at the end of the time period	0.18 (0.00)	0.23 (0.00)	0.70 (0.00)	1.07 (0.00)	0.54 (0.00)
Winter tick					
Prevalence (% of infested moose)	39	14	25	41	42
Tick load (no. ticks/moose)	830 (19)	309 (13)	3,843 (68)	2,713 (41)	5,059 (127)
Years of “severe” infestation (>35,000 ticks/moose)	None	None	None	None	None

[1] Calculated as the number of immigrants divided by the total number of individuals of this age- and sex-class in the Forillon National Park.

DISCUSSION

Our sex- and age-structured model, parameterized applying a pattern-oriented modeling strategy, successfully reproduced the observed dynamics of the moose population of the Forillon National Park over a 38-year period. It allowed us to disentangle the interactions between the different dynamics-driving factors and to highlight the biological mechanisms through which they influenced our high-density population over time in a system without wolves and in a protected area free of hunting and logging. Density-dependence played a key role in shaping the dynamics of this moose population through effects on both survival, reproduction and dispersal, which is in line with our initial hypotheses. Winter climate was also an important factor and alternately interacted with moose density and winter tick load. However, contrary to our hypotheses, the effect of winter tick was restricted to winter calf survival, while the influence of predation and hunting were higher than expected. The relative importance of these factors varied over time, as winter climate and predation appeared to have a greater influence before 2000 (i.e. when moose density was relatively low), while density dependence became the leading factor afterwards.

Moose density as the major factor, impacting survival, reproduction and dispersal

Mean winter survival rates of calves were within the range of values generally observed (Ballard et al., 1991; Keech et al., 2011; Ausilio et al., 2023), although they were lower than could be expected in an area without wolves (e.g. Gasaway et al., 1983; Jolicoeur & Crête, 1988). These survival rates were more variable and sensitive to winter severity and population density than adult survival rates, as reviewed by Gaillard et al. (2000). Mean winter survival rates of calves exhibited a negative density dependence, which is consistent with the results of other studies in which a high population density was associated with higher mortality due to malnutrition (Clutton-Brock et al., 1991; Boertje et al., 2009). Mean winter survival rates of yearlings and adults appeared relatively buffered against variations in winter conditions. Indeed, in large herbivores, the adult survival rate is known to be more stable than the other vital rates, probably because individuals prioritize body maintenance over any

other energy expenditure (Gaillard et al., 2000). However, mean winter survival rates of yearlings and adults decreased in 2017–2019. High-density populations are more sensitive to adverse climatic conditions because of decreased body condition (Coulson et al., 2001; Hansen et al., 2019), which could explain the low winter survival rates for all age classes between 2017 and 2019 when density was over 2.3 moose/km^2.

The reproductive rates of females were similarly high between the first three time periods. Considering the longer and snowier winters between 1990 and 1996, this suggests that when moose abundance is relatively low, reproductive rates can also be buffered against climatic variations, because females remain in good body condition. This was documented by several studies (Gaillard et al., 2000; Desforges et al., 2021). However, when moose abundance was close to the carrying capacity (as in the 2009–2016 and 2017–2019 periods), our model suggested that the parturition rate of yearling females decreased to zero while the twinning and adult parturition rates were reduced. This could indicate that females prioritize survival and maintenance of body condition at the expense of reproduction. This is supported by findings made by other research teams (Boertje et al., 2007; Gingras et al., 2014; Harris et al., 2021). Indeed, sufficiently restoring body fat reserves after calving at high population densities is more difficult due to increased food competition (Clutton-Brock and Coulson, 2002; Simard et al., 2010), so the probability of reproducing the next year may be reduced (Hamel et al., 2011).

Overall, emigration also increased with time, providing partial support to the hypothesis of a "positive density dependence in dispersal", but decreased during the 2009–2016 period. This suggests that, as moose abundance reached carrying capacity, dispersal may have become less advantageous than philopatry. This could be explained by a decrease in body condition resulting from competition for food, decreasing the likelihood of dispersing (Hjeljord, 2001). Alternatively, the high density of females in the area could provide an enhanced access to mates for males of younger age classes and incite them to stay in the park (Røed et al., 2002; Loe et al., 2009). McFarlane et al. (2022) observed a negative density dependence in dispersal in a caribou population and hypothesized that it was due to the presence of remnant patches of high-quality habitat, coupled with an adverse effect of roads.

Moreover, the park is considerably less disturbed than its surroundings (e.g. no hunting, snowmobiling or logging), which makes it attractive for moose despite food competition.

All this evidence was consistent with moose having reached their carrying capacity (i.e. ~3.2 moose/km²). This estimate is in line with the conclusions of Crête (1989), and with recent observations of similar moose densities in the neighbouring region of Bas-St-Laurent (Desgagnés et al., 2022). Our results also suggest that the composition of moose forage in metabolizable energy and nitrogen is fairly balanced in our study region. Studies on other cervids (e.g. *Rangifer*: Barboza and Parker, 2008; Barboza et al., 2018) consistently reported that forage nitrogen is more limiting than energy, in particular during lactation. Parker et al. (2005) speculated that this might not be the case for all north-temperate cervids because the lichens consumed by reindeer and caribou in winter have a much higher energy : protein ratio than more commonly used forage species. Other authors reported more energy-limited (or balanced) diets in winter for several temperate ungulates (Hobbs et al., 1982; Parker et al., 1999). As for the summer season, digestible-energy-based estimates for the summer range carrying capacity for moose in Rocky Mountain National Park (Colorado) were 34% lower than nitrogen-based estimates (Dungan et al., 2010), which is similar to our findings.

Predation as an important source of calf mortality due to high bear density

The proportion of calves killed annually by predators was high in our model (between 25 and 65%) when compared to other studies conducted in areas free of wolves, where moose calf predation is usually < 30% (Boer, 1987; Musante et al., 2010). However, such high values are not unique, as predation rates as high as 70% were observed in caribou populations in the presence of black bears and coyotes (Lewis et al., 2017). This suggests that, despite the black bear being an opportunistic predator for moose, its relatively high density in the park may have resulted in a high calf mortality via a high encounter rate. In addition, the combined kill rate and moose abundance doubled in 2009–2016 (with respect to their values in 1997–2008) while the density of predators remained stable between the 1997–2008 and 2009–2016 periods, which can be interpreted as the probability to kill calves increasing

proportionally to the probability of encounter. Black bears are known to eat more animal prey in early summer, when moose calves are available, before shifting to a mostly plant-based diet later in the summer (Merkle et al., 2017; McLaren et al., 2021). Nevertheless, researchers have noted a great variation in bear diet between individuals, with some individuals "specialized" on mammal prey (Bastille-Rousseau et al., 2011; Edwards et al., 2011; Rioux et al., 2022). Coyotes may have accounted for a significant part of the calf mortality, although they are less abundant in the area than bears. Unfortunately, our model was not able to accurately partition the number of calves killed between these two predators. Indeed, when the black bear kill rate decreased, the associated calf mortality was automatically attributed to coyotes, with kill rates remaining within realistic ranges of values according to the literature. Thus, while predation rates were high at our population scale, the kill rates were low when compared to those observed in other studies for predation on young ungulates by black bears (Ballard, 1992; Rayl et al., 2018) and coyotes (Benson et al., 2017). In addition, implementing a maximum value for the predation rate made us unable to confirm or reject our hypothesis of a slight decline in coyote density after 2015, because 1) a small change in the coyote density no longer influenced the proportion of dying calves, and 2) as mentioned above, the mortality caused by coyotes could not be distinguished from that due to bears.

Winter conditions influence vital rates differently over time

Different scenarios were selected depending on the time period, indicating that the way in which winter conditions influenced the vital rates changed over time, with potential evidence of a carryover effect. Our model clearly identified a 1-year lag in the effect of winter conditions on reproductive rates for the 1982–1989, 1990–1996 and 2009–2016 periods. Several studies conducted on ungulates found such a negative correlation between female fecundity and snow accumulation or persistence in the winter preceding gestation (Mech et al., 1987; Post and Stenseth, 1999; Garroway and Broders, 2007). The associated biological mechanism would be the difficulty of females to sufficiently restore their body fat reserves during summer (especially if they are lactating), redirecting the resources to self-maintenance and inducing a reproductive pause (Clutton-Brock et al., 1989; Parker et al., 2009). Such a

mechanism could have been at play for the 1990–1996 period when winters were relatively snowy, and the snow melted relatively late. However, for 2009–2016, when winters were milder, the capacity of females to reach a body condition sufficient for gestation could have been constrained by intraspecific competition, considering the very high moose densities. In contrast, in 1997–2008 and 2017–2019, the selected scenarios suggested no carryover effect of winter on reproduction, which could appear counter-intuitive regarding the very snowy and long winters of 2017, 2018 and 2019. However, scenarios with a carryover effect of winter conditions on winter calf survival were strongly selected for this time period, suggesting that instead of impacting the ability of females to conceive, severe winter conditions during gestation led to lighter or weaker newborns, which were less likely to survive their first winter. This phenomenon was described in several studies (Adams, 2005; Lamb et al., 2023).

Limited effect of winter tick on population dynamics suggests low tick load in the area

The simulations with the smallest deviation for each time period consistently displayed low mean tick loads. This is consistent with the findings of several authors; at high latitudes, in areas where winters are long (i.e. shorter seasons for questing larvae and decreased probability of egg-laying for adult female ticks), moose tick load is limited by climate and expected to be low, unless moose densities become high (> 1 moose/km²; Samuel, 2007; Dunfey-Ball, 2017). Nevertheless, we believe that our estimates are biased downward, since it is unlikely that a tick load of only 300 ticks/individual caused such a difference in winter survival rate between infested and non-infested calves in 1990–1996. We conclude that our model was more efficient at estimating the effect of tick infestation on moose vital rates than the winter tick load itself. Our results also suggest that the survival rates of infested and non-infested calves were only slightly different, except in the periods 1990–1996 and 2009–2016. Regarding the period 2017–2019, this slight difference is supported by recent observations made by a research team that compared the survival rates of moose calves treated vs. untreated with acaricides in different regions of Quebec (V. Bonin-Palardy, *unpublished data*). They noted that Forillon National Park was among the regions with the smallest

differences between the survival rates of treated and untreated calves. The higher disparity in survival between infested and non-infested calves for the periods 1990–1996 and 2009–2016 can reflect an interaction between tick load and winter climate or density. Indeed, tick-induced self-grooming, hair damage and blood loss can cause a decrease in body condition of infested calves, and make them more sensitive to severe winter conditions (for 1990–1996) or density effects (for 2009–2016), as was documented in several studies (Samuel, 2004; Musante et al., 2007; Ellingwood et al., 2019).

Sex-biased dispersal and hunting shape moose sex ratio

Our model used different dispersal rates between males and females to explain the variations in moose sex ratio between time periods. According to our model, males were more susceptible to disperse in all periods. This is in accordance with the mating strategy typically observed in mammals, where local mate competition, inbreeding avoidance and female mate choice often lead to a male-biased dispersal (Greenwood, 1980; Lawson Handley and Perrin, 2007). Our model also suggested that immigration was mainly composed of females, a finding consistent with the fact that females constituted the major part of the population outside the park: indeed, moose sex ratio in the hunting zone n°1 fell from 0.53 in 2000 to 0.20 in 2017 (Landry and Lavergne, 2007; Dorais and Lavergne, 2017). Females may have used the park as a "refuge" from hunting or other human disturbances, as was observed in other studies (Coppes et al., 2017; Sergeyev et al., 2022). Moreover, as moose density increased, hunting around the park likely further contributed to this bias in sex ratio, as it removed 12% of the males annually from 2017 to 2019.

Limitations and potential research avenues

Having to fix the values of 63 parameters to meet the conditions for use of the POM method may appear as an obvious limit of our study, as it may have constrained the model from exploring combinations of parameter values that include values near the extremes of the ranges. However, fixing 63 parameter values substantially improved the success rates for

all time periods, and the minimum deviations were slightly lower than when we did not use fixed parameters for 3 time periods. One could still argue that we used POM to first estimate 63 parameter values before using it a second time with the remaining 20 variables. However, we consider it a relevant exploratory phase that allowed us to confirm 1) which parameters could be fixed without overly reducing the model's explanatory capacity, and 2) the values to be used, instead of fixing them arbitrarily. Building our model with fewer than 20 variables from the start would have resulted in a less complex model, certainly less explanatory and useful for population managers. Moreover, our results with 83 unfixed parameters were remarkably similar to those with 20 unfixed parameters (see Appendix 2.6). It may thus be valuable to explore more quantitatively under which conditions and with which gain the POM method can be used to estimate more than 20 parameters at a time.

Using the POM method did have some shortcomings: due to scarce data, the parameter ranges to be explored were so wide that POM could always find an adequate combination to reproduce the observed patterns regardless of the value of certain parameters. This is the case of winter tick prevalence and winter tick load, whose values in successful simulations covered wide ranges of possible values for all time periods. This demonstrates the limited capacity of our model to estimate them. As mentioned above, this consideration may also be true for the kill rates of black bears and coyotes (which were used interchangeably by the model to kill a given proportion of calves), and to a certain extent for moose carrying capacity in the park (when taking into account the uncertainties around the values derived from the surveys, the observed moose abundance in 2017 could be reproduced with winter carrying capacities ranging from 2.5 to 5 moose/km^2; see also Appendix 2.10). Investigating how the kill rates vary with the relative densities of black bears, coyotes and moose would be useful for wildlife managers in such areas and for future model builders.

Finally, the validity of our results assumes that the data obtained via aerial surveys (and used as patterns to parameterize our model) are accurate. However, variations in the methods and timing of monitoring between the time periods may have caused a bias in some estimates (see Appendix 2.1). Furthermore, a recent study pointed out that the aerial inventory standards used since the 90s for moose in Quebec do have some weaknesses that might

compromise the precision of density estimates (Gagnon-Labrosse, 2022). Some of these weaknesses were corrected in the park's sampling protocols, so that the values derived from the surveys still provide useful orders of size for modelling.

Implications for management

On the practical level, our model is a tool that could support decision-making. Dividing it into 5 time periods allowed us to obtain several sets of parameters that describe different types of dynamics: "stable low-density population" (1982–1996), "growing moderate-density population" (1997–2008), "growing population near carrying capacity" (2009–2016) and "decreasing high-density population" (2017–2019). These sets of parameters could be used to forecast the population's evolution under different management scenarios. Our model could be adapted to other study areas or cervid species in Canada, provided that the modelers have the relevant data in hand (e.g. climate and hunting data, energy and nitrogen budget, etc.) and the computing capacity needed to perform a new parameterization. On the theoretical level, we provide new information about the biological mechanisms at play for ungulate populations in protected areas in the absence of their apical predator, which should be accounted for by managers for conservation planning.

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SUPPLEMENTARY INFORMATION

Appendix 2.1: Results and methodology of the aerial surveys.

The POM (*Pattern-oriented Modeling*) method involves several patterns observed in the field to build and/or parameterize a model: the latter is "structurally realistic" or correctly parameterized if it can reproduce all the patterns simultaneously (Grimm et al., 2005). In this study, we used the time series of abundance, sex ratio and recruitment rate of our moose population from 1982 to 2020 (obtained with 6 aerial surveys) as patterns in our POM process (Table A1).

Table A1: Results of the 6 aerial surveys performed in Forillon National Park between 1982 and 2020. These data were used as patterns to feed the POM procedure.

Year of the aerial survey	Moose abundance (80% CI)	Sex ratio M : F[1] (80% CI)	Recruitment rate (80% CI)
1982	147 (137 – 157)	0.38 (0.30 – 0.46)	0.56 (0.48 – 0.64)
1990	108 (100 – 115)	0.63 (0.54 – 0.72)	0.22 (0.13 – 0.31)
1997	137 (127 – 147)	0.77 (0.71 – 0.83)	0.21 (0.14 – 0.28)
2009	433 (411 – 453)	0.33 (0.29 – 0.37)	0.33 (0.29 – 0.37)
2017	842 (800 – 884)	0.49 (0.46 – 0.52)	0.26 (0.23 – 0.29)
2020	551 (409 – 854)	0.47 (0.43 – 0.51)	0.26 (0.22 – 0.30)

[1] Although the park is a protected area, the sex ratio of the moose population was always skewed towards females.

The 1982 and 1990 surveys were conducted using a helicopter in late January – early February. The entire park area was overflown in one session following equally spaced flight lines of 500 m to count and locate all the moose winter yards (Bujold et al., 1986; Argus Groupe-Conseil and Yves Garant Consultants, 1991). Two independent observers (one on each side of the aircraft) watched and transmitted data to a navigator who noted them on a map. In addition, they counted moose and identified the sex of each individual (using the presence or absence of the vulva patch) and attributed them to an age class (young or adult, based on the body size).

The 1997 and 2009 surveys were carried out in mid/late February (Comeau, 1997; Sigouin, 2009). Unlike previous surveys, they included three flights. During the first flight, the transects were sampled to localize the track networks in the snow using GPS (no count was made at that time). The next day, the second flight allowed to delineate moose winter yards, count moose and identify their sex and age class. The third flight had the sole objective of estimating the moose sightability rate using the double-count method, as described by Lahaise et al. (2010). This sightability rate (70±7%) was retrospectively applied to the results of the 1982 and 1990 surveys. The confidence intervals around the values of moose abundance are directly derived from the uncertainty around the sightability rate (e.g. for the survey of 1997, 137 + 7% is 147 moose, and 137 – 7% is 127 moose).

In 2017, the same methodology as in 1997 and 2009 was used, except that it was conducted by the MELCCFP in only one flight (Courtois, 1996; Sebbane et al., 2013), using the same sightability rate as the one applied in 1997 and 2009 (Sigouin, 2018).

The aerial survey of 2020 was conducted in early March (Sigouin and Samson, 2022). In this context, the sightability rate previously used was no longer adequate. Indeed, moose tend to decrease their movements and spend more time under canopy cover as the winter progresses and snow depth increases, which reduces the moose sightability rate when compared to early winter (early January to mid-February) estimates (Crête et al., 1986; Peterson and Page, 1993). Thus, a new sightability rate had to be estimated for this particular survey. Fifteen female moose had been radio-collared a few weeks before the survey, which allowed to use the proportion of resighted marked females as an adapted estimation of the sightability rate (47%). However, the low number of marked individuals led to a larger confidence interval on the sightability rate (±35%). Again, this uncertainty around the sightability rate was integrated in the calculation of the confidence interval around the value of moose abundance.

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Appendix 2.2: List of the 83 parameters estimated with the POM method, their range and associated equations.

Abbreviated name of the parameter	**Range of values**	**Explanation / associated equation**
Winter survival		
Basic equations		
$non\_infest\_calf_1$	[31 ; 37]	Survival rate of calves non-infested by winter tick = $1 - \exp((I^1 - non\_infest\_calf_1) / non\_infest\_calf_2)$
$non\_infest\_calf_2$	[5 ; 8]	
$infest\_calf_1$	[43 ; 49]	Survival rate of calves infested by winter tick = $1 - \exp((I_{bis}^1 - infest\_calf_1) / infest\_calf_2)$
$infest\_calf_2$	[8 ; 15]	
$yearling\_f_1$	[43.75 ; 49]	Survival rate of yearling females = $1 - \exp((I^1 - yearling\_f_1) / yearling\_f_2)$
$yearling\_f_2$	[6 ; 9.25]	
$yearling\_m_1$	[43.75 ; 49]	Survival rate of yearling males = $1 - \exp((I^1 - yearling\_m_1) / yearling\_m_2)$
$yearling\_m_2$	[6 ; 9.25]	
$senescent\_f_1$	[43.75 ; 49]	Survival rate of adult females = $1 - \exp((I^1 - senescent\_f_1) / senescent\_f_2)$
$senescent\_f_2$	[6 ; 9.25]	
$senescent\_m_1$	[43.75 ; 49]	Survival rate of adult males = $1 - \exp((I^1 - senescent\_m_1) / senescent\_m_2)$
$senescent\_m_2$	[6 ; 9.25]	

Winter tick		
$coef_{snowmelt}$	[0 ; 3]	Multipliers involved in the calculation of the suitability index for female tick survival[2]: $I_{tick} = coef_{snowmelt} * I_{snowmelt} + coef_{first\_snow} * I_{first\_snow} + coef_{moose\_density} * I_{moose\_density}$
$coef_{first\_snow}$	[0 ; 3 – $coef_{snowmelt}$]	
$coef_{moose\_density}$	/	$coef_{moose\_density} = 3 - coef_{snowmelt} - coef_{first\_snow}$
$tick_1$	[1,000 ; 5,000]	Mean winter tick load = $tick_1 * (\exp(I_{tick} / tick_2) - 1)$, where $tick_2 = 21/\log((45{,}000 / tick_1) + 1)$
prop_infested	[0 ; 70]	Winter tick prevalence (percentage of moose that are infested by winter tick)
mean_yf_tick	[0.05 ; 0.1]	Mean and standard deviation to be used (annually) in a normal distribution random sampling, which yields a number to be subtracted from the winter survival rate of yearling females, i.e. additive mortality due to winter tick. Conditional to the fact that the mean winter tick load has been > 35,000 for 2 consecutive years or more.
sd_yf_tick	[0 ; 0.05]	
mean_ym_tick	[0.05 ; 0.1]	Same for yearling males.
sd_ym_tick	[0 ; 0.05]	
mean_af_tick	[0.05 ; 0.1]	Same for adult females.
sd_af_tick	[0 ; 0.05]	
mean_am_tick	[0.05 ; 0.1]	Same for adult males.
sd_am_tick	[0 ; 0.05]	
Density dependence		
mean_nic_density	[0.02 ; 0.15]	Mean and standard deviation to be used (annually) in a normal distribution random sampling, which yields a number to be subtracted from the winter survival rate of non-infested calves, i.e. additive mortality due to density dependence. Conditional to the fact that the ratio moose requirements/browse availability is > 0.5.
sd_nic_density	[0 ; 0.05]	

mean_ic_density	[0.02 ; 0.15]	Same for infested calves. Conditional to the fact that the ratio moose requirements/browse availability is > 0.5.
sd_ic_density	[0 ; 0.05]	
mean_yf_density	[0.02 ; 0.15]	Same for yearling females. Conditional to the fact that the ratio moose requirements/browse availability is > thresh_KCC$_4$ (see below).
sd_yf_density	[0 ; 0.05]	
mean_ym_density	[0.02 ; 0.15]	Same for yearling males. Conditional to the fact that the ratio moose requirements/browse availability is > thresh_KCC$_4$ (see below).
sd_ym_density	[0 ; 0.05]	
mean_af_density	[0.02 ; 0.15]	Same for adult females. Conditional to the fact that the ratio moose requirements/browse availability is > thresh_KCC$_4$ (see below).
sd_af_density	[0 ; 0.05]	
mean_am_density	[0.02 ; 0.15]	Same for adult males. Conditional to the fact that the ratio moose requirements/browse availability is > thresh_KCC$_4$ (see below).
sd_am_density	[0 ; 0.05]	
Predation		
bear_kill_rt$_1$	[0.25 ; 1.5]	Kill rate of bears (i.e. no. moose calves killed per bear per day) = 1 – 1/exp(((moose density / bear density) – bear_kill_rt$_1$) / bear_kill_rt$_2$)
bear_kill_rt$_2$	[120 ; 950]	
bear_age	[0.60 ; 0.85]	Proportion of the bear population represented by adult bears (> 2 years old)
vuln_to_bears	[30 ; 90]	No. days during which moose calves can be preyed on by bears
coyote_kill_rt$_1$	[2 ; 8]	Kill rate of coyotes (i.e. no. moose calves killed per coyote per day) =
coyote_kill_rt$_2$	[300 ; 6,000]	1 – 1/exp(((moose density / coyote density) – coyote_kill_rt$_1$) / coyote_kill_rt$_2$)
vuln_to_coyotes	[180 ; 365]	No. days during which moose calves can be preyed on by coyotes

Reproduction		
Basic equations		
repro_y_1	[24 ; 28]	Parturition rate of yearling females = $1 - \exp((I^1 - \text{repro\_}y_1) / \text{repro\_}y_2)$
repro_y_2	[18 ; 22]	
repro_a_1	[39 ; 43]	Parturition rate of adult females = $1 - \exp((I^1 - \text{repro\_}a_1) / \text{repro\_}a_2)$
repro_a_2	[9 ; 14]	
twin_rt_1	[26 ; 31]	Twinning rate of adult females = $1 - \exp((I^1 - \text{twin\_}rt_1) / \text{twin\_}rt_2)$
twin_rt_2	[14 ; 19]	
Density dependence		
mean_abor_twin	[0.05 ; 0.2]	Mean and standard deviation to be used (annually) in a normal distribution random sampling, which yields a number to be subtracted from the twinning rate of adult females, i.e. decrease in litter size due to density dependence. Conditional to the fact that the ratio moose requirements/browse availability is > thresh_KCC_2 (see below).
sd_abor_twin	[0 ; 0.05]	
mean_abor	[0.05 ; 0.2]	Mean and standard deviation to be used (annually) in a normal distribution random sampling, which yields a number to be subtracted from the parturition rate of adult females, i.e. spontaneous abortion due to density dependence. Conditional to the fact that the ratio moose requirements/browse availability is > thresh_KCC_3 (see below).
sd_abor	[0 ; 0.05]	
Immigration		
mean_yf_immi	[0 ; 9]	The no. yearling females immigrating annually is estimated using a normal distribution (mean = mean_yf_immi; SD = sd_yf_immi).
sd_yf_immi	[0 ; 2.5]	
mean_ym_immi	[0 ; 4]	The no. yearling males immigrating annually is estimated using a normal distribution (mean = mean_ym_immi; SD = sd_ym_immi).
sd_ym_immi	[0 ; 1]	

mean_af_immi	[0 ; 7.5]	The no. adult females immigrating annually is estimated using a normal distribution (mean = mean_af_immi; SD = sd_af_immi).
sd_af_immi	[0 ; 2]	
mean_am_immi	[0 ; 3]	The no. adult males immigrating annually is estimated using a normal distribution (mean = mean_am_immi; SD = sd_am_immi).
sd_am_immi	[0 ; 1]	
Emigration		
Positive density dependence (PDD)		
yf_emi_1	[0.1 ; 0.95]	Yearling female emigration rate = exp((moose density + yf_emi_1) / yf_emi_2) – 1
yf_emi_2	[4 ; 30]	
ym_emi_1	[0.1 ; 0.95]	Yearling male emigration rate = exp((moose density + ym_emi_1) / ym_emi_2) – 1
ym_emi_2	[4 ; 25]	
af_emi_1	[0.1 ; 0.9]	Adult female emigration rate = exp((moose density + af_emi_1) / af_emi_2) – 1
af_emi_2	[8 ; 215]	
am_emi_1	[0.1 ; 0.9]	Adult male emigration rate = exp((moose density + am_emi_1) / am_emi_2) – 1
am_emi_2	[8 ; 205]	
Negative density dependence (NDD)		
yf_emi_1	[-2.75 ; -2]	Yearling female emigration rate = 1 – exp((moose density + yf_emi_1) / yf_emi_2)
yf_emi_2	[9 ; 11]	
ym_emi_1	[-3.5 ; -2.25]	Yearling male emigration rate = 1 – exp((moose density + ym_emi_1) / ym_emi_2)
ym_emi_2	[6 ; 9]	

af_emi_1	[-2.75 ; -2]	Adult female emigration rate = 1 – exp((moose density + af_emi_1) / af_emi_2)
af_emi_2	[40 ; 55]	
am_emi_1	[-3.5 ; -2.25]	Adult male emigration rate = 1 – exp((moose density + am_emi_1) / am_emi_2)
am_emi_2	[25 ; 40]	
Carrying capacity		
prop_bafi	[0 ; 1]	Proportion of balsam fir available to moose
DE_deci_S	[2.3 ; 3.3]	Digestible energy content (kcal/g – dry weight) of deciduous leaves in summer
DE_bafi	[2.7 ; 3.1]	Digestible energy content (kcal/g – dry weight) of balsam fir in both winter and summer
CP_deci_S	[5.75 ; 15]	Crude protein content (g/100g – dry weight) of deciduous leaves in summer
CP_bafi_S	[7.5 ; 10.2]	Crude protein content (g/100g – dry weight) of balsam fir needles in summer
DE_deci_W	[1.9 ; 3.3]	Digestible energy content (kcal/g – dry weight) of deciduous twigs in winter
CP_deci_W	[5.75 ; 7.8]	Crude protein content (g/100g – dry weight) of deciduous twigs in winter
CP_bafi_W	[7.5 ; 9.2]	Crude protein content (g/100g – dry weight) of balsam fir twigs in winter
mean_age_AF	[5 ; 12]	Mean age (in years) of adult females and males, respectively. Used to calculate their body weight and then their daily requirements in metabolizable energy and nitrogen.
mean_age_AM	[5 ; 12]	
$thresh\_KCC_2$	[0.5 ; 0.8]	Threshold value of the ratio moose requirements/browse availability above which density-dependent effects on the parturition rate of yearling females and the twinning rate occur.
$thresh\_KCC_3$	[$thresh\_KCC_2$; 0.9]	Threshold value of the ratio moose requirements/browse availability above which density-dependent effects on the parturition rate of adult females occur.
$thresh\_KCC_4$	[$thresh\_KCC_3$; 1]	Threshold value of the ratio moose requirements/browse availability above which density-dependent effects on winter survival rates of yearlings and adults occur.

[1] I is an index of winter severity, ranging from 12 to 32. It is calculated based on NIVA and date of snowmelt as follows. NIVA ranged approximately from 6,000 to 16,000 days-cm in our study area between 1982 and 2020. We thus obtained a scale from 6 to 16 by dividing NIVA by 1,000. Date of snowmelt ranged from May 14th to June 9th in our study area between 1982 and 2020. We divided the total number of days separating these dates (27 days) by the number of figures separating 6 and 16 (11) to put the date of snowmelt on the same scale as NIVA. This gave us around 2.45 days separating each figure from 6 to 16. We alternatively attributed a 2-day or 3-day period of time to each figure: e.g. if the date of snowmelt in the year *t* was May 16th, May 17th or May 18th, this part of the index was 7, but if the date of snowmelt was May 19th or May 20th, this part of the index was 8. The index I is thus the sum of scaled NIVA and scaled date of snowmelt.

I_{bis} is the same as I, but adapted to infested calves, involving mean winter tick load in the calculation. Mean winter tick load was put on the same scale as NIVA and date of snowmelt with a cross multiplication: scaled winter tick load = (winter tick load * 10)/45,000 + 6. I_{bis} is the sum of scaled NIVA, scaled date of snowmelt and scaled winter tick load, and ranges from 18 to 48.

[2] I_tick (i.e. the suitability index for female tick survival) is used to estimate winter tick abundance in the park (and thus winter tick load on moose) annually based on weather and moose density. It ranges from 0 to 21, and is composed of $I_{snowmelt}$, I_{first_snow} and $I_{moose\_density}$. The higher is I_tick value, the higher will be winter tick load.

$I_{snowmelt}$ indexes the date of snowmelt in the spring previous of the winter during which moose mortality is occurring (i.e. winter tick load in the winter of year *t* depends on the survival rate of adult female winter ticks in the spring of year *t-1*). The scale is from 0 to 7 with a weekly time step, with 0 corresponding to a snowmelt after May 8th, and 7 to a snowmelt before March 23rd.

I_{first_snow} indexes the date of first snow in the autumn previous of the winter during which moose mortality is occurring (i.e. winter tick load in the winter of year *t* depends on the length of larvae questing period in the autumn of year *t-1*). The scale is from 0 to 7 with a weekly time step, with 0 corresponding to a first snow before October 23rd, and 7 to a first snow after December 8th.

$I_{moose\_density}$ indexes the moose density in the area. The scale is from 0 to 7 with growing intervals as moose density increases (following Samuel, 2004, 2007; Dunfey-Ball, 2017; Healy et al., 2020). A value of 0 corresponds a moose density < 0.2/km², while a value of 7 corresponds to a moose density > 2.6/km².

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Appendix 2.3: Variations in the density of twigs (no./ha) between 1995 and 2015 in Forillon National Park.

The density of twigs (no./ha) of saplings (11–90 mm in DBH, i.e. diameter at breast height) and trees (DBH > 90 mm) was assessed in 38 sample plots of 400 m² randomly distributed in the park in 1995, and was re-evaluated in 2006 in 35 of these same plots (3 of them could not be accurately relocated). In 2015, 61 additional plots were added to the first 38, for a total of 99 sample plots, and the surveys were repeated over 5 years (from 2015 to 2019). DBH, density of twigs (no./ha) and basal area were determined on living trees and on dead trees that were still standing. The trees were measured in the entire 400 m² plots (11.28 m in radius), while the saplings were measured in 40 m² subplots (3.57 m in radius) at the center of each 400 m² plot. Targeted species were balsam fir (*Abies balsamea*), striped maple (*Acer pensylvanicum*), red maple (*Acer rubrum*), sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*), white birch (*Betula papyrifera*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), balsam poplar (*Populus balsamifera*), quaking aspen (*Populus tremuloides*) and eastern white cedar (*Thuja occidentalis*). White and black spruce and eastern white cedar are not commonly eaten by moose (Routledge & Roese, 2004; Desgagnés et al., 2022), and considering that no evidence of browsing on these species was found in our study area, we discarded these species from our subsequent analyses. We also removed balsam poplar, which we considered a negligible source of forage for moose in our study area because this species was only found in 1 sample plot in 1995 and 2006, and in 3 plots in 2015.

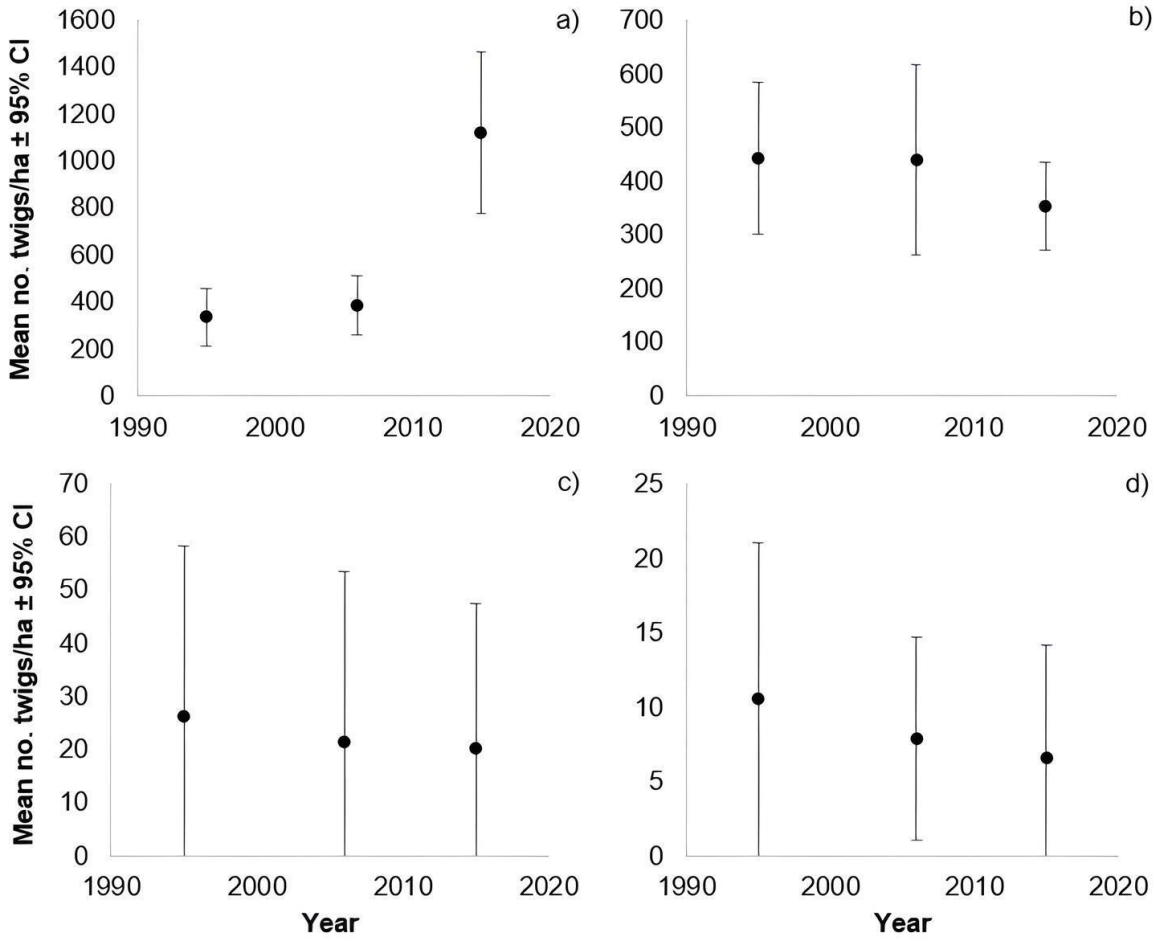

Figure A1: Variation of mean density of twigs (no./ha) between 1995 and 2015 in Forillon National Park for two tree species and height classes commonly eaten by moose: a) balsam fir saplings; b) balsam fir trees; c) striped maple saplings; d) striped maple trees.

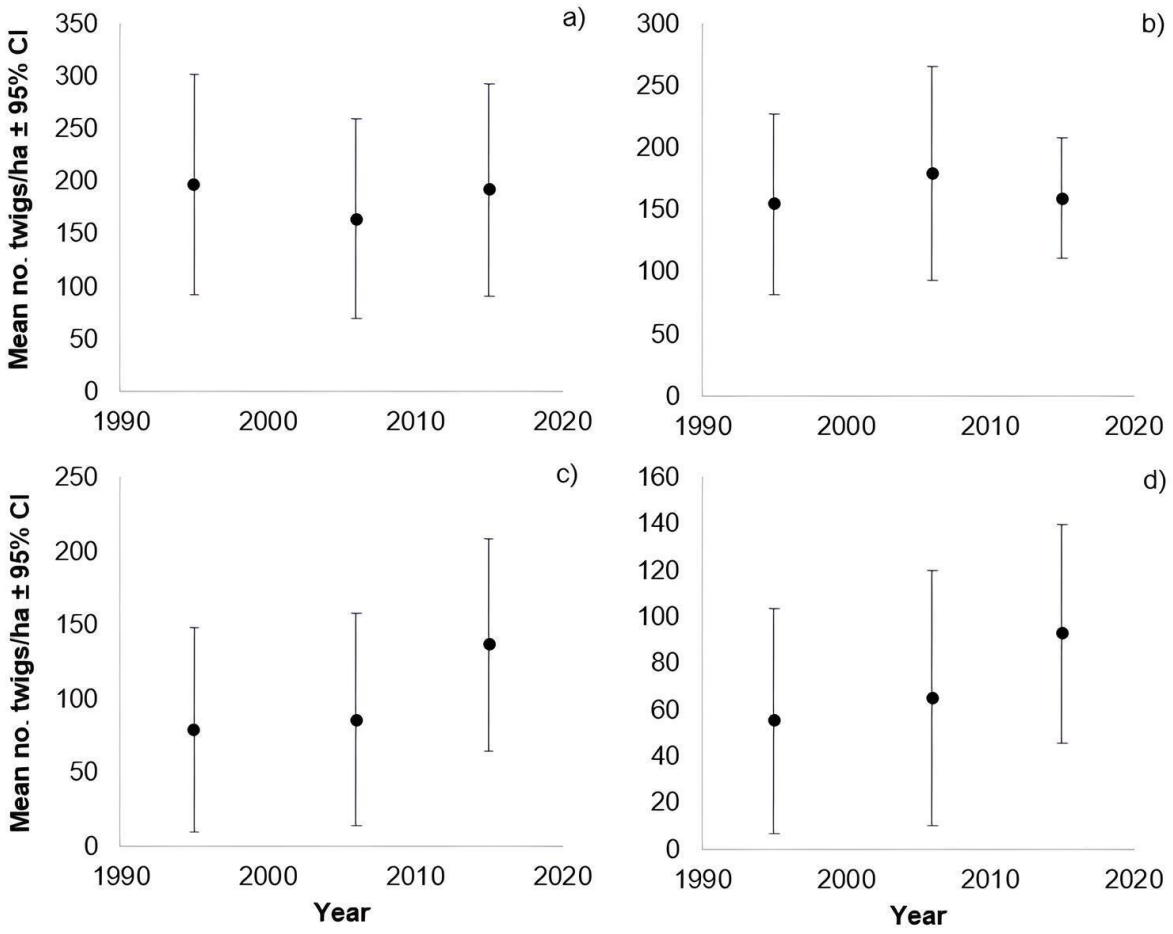

Figure A2: Variation of mean density of twigs (no./ha) between 1995 and 2015 in Forillon National Park for two tree species and height classes commonly eaten by moose: a) red maple saplings; b) red maple trees; c) sugar maple saplings; d) sugar maple trees.

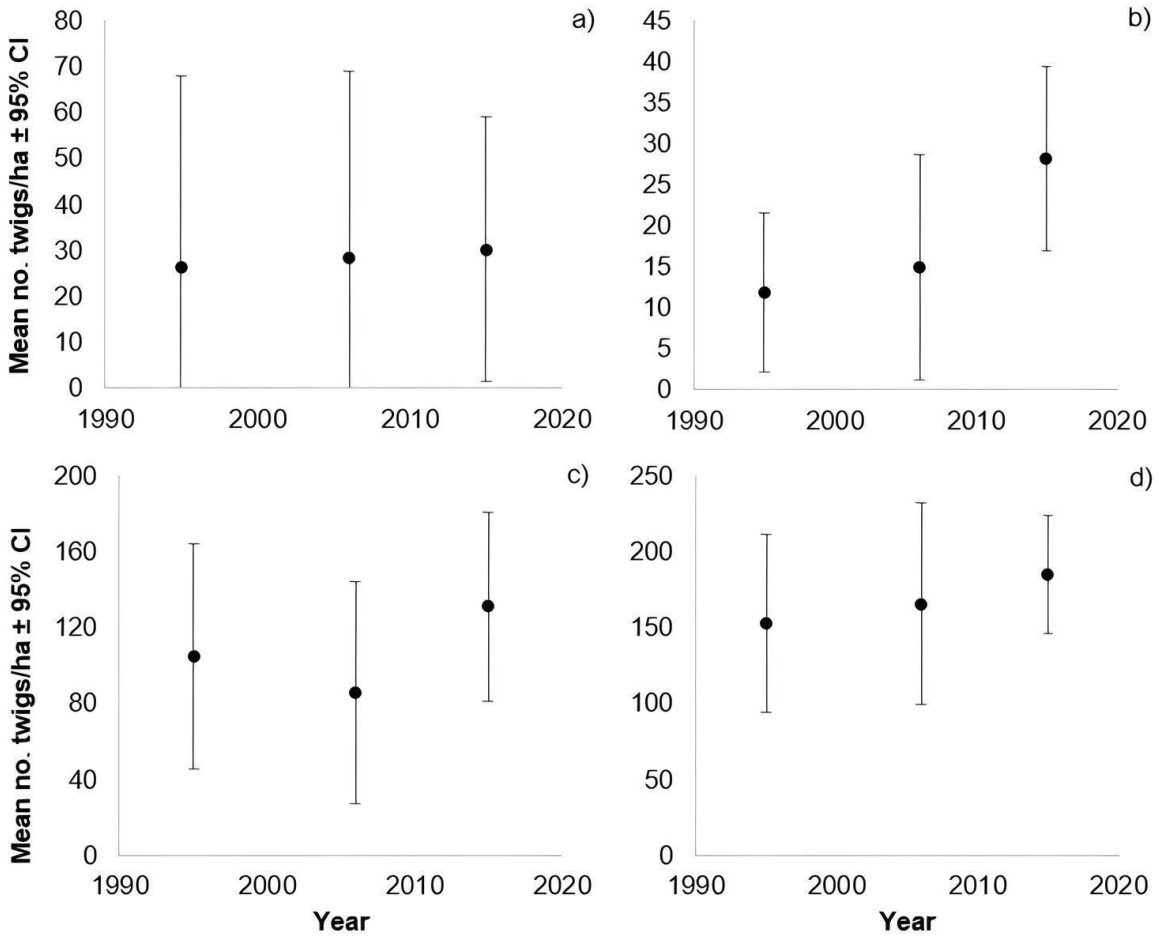

Figure A3: Variation of mean density of twigs (no./ha) between 1995 and 2015 in Forillon National Park for two tree species and height classes commonly eaten by moose: a) yellow birch saplings; b) yellow birch trees; c) white birch saplings; d) white birch trees.

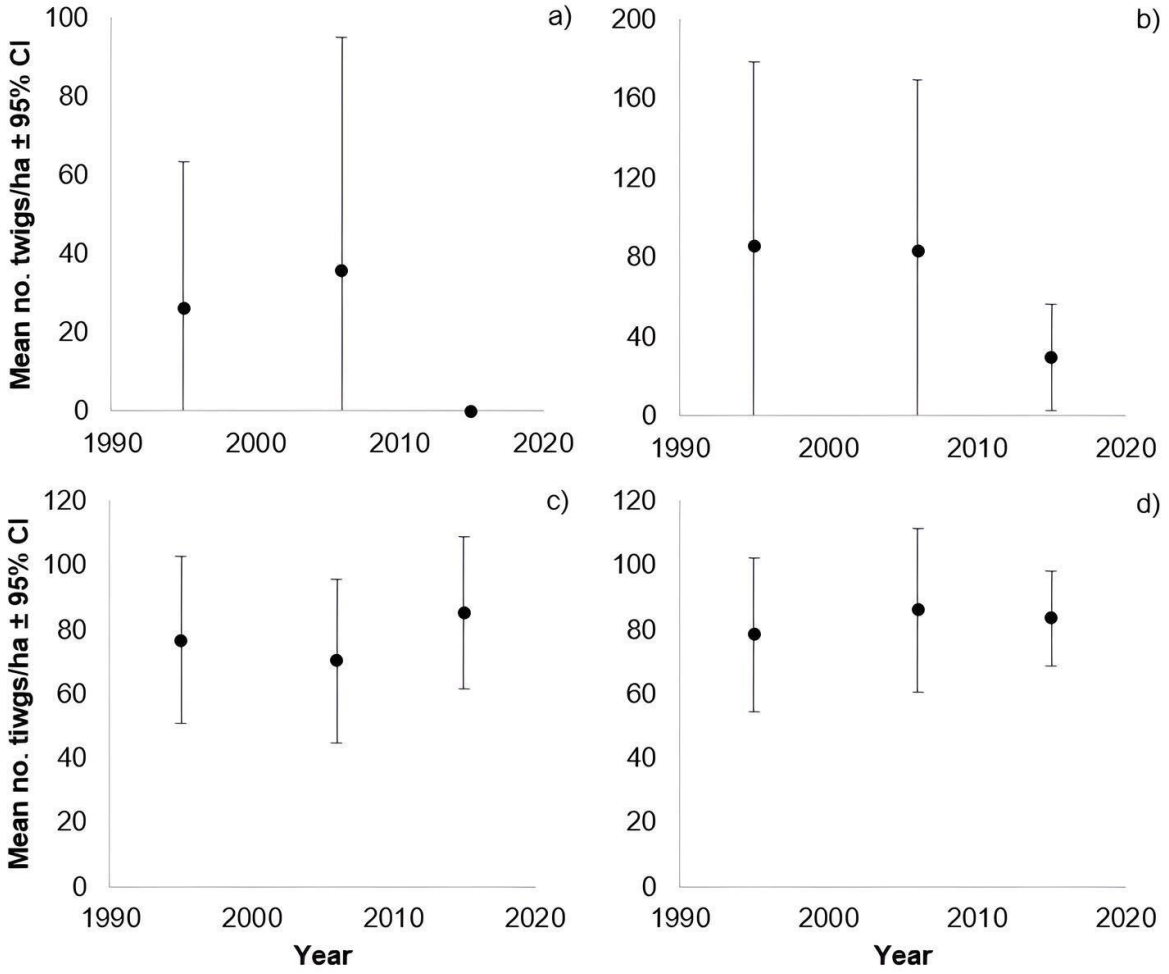

Figure A4: Variation of mean density of twigs (no./ha) between 1995 and 2015 in Forillon National Park for several tree species and height classes commonly eaten by moose: a) quaking aspen saplings; b) quaking aspen trees; c) all the deciduous species together (saplings); d) all the deciduous species together (trees).

We sought to perform one-way ANOVAs in order to compare the means of the no. twigs/ha between the surveys, but the assumption of normal distribution of the residuals was not met in our data. We thus performed nonparametric tests (Wilcoxon tests) instead. We found a (marginally) significant increase in the density of twigs (no./ha) for balsam fir saplings between 1995 and 2015 (W = 1,491.5; *P*-value = 0.054). This difference of production seems to be mainly explained by some outliers, i.e. 11 sample plots out of 99 in 2015 had values over 3,000 twigs/ha, as illustrated in the following boxplot (Figure A5).

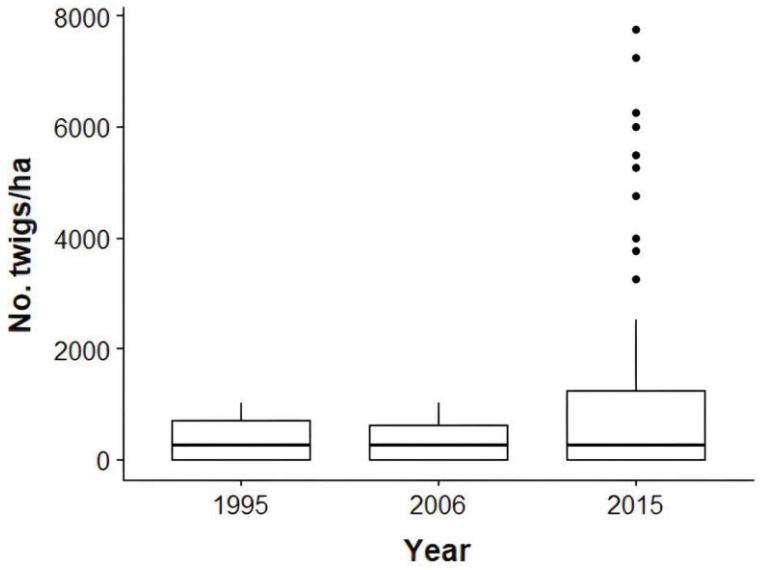

Figure A5: Boxplot of the distribution of the number of twigs/ha for balsam fir saplings in sample plots in 1995, 2006 and 2015 in Forillon National Park.

Moreover, we found a significant decrease in the number of twigs/ha for striped maple trees between 1995 and 2015 (W = 2,077; *P*-value = 0.046) and between 2006 and 2015 (W = 1,981; *P*-value = 0.011). Finally, the number of twigs/ha for quaking aspen saplings also significantly decreased between 1995 and 2015 (W = 1,980; *P*-value = 0.023) and between 2006 and 2015 (W = 1,831.5; *P*-value = 0.018). However, these differences did not influence the productivity of the 6 deciduous species taken all together, for saplings or for trees (see the panels c) and d) of Figure A4). Our calculation of the annual production in the model does not distinguish the amount of forage between the different deciduous species, and the observed differences in the number of twigs/ha are in the order of 5 twigs/ha for striped maple trees and 30 twigs/ha for quaking aspen saplings (Figures A1–4) compared to 700 twigs/ha for balsam fir saplings. Therefore, we decided not to account for the decrease of striped maple and quaking aspen forage between 2006 and 2015 in our model.

Appendix 2.4: Processing road mortality data.

We accessed two different databases synthesizing the number of moose killed annually on Highways 132 and 197 (Figure 2.1a) during our study period: 1) traffic accidents involving wildlife from the Ministère des Transports du Québec, which covered the years 1990–2016 and 2018–2020, and 2) carcass surveys for large mammals in the Forillon National Park (2015–2020). We took the greater of the two mortality values when they differed between the datasets.

The sex and age class of dead moose were only available in the carcass survey database of the Forillon National Park. Therefore, we summed the number of individuals killed between 2015 and 2020 separately for females older than 1 year old, males older than 1 year old and calves to be as accurate as possible regarding the effect of moose-vehicle collisions on the sex ratio and recruitment of our moose population. The percentage of all road mortalities represented by each of the three categories was 63% for females, 12% for males and 25% for calves. We compared these percentages with those calculated for the entire population using the aerial survey data of 2017, considering that the population structure did not change between this survey and the one conducted in 2020 (i.e. 57%, 28% and 15%, for females, males and calves, respectively). We concluded that females > 1 year old were involved in road accidents in the same percentage as their presence in the population (63% vs. 57%), but that males were less impacted (12% vs. 28%) and calves were more impacted (25% vs. 15%). In order to distribute the number of individuals killed on the road each year from 1990 to 2014 between the three categories, we multiplied this number by the percentage of females in the entire population (progressively updating it backwards in time using the results of the surveys from 1990, 1997 and 2009) and by the ratio 63/57=1.11, and rounded the result to the nearest integer. We repeated this process for males and confirmed the results with the calves.

Data were missing for the 1982–1989 period. Since the mortality was expected to be very low in these years compared to the size of the population, we explored the possibility of

extrapolating our values to this period by fitting models to our dataset for each category of individuals.

The most suitable model for females over 1 year old was a cubic equation (R^2=0.565, *P*-value=4.384e^{-05}; see Figure A6), which indicated that no females were killed in a collision with a vehicle between 1982 and 1989.

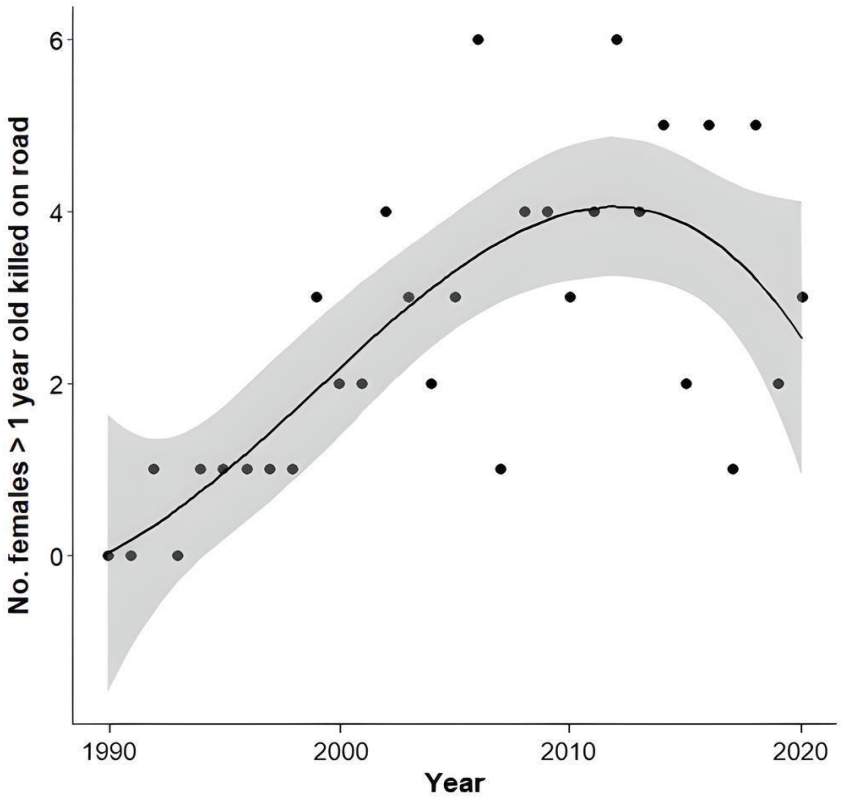

Figure A6: Number of females > 1 year old killed on Highways 132 and 197 between 1990 and 2020. Black points are the raw data, and the curve represents the fitted model (cubic equation).

The most adequate model for males over 1 year old was a logistic regression (AUC=0.765; see Figure A7) that was significantly different from the null model ($\chi_{2,1}$=6.837, *P*-value=0.009). It also suggested that no males died in a road accident between 1982 and 1989.

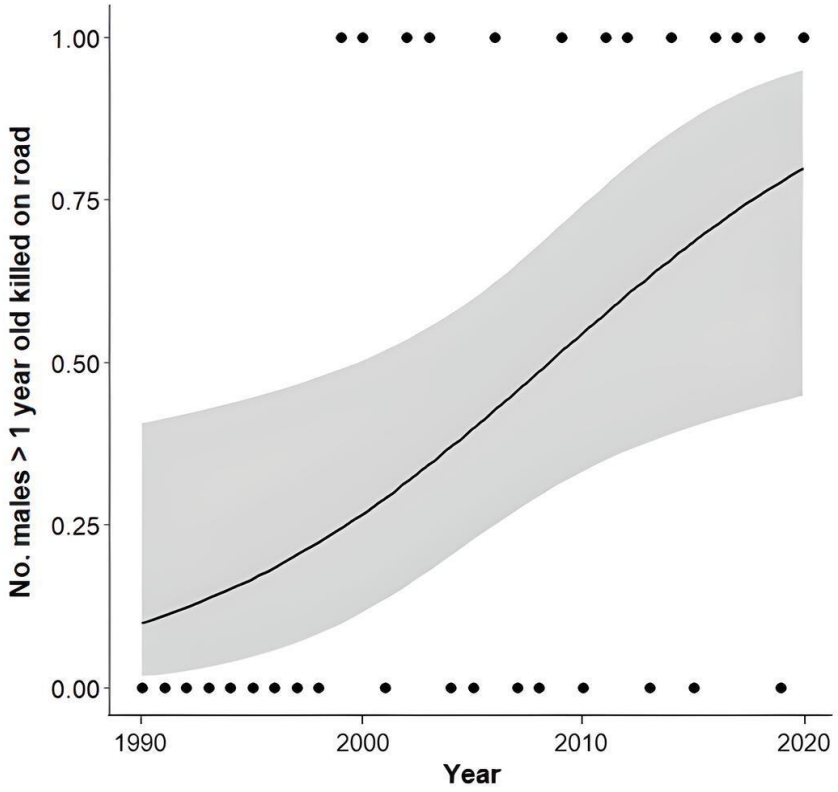

Figure A7: Number of males > 1 year old killed on Highways 132 and 197 between 1990 and 2020. Black points are the raw data, and the curve represents the fitted model (logistic regression).

Finally, the most appropriate model for calves was a cubic equation (R^2=0.470, *P*-value=0.001; see Figure A8) that suggests that 2 calves may have died in an accident in 1982, 1 calf per year died from 1983 to 1986, and 0 calves died in a road collision from 1987 to 1989.

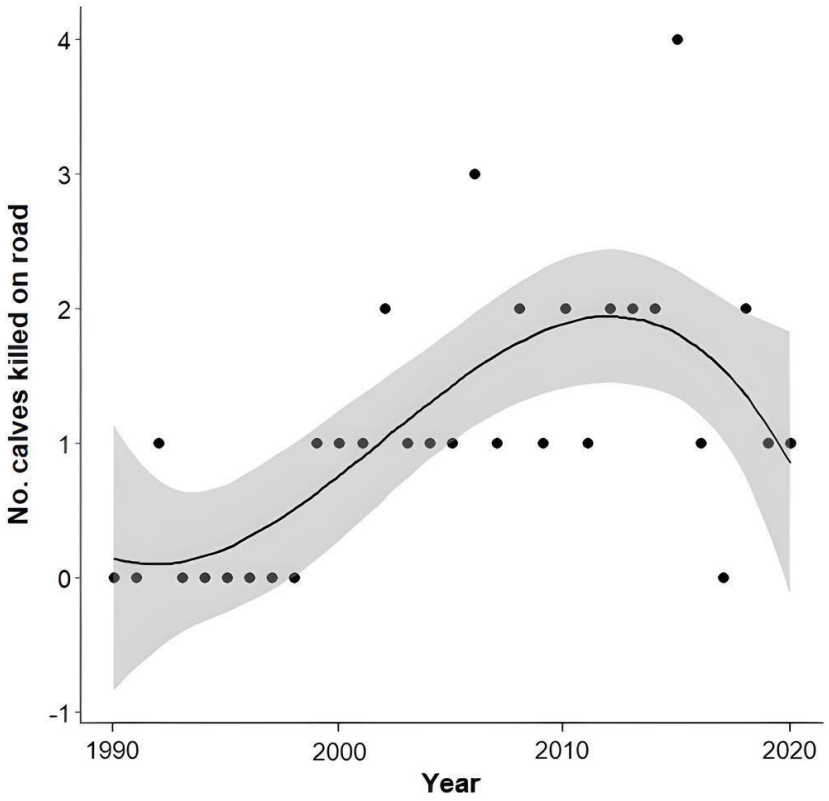

Figure A8: Number of calves killed on Highways 132 and 197 between 1990 and 2020. Black points are the raw data, and the curve represents the fitted model (cubic equation).

Appendix 2.5: Details about the stability of the results.

We mentioned in the section **Model parameterization** of our article that when determining the no. replicates to be used for the simulations of each time period, there was a remnant stochasticity in the moose abundance pattern for the last three periods (1997–2008, 2009–2016 and 2017–2019) whatever the no. replicates. For these cases, it may have led us to select the second- or third-closest parameter set to zero deviation because, for instance, the mean of the replicates was 434 moose for the 1997–2008 period for one replicate, but was closer to 437 moose the other times. However, the consequences of this on our results are very limited for two reasons. First, when a simulation was successful, and the associated results were saved, these results corresponded exactly to *the* time that this parameter set produced *this* deviation between simulated and observed patterns. Therefore, even if the value of the moose abundance pattern giving the minimum deviation cannot be reproduced afterwards with the corresponding parameter set, the results that we present in our Table 2.3 do correspond to the minimum deviation that could be obtained. Second, the combinations of values for the vital rates for which the deviation between simulated and observed patterns is close to 0 are very similar (i.e. with differences of one centimal place here and there). Thus, while the results presented in Table 2.3 may not perfectly minimize the deviation between simulated and observed patterns, they are very close to what the best combination would have been.

For this reason, and as mentioned in the last paragraph of the section **Model parameterization**, increasing the no. simulations to exceed 10,000 successful parameter sets and perhaps find a slightly lower deviation value would not have changed the results meaningfully.

Appendix 2.6: Results without fixing parameters.

Table A2: Mean values of the vital rates and some environmental parameters from the selected simulation for each subperiod. The selected simulation is the one for which the weighted deviation between the observed and simulated values of our three patterns is smallest. The 95% confidence intervals are shown in parentheses. For each vital rate in the "winter/spring survival" and "reproduction" sections, the first line indicates the "gross value"; the line "*after winter tick*" indicates the value of the vital rate after considering the effect of winter tick; and the line "*after density dependence*" indicates the "final value" after taking into account the effect of winter tick AND the effect of moose density. A "-" indicates that the value is identical to that of the line above.

	Time period				
	1982–1989	**1990–1996**	**1997–2008**	**2009–2016**	**2017–2019**
Survival					
Winter/spring (*end of hunting season – May 31st*)					
Calves not infested by winter tick	0.73 (0.01)	0.70 (0.01)	0.70 (0.01)	0.80 (0.01)	0.64 (0.02)
after density dependence	-	-	0.68 (0.01)	0.78 (0.01)	0.50 (0.02)
Calves infested by winter tick	0.71 (0.01)	0.60 (0.01)	0.65 (0.01)	0.66 (0.01)	0.61 (0.02)
after density dependence	-	-	0.60 (0.01)	0.54 (0.01)	0.46 (0.02)
Yearling females	0.94 (0.00)	0.95 (0.00)	0.99 (0.00)	0.95 (0.00)	0.93 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	0.97 (0.00)	0.92 (0.00)	0.85 (0.00)
Yearling males	0.94 (0.00)	0.97 (0.00)	0.94 (0.00)	0.95 (0.00)	0.96 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	0.91 (0.00)	0.94 (0.00)	0.88 (0.00)
Adult females	0.92 (0.00)	0.94 (0.00)	0.95 (0.00)	0.96 (0.00)	0.93 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	0.94 (0.00)	0.95 (0.00)	0.83 (0.00)
Adult males	0.96 (0.00)	0.96 (0.00)	0.95 (0.00)	0.94 (0.00)	0.93 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	0.93 (0.00)	0.90 (0.00)	0.87 (0.00)

Summer (*June 1st – start of hunting season*)					
Proportion of calves killed by predators	0.57 (0.00)	0.60 (0.00)	0.28 (0.00)	0.25 (0.00)	0.30 (0.00)
Combined kill rate (calves/predator/year)	0.54 (0.01)	0.53 (0.02)	0.53 (0.01)	0.68 (0.02)	0.58 (0.02)
Total summer survival of calves (*predation + vehicle collisions*)	0.38 (0.00)	0.40 (0.00)	0.71 (0.00)	0.74 (0.00)	0.69 (0.00)
Yearling females (*vehicle collisions*)	1.00 (0.00)	1.00 (0.00)	0.99 (0.00)	0.99 (0.00)	1.00 (0.00)
Yearling males (*vehicle collisions*)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)	1.00 (0.00)
Adult females (*vehicle collisions*)	1.00 (0.00)	0.99 (0.00)	0.99 (0.00)	0.99 (0.00)	0.99 (0.00)
Adult males (*vehicle collisions*)	1.00 (0.00)	1.00 (0.00)	0.99 (0.00)	0.99 (0.00)	1.00 (0.00)
Autumn (*hunting season*)					
Calves	0.98 (0.00)	0.98 (0.00)	0.98 (0.00)	0.94 (0.00)	0.95 (0.00)
Yearling females	1.00 (0.00)	1.00 (0.00)	0.99 (0.00)	0.98 (0.00)	0.97 (0.00)
Yearling males	0.97 (0.01)	0.99 (0.00)	0.92 (0.00)	0.91 (0.00)	0.86 (0.00)
Adult females	0.98 (0.00)	0.98 (0.00)	0.99 (0.00)	0.98 (0.00)	0.97 (0.00)
Adult males	0.94 (0.00)	0.96 (0.00)	0.92 (0.00)	0.91 (0.00)	0.87 (0.00)
Annual					
Calves not infested by winter tick	0.32 (0.01)	0.27 (0.01)	0.51 (0.01)	0.58 (0.01)	0.33 (0.00)
Calves infested by winter tick	0.31 (0.00)	0.23 (0.01)	0.48 (0.00)	0.48 (0.00)	0.32 (0.00)
Yearling females	0.95 (0.00)	0.94 (0.00)	0.95 (0.00)	0.90 (0.00)	0.80 (0.00)
Yearling males	0.91 (0.01)	0.96 (0.01)	0.84 (0.00)	0.85 (0.00)	0.74 (0.00)
Adult females	0.91 (0.00)	0.91 (0.00)	0.92 (0.00)	0.92 (0.00)	0.78 (0.00)
Adult males	0.91 (0.00)	0.91 (0.00)	0.87 (0.00)	0.80 (0.00)	0.73 (0.00)
Reproduction					
Parturition rate of yearling females	0.20 (0.01)	0.19 (0.01)	0.17 (0.01)	0.16 (0.01)	0.00 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	0.12 (0.01)	0.00 (0.00)	-
Parturition rate of adult females	0.76 (0.01)	0.82 (0.01)	0.85 (0.00)	0.67 (0.01)	0.59 (0.01)
after density dependence	-	-	0.83 (0.00)	0.62 (0.01)	0.54 (0.01)

Twinning rate	0.24 (0.01)	0.32 (0.01)	0.25 (0.01)	0.22 (0.01)	0.00 (0.00)
after winter tick	-	-	-	-	-
after density dependence	-	-	0.23 (0.01)	0.15 (0.01)	-
Immigration					
Yearling females (no. individuals/year)	1.00 (0.00)	1.00 (0.02)	5.47 (0.08)	8.86 (0.09)	7.14 (0.12)
Yearling males (no. individuals/year)	0.03 (0.01)	0.45 (0.04)	0.90 (0.04)	2.10 (0.02)	2.37 (0.06)
Adult females (no. individuals/year)	0.08 (0.02)	0.78 (0.03)	2.63 (0.05)	5.28 (0.11)	5.73 (0.11)
Adult males (no. individuals/year)	0.28 (0.03)	0.21 (0.03)	0.00 (0.00)	0.90 (0.05)	1.75 (0.08)
Proportion of yearling female immigrants[1]	0.21 (0.01)	0.13 (0.00)	0.21 (0.01)	0.18 (0.00)	0.22 (0.01)
Proportion of yearling male immigrants[1]	0.01 (0.00)	0.06 (0.01)	0.06 (0.00)	0.06 (0.00)	0.09 (0.00)
Proportion of adult female immigrants[1]	0.00 (0.00)	0.01 (0.00)	0.02 (0.00)	0.02 (0.00)	0.02 (0.00)
Proportion of adult male immigrants[1]	0.01 (0.00)	0.00 (0.00)	0.00 (0.00)	0.01 (0.00)	0.01 (0.00)
Emigration					
Yearling females (no. individuals/year)	2.64 (0.08)	0.86 (0.02)	2.33 (0.08)	0.25 (0.02)	5.81 (0.29)
Yearling males (no. individuals/year)	2.10 (0.08)	1.43 (0.03)	7.77 (0.26)	0.48 (0.05)	5.64 (0.29)
Adult females (no. individuals/year)	3.00 (0.00)	1.58 (0.03)	1.00 (0.04)	1.00 (0.07)	5.75 (0.15)
Adult males (no. individuals/year)	2.88 (0.02)	1.00 (0.00)	2.99 (0.07)	0.50 (0.05)	4.97 (0.15)
Proportion of yearling female emigrants	0.31 (0.01)	0.11 (0.00)	0.07 (0.00)	0.01 (0.00)	0.17 (0.00)
Proportion of yearling male emigrants	0.22 (0.01)	0.18 (0.00)	0.24 (0.00)	0.02 (0.00)	0.16 (0.00)
Proportion of adult female emigrants	0.06 (0.00)	0.03 (0.00)	0.01 (0.00)	0.00 (0.00)	0.02 (0.00)
Proportion of adult male emigrants	0.11 (0.00)	0.02 (0.00)	0.04 (0.00)	0.01 (0.00)	0.03 (0.00)
Environmental parameters					
Carrying capacity					
Distance to carrying capacity (requirements/availability ratio) at the end of the time period	0.21 (0.00)	0.27 (0.00)	0.76 (0.00)	0.97 (0.00)	0.64 (0.01)
Winter tick					
Prevalence (% of infested moose)	30	19	65	42	11

Tick load (no. ticks/moose)	1,582 (35)	403 (9)	8,968 (234)	586 (5)	11,560 (55)
Years of “severe” infestation (>35,000 ticks/moose)	None	None	None	None	None

[1] Calculated as the number of immigrants divided by the total number of individuals of this age- and sex-class in the Forillon National Park.

Appendix 2.7: Results of the sensitivity analysis.

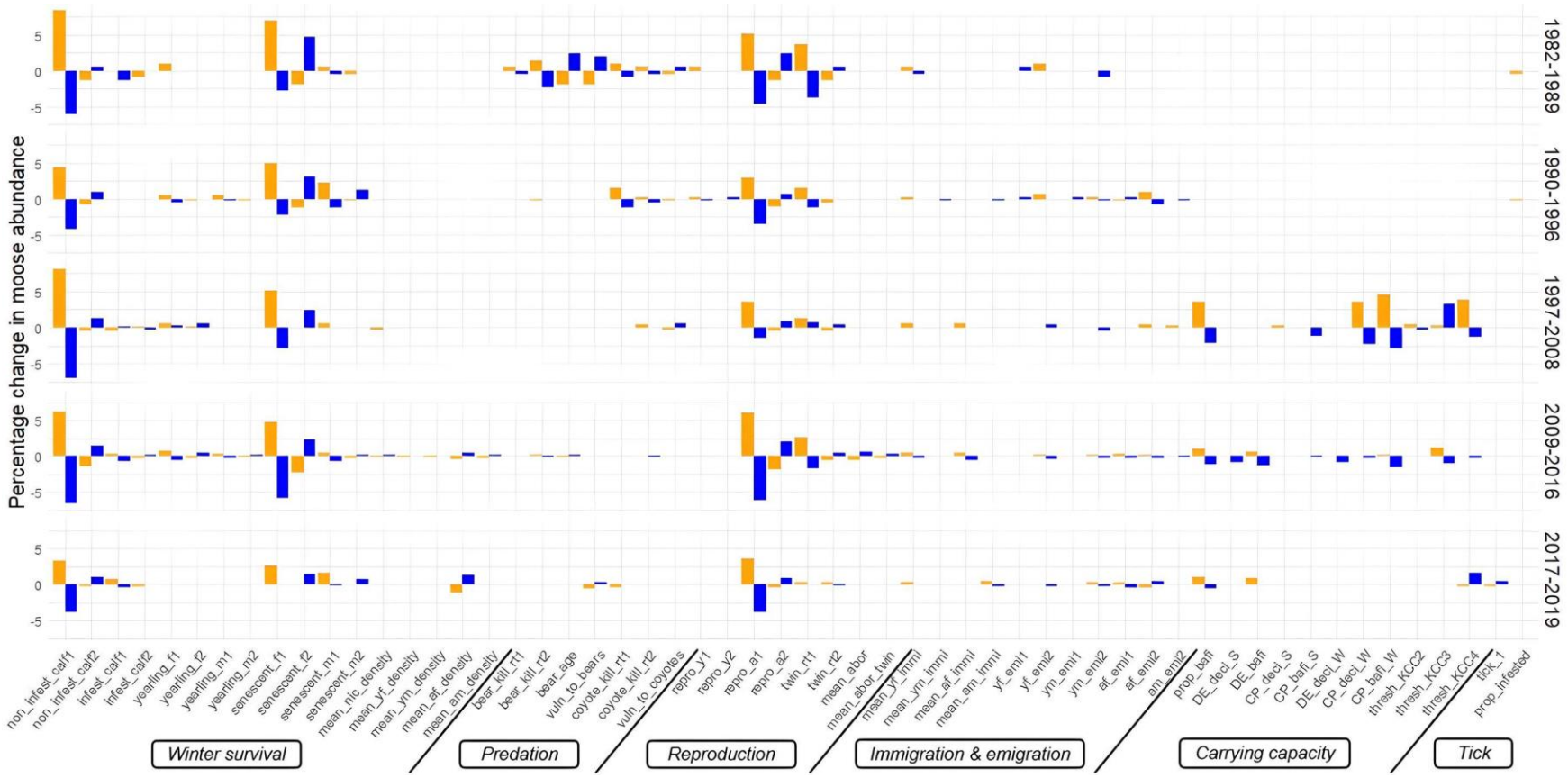

Figure A9: Response of moose abundance to a +5% (orange bars) and -5% (blue bars) change in parameter values (see Appendix 2.2 for a description of all the parameters on the x–axis). Only the parameters for which the effect on moose abundance was not zero are displayed.

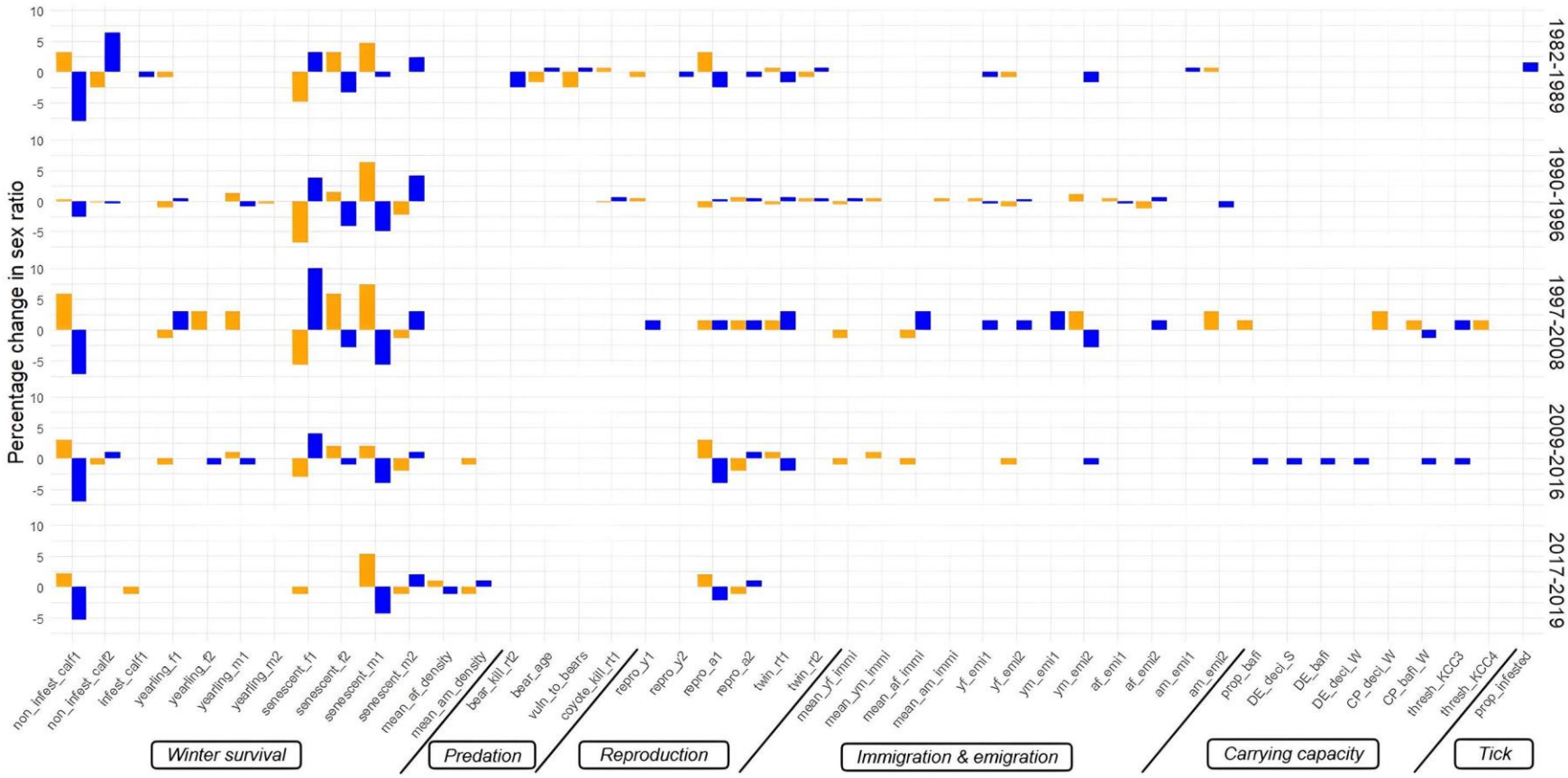

Figure A10: Response of moose sex ratio to a +5% (orange bars) and -5% (blue bars) change in parameter values (see Appendix 2.2 for a description of all the parameters on the x–axis). Only the parameters for which the effect on moose sex ratio was not zero are displayed.

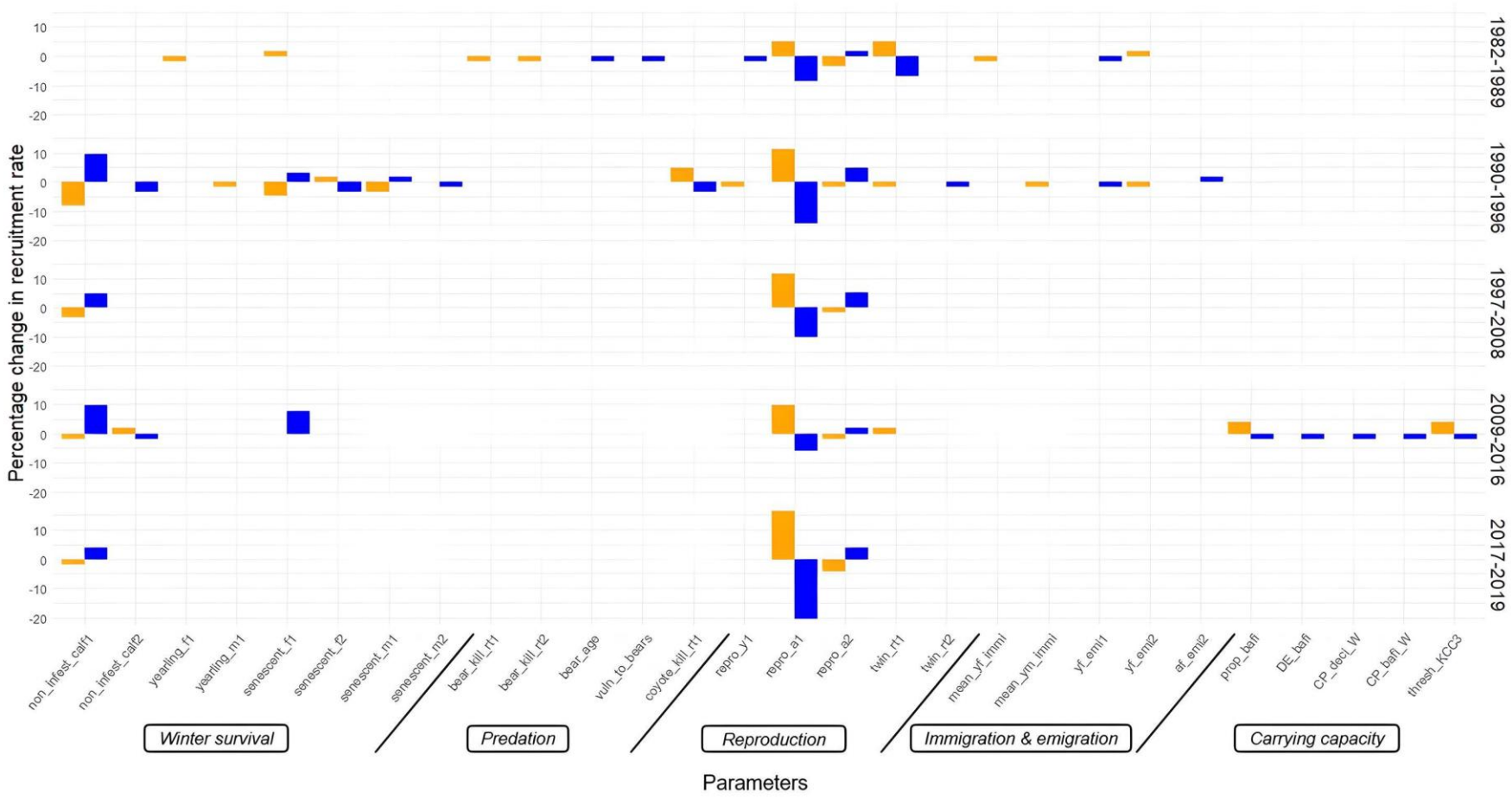

Figure A11: Response of moose recruitment rate to a +5% (orange bars) and -5% (blue bars) change in parameter values (see Appendix 2.2 for a description of all the parameters on the x–axis). Only the parameters for which the effect on moose recruitment rate was not zero are displayed.

Appendix 2.8: Summary of the fixed parameters and their values for each time period (from the scenario that yielded the smaller deviation). The "range" corresponds to the range of values that was explored with pattern-oriented modeling for each parameter (see Appendix 2.2 for a description of the parameters).

	Time period									
	1982–1989		**1990–1996**		**1997–2008**		**2009–2016**		**2017–2019**	
Abbreviated name of the parameter	**Range tested**	**Fixed value**	**Range tested**	**Fixed value**	**Range tested**	**Fixed value**	**Range tested**	**Fixed value**	**Range tested**	**Fixed value**
Winter survival										
Basic equations										
non_infest_calf$_1$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
non_infest_calf$_2$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
infest_calf$_1$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		[43;48]	45.6
infest_calf$_2$	*Not fixed*		*Not fixed*		[8;15]	11.8	*Not fixed*		*Not fixed*	
yearling_f$_1$	[43.75;48.5]	46.1	[44;49]	46.5	[44;49]	46.5	[44;49]	46.6	[44;49]	46.5
yearling_f$_2$	[6.5;9.25]	7.92	[6;9]	7.51	[6;9]	7.44	[6;9]	7.38	[6;9]	7.52
yearling_m$_1$	[43.75;48.5]	46.1	[44;49]	46.5	[44;49]	46.4	[44;49]	46.4	[44;49]	46.5
yearling_m$_2$	[6.5;9.25]	7.88	[6;9]	7.52	[6;9]	7.62	[6;9]	7.57	[6;9]	7.45
senescent_f$_1$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
senescent_f$_2$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
senescent_m$_1$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
senescent_m$_2$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
Winter tick										
coef$_{snowmelt}$	[0;3]	1.49	[0;3]	1.51	[0;3]	1.44	[0;3]	1.56	[0;3]	1.55
coef$_{first_snow}$	[0;3-coef$_{snowmelt}$]	0.75	[0;3-coef$_{snowmelt}$]	0.75	[0;3-coef$_{snowmelt}$]	0.76	[0;3-coef$_{snowmelt}$]	0.75	[0;3-coef$_{snowmelt}$]	0.76
coef$_{moose_density}$	/	0.76	/	0.74	/	0.80	/	0.69	/	0.69
tick$_1$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
prop_infested	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	

mean_yf_tick	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075
sd_yf_tick	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025
mean_ym_tick	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075
sd_ym_tick	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025
mean_af_tick	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075
sd_af_tick	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025
mean_am_tick	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075	[0.05;0.1]	0.075
sd_am_tick	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025
Density dependence										
mean_nic_density	[0.02;0.15]	0.085	[0.02;0.15]	0.085	[0.02;0.15]	0.097	[0.02;0.15]	0.078	[0.02;0.15]	0.096
sd_nic_density	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025
mean_ic_density	[0.02;0.15]	0.085	[0.02;0.15]	0.085	[0.02;0.15]	0.086	[0.02;0.15]	0.083	[0.02;0.15]	0.099
sd_ic_density	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025
mean_yf_density	[0.02;0.15]	0.085	[0.02;0.15]	0.085	[0.02;0.15]	0.084	[0.02;0.15]	0.077	[0.02;0.1]	0.075
sd_yf_density	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.04]	0.020
mean_ym_density	[0.02;0.15]	0.085	[0.02;0.15]	0.085	[0.02;0.15]	0.090	[0.02;0.15]	0.091	[0.02;0.1]	0.075
sd_ym_density	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.04]	0.020
mean_af_density	[0.02;0.15]	0.085	[0.02;0.15]	0.085	[0.02;0.15]	0.073	[0.02;0.15]	0.046	*Not fixed*	
sd_af_density	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.04]	0.020
mean_am_density	[0.02;0.15]	0.085	[0.02;0.15]	0.085	[0.02;0.15]	0.102	[0.02;0.15]	0.101	[0.02;0.1]	0.072
sd_am_density	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.04]	0.020
Predation										
bear_kill_rt$_1$	[0.25;1.5]	0.82	*Not fixed*		[0.5;1.5]	1.00	[0.5;1.5]	1.00	[0.5;1.5]	1.00
bear_kill_rt$_2$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
bear_age	[0.60;0.85]	0.73	[0.60;0.85]	0.73	[0.60;0.85]	0.72	[0.60;0.85]	0.73	[0.60;0.85]	0.73
vuln_to_bears	[30;90]	68.7	*Not fixed*		[30;90]	60.8	[30;90]	64.2	[30;90]	60.9

coyote_kill_rt$_1$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
coyote_kill_rt$_2$	[300;2,000]	954	[300;2,000]	1,120	[1,000;10,000]	5,290	[1,200;6,000]	3,600	[1,200;6,000]	3,580
vuln_to_ coyotes	[180;365]	281	*Not fixed*		[180;365]	274	[180;365]	272	[180;365]	272
Reproduction										
Basic equations										
repro_y$_1$	*Not fixed*		[24;28]	26.0	[24;28]	26.0	[24;27.5]	25.7	[24;27.5]	25.7
repro_y$_2$	[18.5;21.25]	19.9	[18;22]	20.0	[18;22]	20.0	[18.5;22]	20.2	[18.5;22]	20.2
repro_a$_1$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
repro_a$_2$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*	
twin_rt$_1$	*Not fixed*		*Not fixed*		*Not fixed*		*Not fixed*		[26;30.5]	28.3
twin_rt$_2$	*Not fixed*		[14;19]	16.6	[14;19]	16.6	[14.5;19]	16.7	[14.5;19]	16.7
Density dependence										
mean_abor_ twin	[0.05;0.2]	0.125	[0.05;0.2]	0.125	[0.05;0.2]	0.128	[0.05;0.2]	0.124	[0.05;0.2]	0.124
sd_abor_twin	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025
mean_abor	[0.05;0.2]	0.125	[0.05;0.2]	0.125	[0.05;0.2]	0.117	[0.05;0.2]	0.125	[0.05;0.17]	0.112
sd_abor	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025	[0;0.05]	0.025
Immigration										
mean_yf_ immi	*Not fixed*		[0;2]	1.01	[3;6]	4.63	[4;9]	6.97	[5.5;9]	7.24
sd_yf_immi	[0;0.7]	0.330	[0;1]	0.503	[1;2]	1.50	[1;2.5]	1.75	[1;2]	1.50
mean_ym_ immi	*Not fixed*		[0;2]	0.917	[0.5;1.5]	0.963	[1;2.5]	1.72	[2;4]	3.03
sd_ym_immi	[0;0.7]	0.341	[0;1]	0.494	[0;1]	0.498	[0;1]	0.500	[0;1]	0.502
mean_af_immi	[0;0.6]	0.244	[0;1.5]	0.729	[2;5]	3.62	[3;7]	5.22	[4;7.5]	5.69
sd_af_immi	[0;0.5]	0.226	[0;1]	0.502	[0.5;1.5]	1.00	[1;2.5]	1.75	[1;2]	1.50
mean_am_ immi	[0;0.6]	0.281	*Not fixed*		[0;1]	0.458	[0.5;1.5]	0.990	[1;3]	2.05
sd_am_immi	[0;0.5]	0.247	[0;1]	0.493	[0;1]	0.490	[0;1]	0.501	[0;1]	0.502

Emigration										
yf_emi$_1$	[0.5;0.95]	0.756	[0.1;0.85]	0.473	[0.1;0.3]	0.199	[-2.5;-2]	-2.25	[0.1;0.25]	0.175
yf_emi$_2$	*Not fixed*		[4;16]	9.98	[19;30]	24.7	[9;11]	10.0	[20;30]	24.9
ym_emi$_1$	[0.5;0.95]	0.735	[0.1;0.85]	0.483	[0.45;0.8]	0.646	[-3;-2.5]	-2.75	[0.15;0.40]	0.273
ym_emi$_2$	[4;8]	5.76	*Not fixed*		[9;13]	10.3	[6.5;9]	7.74	[18;28]	23.4
af_emi$_1$	[0.45;0.9]	0.690	[0.1;0.7]	0.400	[0.1;0.3]	0.201	[-2.5;-2]	-2.25	[0.1;0.3]	0.201
af_emi$_2$	[8;24]	15.3	[20;65]	42.2	[160;215]	188	[45;55]	50.0	[150;210]	180
am_emi$_1$	[0.5;0.9]	0.713	[0.1;0.7]	0.407	[0.45;0.7]	0.578	[-3;-2.5]	-2.75	[0.15;0.40]	0.274
am_emi$_2$	[8;26]	15.5	[20;65]	41.3	[55;100]	73.9	[30;40]	35.0	[100;180]	142
Carrying capacity										
prop_bafi	[0.05;0.08]	0.065	[0.05;0.08]	0.065	*Not fixed*		*Not fixed*		*Not fixed*	
DE_deci_S	[2,300;3,300]	2,800	[2,300;3,300]	2,800	[2,300;3,300]	2,800	[2,300;3,300]	2,790	[2,300;3,300]	2,800
DE_bafi	[2,700;3,100]	2,900	[2,700;3,100]	2,900	*Not fixed*		*Not fixed*		*Not fixed*	
CP_deci_S	[5.75;15]	10.3	[5.75;15]	10.4	[5.75;15]	10.3	[5.75;15]	10.4	[5.75;15]	10.4
CP_bafi_S	[7.5;10.2]	8.60	[7.5;10.2]	8.84	[7.5;10.2]	8.77	[7.5;10.2]	8.88	[7.5;10.2]	8.84
DE_deci_W	[1,900;3,300]	2,480	[1,900;3,300]	2,480	[1,900;3,300]	2,460	[1,900;3,300]	2,470	[1,900;3,300]	2,480
CP_deci_W	[5.75;7.8]	6.34	[5.75;7.8]	6.70	[5.75;7.8]	6.56	[5.75;7.8]	6.76	[5.75;7.8]	6.68
CP_bafi_W	[7.5;9.2]	7.84	[7.5;9.2]	8.17	*Not fixed*		*Not fixed*		*Not fixed*	
mean_age_AF	[5.75;12.75]	9.75	[5.75;12.75]	8.75	[5.75;12.75]	9.75	[5.75;12.75]	8.75	[5.75;12.75]	9.75
mean_age_AM	[5.75;12.75]	8.75	[5.75;12.75]	9.75	[5.75;12.75]	9.75	[5.75;12.75]	9.75	[5.75;12.75]	9.75
thresh_KCC$_2$	[0.5;0.8]	0.65	[0.5;0.8]	0.65	*Not fixed*		[0.5;0.8]	0.65	*Not fixed*	
thresh_KCC$_3$	[thresh_KCC$_2$;0.9]	0.77	[thresh_KCC$_2$;0.9]	0.78	*Not fixed*		*Not fixed*		*Not fixed*	
thresh_KCC$_4$	[thresh_KCC$_3$;1.0]	0.89	[thresh_KCC$_3$;1.0]	0.89	*Not fixed*		*Not fixed*		*Not fixed*	

Appendix 2.9: Evolution of the mean values of our indices of winter severity over time (95% confidence intervals are shown in brackets).

	Time period				
	1982–1989	**1990–1996**	**1997–2008**	**2009–2016**	**2017–2019**
Environmental parameters					
Winter weather					
NIVA index (days-cm)	10,736 (2,424)	12,381 (2,513)	10,928 (1,511)	10,586 (2,781)	15,009 (2,313)
Mean date of snowmelt	May 24th	May 30th	May 28th	May 25th	June 3rd

Appendix 2.10: Details about the proportion of balsam fir included in the calculation of carrying capacity.

Our model was not able to converge for the period 2009–2016 if the proportion of balsam fir available for moose to browse was beyond 10%. This could be due to an overestimation of the annual production (kg/ha) of balsam fir in our study area, or an underestimation of the decrease of the nutritional value of balsam fir caused by tannins (Windels and Hewitt, 2011). Moreover, this threshold value of 10% was conditional to a 100% browsing of the annual production of deciduous forage species, which is unlikely. Conversely, moose do not browse only on current-year growth. Several modelers took these reflections into account by testing several browse scenarios (Wolfe et al., 1983; Dungan et al., 2010; Smythe et al., 2019). We tested them, and some yielded a very low carrying capacity (< 0.1 moose/km²) while others resulted in impossible values (several thousand moose per km²). Thus, we would have had to add the associated parameters (e.g. maximum percentage of available deciduous browse) to those estimated with POM in order to keep these scenarios in our model structure. But considering the already complex structure of our carrying capacity module, it would have given additional ways for POM to combine parameter values, and our window of 2.5 to 5 moose/km² for the carrying capacity would have remained unchanged. Therefore, we kept this threshold value of 10% in our calculation.

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CONCLUSION GÉNÉRALE

RETOUR SUR LE CONTEXTE DE L'ÉTUDE

Les mécanismes biologiques qui gouvernent les variations spatiotemporelles d'abondance au sein des populations animales et végétales demeurent un vaste champ d'investigation, d'importance pour plusieurs autres domaines scientifiques (Alexander et al., 2012 ; Leopold, 2019 ; Krebs, 2020). Les paramètres démographiques (survie, recrutement et dispersion) qui déterminent la taille d'une population peuvent être influencés par divers facteurs environnementaux (Saether, 1997 ; Olsson et al., 2019 ; Canales et al., 2020). Dans le cas des populations de grands herbivores, les conditions climatiques hivernales et printanières, la compétition intra- et interspécifique, la maladie, le parasitisme, la prédation et la chasse sont les principaux facteurs qui, en modifiant la condition physique et l'état nutritionnel des individus, impactent la survie (Smith et al., 2006 ; Monteith et al., 2014 ; Bassi et al., 2020) et le recrutement (Budischak et al., 2018 ; Lukacs et al., 2018 ; Holmes et al., 2021). Quant à la dispersion, elle peut notamment être affectée par des changements dans le rapport des sexes, la structure d'âge ou la densité de la population, ainsi que par la qualité de l'habitat et les activités humaines (Bowler & Benton, 2005 ; Long et al., 2008 ; Beauchesne et al., 2013).

Ces connaissances sont essentielles en gestion de la faune, particulièrement lors de l'élaboration de modèles à visée rétrospective ou pour tester l'effet de différentes stratégies de gestion (McLane et al., 2011 ; Lacy, 2019 ; Niemuth et al., 2021). Ces derniers constituent un outil fréquemment employé pour la gestion de populations surabondantes (p. ex. Gogan et al., 2001 ; Raiho et al., 2015 ; Franklin et al., 2020). En effet, celles-ci ont le potentiel de perturber le fonctionnement des écosystèmes et d'en altérer la biodiversité (Brousseau et al., 2013 ; Dolman et al., 2010 ; Crystal-Ornelas et al., 2021), et peuvent présenter plusieurs autres risques pour les populations humaines (p. ex. propagation d'agents infectieux,

collisions avec des véhicules : Côté et al., 2004 ; Valente et al., 2020). Cela justifie la nécessité d'en effectuer un suivi attentif et d'élaborer des mesures de gestion adaptées (McLaren et al., 2004 ; Carpio et al., 2021). L'orignal (*Alces alces americana*) fait partie de ces espèces pour lesquelles des densités très élevées ont récemment été observées dans certaines zones d'Amérique du Nord (Sigouin, 2018 ; Desgagnés et al., 2022). De nombreux modèles de dynamique des populations ont été développés pour l'orignal, mais très peu parmi eux sont applicables dans une aire protégée, sans prélèvement ni aménagement forestier, et en l'absence du prédateur principal (le loup gris, *Canis lupus*).

RAPPEL DES OBJECTIFS ET DES PRINCIPAUX RÉSULTATS

Mon projet de maîtrise avait pour premier objectif d'identifier les facteurs environnementaux, ainsi que leurs interactions, qui régissent la dynamique d'une population d'orignaux vivant dans un tel contexte. Le second objectif était de développer un modèle de dynamique des populations adapté, utile à des fins de gestion. Mon cas d'étude était la population d'orignaux du Parc national Forillon, en Gaspésie (Québec, Canada), qui a connu une croissance rapide entre 1982 et 2017, passant de 0,6 orignaux/km² à 3,5/km². Mes hypothèses stipulaient que le climat, la compétition intraspécifique et le parasitisme expliqueraient la plus grande part de la variation dans la taille de la population d'orignaux, et que leur influence relative varierait dans le temps et selon la densité de la population. Mon approche méthodologique a consisté, sur la base d'une revue de littérature des facteurs environnementaux pertinents pour mon aire d'étude, à assembler ces facteurs (et leurs interactions probables) en un modèle qui en simulerait l'impact sur la population annuellement de 1982 à 2020. Un certain nombre de paramètres du modèle ont été calibrés grâce à la méthode de modélisation orientée par patrons (*Pattern-oriented Modelling* ; Grimm et al., 1996, 2005 ; Gallagher et al., 2021), en m'appuyant sur les séries temporelles d'abondance, de rapport des sexes et de taux de recrutement recueillies au cours de cette période dans le parc lors d'inventaires aériens. Cela m'a permis d'observer les liens existants entre la trajectoire de la population et l'intensité de chaque facteur, et d'identifier les combinaisons de paramètres reproduisant au plus près les données des inventaires.

L'utilisation de cette approche méthodologique m'a permis d'atteindre mes deux objectifs : une fois le modèle construit et l'étape de paramétrisation achevée, j'ai pu mettre en évidence les principaux mécanismes biologiques à l'œuvre dans mon système d'étude. La compétition intraspécifique a été le facteur le plus déterminant pour la dynamique de cette population. En effet, mes résultats suggèrent un effet négatif marqué de la densité sur le taux de survie à l'hiver pour toutes les catégories de sexe et d'âge, avec une magnitude d'effet croissante entre 1997 et 2019. Des effets de densité-dépendance sur la reproduction ont également été constatés, réduisant successivement le taux de mise bas des femelles d'un an, le taux de gémellité et le taux de mise bas des femelles adultes, à mesure que la densité de la population augmentait. La densité a aussi affecté les patrons de dispersion des orignaux : la proportion d'individus sortant du parc est restée à peu près constante au cours du temps pour chaque catégorie de sexe et d'âge, à l'exception d'une forte diminution dans les années où le niveau de population est devenu très proche de la capacité support. Tous ces effets négatifs de la densité sur les paramètres démographiques peuvent être attribués à une diminution de la condition corporelle des orignaux due une intensification de la compétition intraspécifique, tel qu'observé dans d'autres études (Hjeljord, 2001 ; Boertje et al., 2009 ; Harris et al., 2021). Cela est cohérent avec les indices de surbroutement relevés dans certaines zones du parc, dont la capacité de support nutritionnelle pour les orignaux, qui elle a été estimée à 3,5/km² en 2017.

La prédation par l'ours (*Ursus americanus*) et le coyote (*Canis latrans*) a eu un effet plus important qu'escompté sur la dynamique de la population, retirant entre 25 et 60% des veaux chaque année. Bien qu'en l'absence de loup les taux de prédation sur les veaux orignaux soient généralement inférieurs à 30% (Boer, 1987 ; Musante et al., 2010), des taux de prédation similaires aux nôtres (entre 40 et 70%) ont été observés dans des populations de caribous en présence d'ours et de coyotes (Leclerc et al., 2014 ; Lewis et al., 2017). Il est probable que la haute densité d'ours dans le parc (entre 0,20 et 0,54/km² pendant toute la durée de l'étude) ait favorisé une forte probabilité de rencontre avec les veaux, en particulier à la fin du printemps. En effet, les alternatives alimentaires sont encore peu nombreuses pour l'ours à cette période de l'année, ce qui peut les pousser à augmenter leur ingestion de

protéines animales (Merkle et al., 2017 ; McLaren et al., 2021). Il a malheureusement été impossible de déterminer quelle part de la mortalité des veaux par prédation était imputable au coyote. En effet, lors de la paramétrisation de mon modèle, une diminution de la proportion de veaux prédatés par l'ours noir se trouvait compensée par une augmentation de la proportion de veaux prédatés par le coyote et vice versa, et ce tout en gardant des taux de prédation réalistes du point de vue de la littérature.

Le climat hivernal avait un impact négatif marqué sur le taux de survie des veaux à l'hiver, mais pas sur la survie des adultes, excepté durant les hivers 2017, 2018 et 2019 qui ont été plus sévères et pendant lesquels la densité de la population était élevée. De plus, les scénarios sélectionnés par le modèle indiquent que, pour certaines périodes de temps, l'effet des conditions hivernales sur les taux de reproduction s'est fait sentir avec un délai d'un an. En effet, l'accumulation et/ou la persistance du couvert de neige durant l'hiver précédant la conception peut faire en sorte que les réserves corporelles des femelles soient si épuisées qu'elles n'aient pas le temps de les reconstituer complètement avant l'hiver suivant, causant une pause reproductrice (Clutton-Brock et al., 1989 ; Parker et al., 2009). Pour d'autres périodes de temps, les scénarios sélectionnés étaient plutôt en faveur d'un effet reporté des conditions hivernales sur la survie des veaux. Cela peut être expliqué par un impact négatif de la sévérité de l'hiver sur le poids des veaux à la naissance, diminuant leur probabilité de survie l'hiver suivant, comme cela a été constaté dans d'autres études (Adams, 2005 ; Lamb et al., 2023).

La tique d'hiver (*Dermacentor albipictus*) n'a pas eu d'effet marqué sur les taux de survie à l'hiver, sauf pour les veaux entre 1990 et 1996 (années durant lesquelles les hivers étaient en moyenne plus neigeux et le printemps plus tardif) et entre 2009 et 2016 (lorsque la densité de la population était à son niveau le plus élevé). Aucun impact négatif de la tique d'hiver sur les taux vitaux des individus âgés de plus d'un an n'a été décelé. Cela suggère que la charge de tiques à Forillon est restée suffisamment faible pour que son impact négatif sur la condition corporelle des orignaux se limite à une augmentation de la vulnérabilité des veaux infestés aux autres facteurs environnementaux (tels que le climat et la compétition intraspécifique : Musante et al., 2007 ; Ellingwood, 2018). Ces résultats sont cohérents avec

de récentes données montrant que la charge de tiques, de même que la prévalence, à Forillon sont parmi les plus bas de tout le Québec (Pouchet, 2023).

L'immigration d'un nombre croissant de jeunes femelles chaque année pendant toute la durée de mon étude, ainsi que l'émigration annuelle d'un certain nombre de mâles, ont constitué les principales sources de variation du rapport des sexes de la population du parc au cours du temps. En effet, la pratique de la chasse sportive a fortement biaisé le rapport des sexes de la population d'orignaux hors du parc (qui est passé de 0,53 mâle par femelle en 2000 à 0,20 en 2017 : Landry et Lavergne, 2007 ; Dorais et Lavergne, 2017). En plus de la pression de chasse, la forte occurrence d'autres activités humaines à l'extérieur du parc (p. ex. exploitation forestière, motoneige) a certainement contribué à la création d'un « effet refuge », où les femelles immigrantes étaient relativement dissuadées de ressortir du parc par tous ces dérangements (voir p. ex. Coppes et al., 2017 ; Sergeyev et al., 2022). L'impact direct de la chasse en périphérie du parc sur notre population semble s'être intensifié avec le temps et la hausse des densités : en effet, 12% des mâles du parc ont été tués chaque année de 2017 à 2019.

CONTRIBUTIONS THÉORIQUES ET APPLIQUÉES

Sur le plan théorique, mon étude apporte sa pierre à l'édifice de la compréhension de la dynamique des populations de grands herbivores, à travers l'exploration des facteurs limitants et régulateurs et des changements de magnitude d'effet de ces facteurs au cours du temps. L'un des aspects novateurs de mon étude a été de s'intéresser à une population de cervidés vivant à haute densité dans une aire protégée (donc sans prélèvement ni aménagement forestier) et en l'absence de son prédateur principal, le loup gris. J'ai montré que les effets de densité-dépendance jouent un rôle primordial dans ce contexte, avec la possibilité d'affecter négativement tous les taux vitaux. Selon mes résultats, l'azote n'est pas plus limitant pour l'orignal que l'énergie métabolisable dans notre région d'étude, suggérant une composition équilibrée du fourrage. J'ai aussi mis en évidence des interactions marquées entre la densité de population, le parasitisme par la tique d'hiver et les conditions climatiques

hivernales en ce qui concerne la survie des veaux. Mes résultats supportent ceux d'autres études selon lesquels l'impact des conditions climatiques hivernales sur les taux vitaux d'une population d'herbivores peut se manifester avec un délai d'un an (Crête & Courtois, 1997 ; Parker et al., 2009), et montrent de plus que ce délai peut concerner différents taux vitaux en alternance au cours du temps, en interaction avec la densité de population.

Contrairement à nos hypothèses de départ, l'effet de certains facteurs tels que la prédation par les prédateurs dits opportunistes (ours, coyote) et la chasse en périphérie de l'aire protégée n'est pas à négliger. Mes résultats montrent en effet que le pourcentage de veaux orignaux prédatés par an peut être supérieur à 30% (et atteindre 65%) même en l'absence du loup gris, si la densité de prédateurs opportunistes devient relativement élevée. De plus, à densité égale de prédateurs, le pourcentage de veaux tués par an peut augmenter si la densité d'orignaux augmente, reflétant une prédation opportuniste proportionnelle à la probabilité de rencontre. D'autre part, la chasse en périphérie du parc a eu un effet croissant sur la dynamique de la population, allant jusqu'à retirer en moyenne 12% des mâles adultes par an entre 2017 et 2019. Ce résultat souligne que malgré l'interdiction de la chasse à l'intérieur des aires protégées, les populations (en particulier leur rapport des sexes) peuvent tout de même être fortement impactées par la chasse à l'extérieur en raison de déplacements importants d'orignaux de part et d'autre des frontières des aires protégées. À ce titre, mes résultats soutiennent ceux obtenus dans d'autres études selon lesquelles, dans le cas de l'orignal, les mâles constituent la plus grande part des individus émigrants (Ballard et al., 1991 ; Hundertmark, 2007 ; Dunfey-Ball, 2017).

D'un point de vue appliqué, mon modèle répond au besoin des gestionnaires du Parc national Forillon de disposer d'un outil prédictif simple d'utilisation, pouvant leur permettre de tester l'effet de plusieurs scénarios de gestion sur l'avenir de la population d'orignaux. Notamment, mon modèle permettra aux gestionnaires d'en modifier les paramètres pour simuler, par exemple, une augmentation de l'émigration (par translocation ou rabattage des orignaux vers l'extérieur du parc), de la prédation (par réintroduction du loup gris) ou de la chasse (dans le cas d'une chasse de conservation par exemple), ou encore une diminution de la capacité de support du parc (via une conversion forestière ou une accélération du

vieillissement de la forêt) ou de la performance reproductive des femelles (contrôle de la fertilité). Toutes ces mesures figurent parmi celles envisagées pour favoriser la décroissance de la population d'orignaux (Etcheverry et al., 2023).

De plus, mon étude fournit une estimation récente de la capacité de support pour les orignaux à la pointe est de la Gaspésie, corroborant les résultats de précédentes études à ce sujet (Crête, 1989 ; Desgagnés et al., 2022). Mon projet de recherche a également permis de dégager plusieurs informations complémentaires pouvant être utiles aux gestionnaires du parc. En particulier, l'utilisation de données issues des inventaires de végétation dans le parc a mis en évidence une augmentation de la capacité de support pour les orignaux depuis la dernière épidémie de tordeuse des bourgeons d'épinette, découlant d'une forte régénération du sapin baumier dans certaines parcelles. Une épidémie similaire étant en cours dans la région depuis 2016, mon étude permet d'envisager la possibilité qu'un tel scénario de rehaussement de la capacité support se reproduise. Mes résultats offrent de plus une meilleure appréciation de l'impact de la chasse et de la prédation sur la population du parc, et mettent en évidence l'importance des mouvements d'individus depuis le – et vers l'extérieur du – parc, de même que leur effet sur le rapport des sexes. Enfin, mes résultats viennent appuyer ceux d'études récentes concernant l'impact de la tique d'hiver sur la dynamique de la population d'orignaux de Forillon, qui pour l'instant semble faible et limité au taux de survie des veaux à l'hiver, probablement du fait d'une faible charge de tiques (Pouchet, 2023 ; V. Bonin-Palardy, *données non publiées*).

Finalement, mon étude constitue un exemple supplémentaire de l'utilisation de la méthode de modélisation orientée par patrons pour estimer des paramètres dont la valeur est incertaine et par conséquent bonifie les appuis à cette méthode dans la littérature scientifique. De plus, l'exercice de paramétrisation que j'ai réalisé soulève de nouvelles réflexions quant aux conditions d'application de cette méthode, notamment le nombre maximum de paramètres à estimer (voir ci-dessous dans les limites de l'étude).

LIMITES DE L'ÉTUDE

La méthode de modélisation orientée par patrons s'avère très utile pour surmonter l'enjeu d'un manque de données ou d'informations permettant la paramétrisation d'un modèle, mais la littérature suggérait de n'estimer qu'un maximum de 20 paramètres à l'aide de cette approche (Grimm & Railsback, 2012). En effet, d'après mes observations personnelles (et celles de ma coautrice), à chaque nouvelle variable ajoutée, le nombre de combinaisons de valeurs possibles se trouve démultiplié, de sorte que les patrons peuvent être reproduits quelle que soit la valeur de certains paramètres moins sensibles. De ce fait, il m'a par exemple été impossible d'estimer avec précision la capacité de support du parc pour les orignaux, bien que mon modèle ait fourni une fenêtre de valeurs variant de 2,5 à 5 orignaux/km². De même, je n'ai pas pu distinguer efficacement la part des veaux prélevée par les ours noirs de celle prédatée par les coyotes car les diverses combinaisons possibles (impliquant tantôt davantage les ours, tantôt davantage les coyotes) étaient de probabilité équivalente, les intervalles de valeurs testés pour les taux de prédation des ours et des coyotes étant très larges. La prévalence de la tique d'hiver ainsi que, dans une certaine mesure, la charge de tiques des orignaux, ont également été difficiles à estimer. Disposer de données additionnelles sur un ou plusieurs de ces thèmes permettrait certainement de réduire la taille des plages de valeurs ou de fixer certaines variables, ce qui améliorerait la précision de mes estimés.

Afin de respecter les conditions d'utilisation de la méthode de modélisation orientée par patrons, j'ai donc dû fixer 63 paramètres parmi les 83 que j'avais à estimer. Cela constitue une limite puisque des combinaisons de valeurs offrant des résultats plus près de la réalité, qui auraient pu utiliser des valeurs extrêmes au sein de certaines plages, n'ont pas pu être explorées. Néanmoins, mes résultats obtenus en faisant varier la totalité des 83 variables sont remarquablement similaires à ceux où l'estimation orientée par patrons n'était utilisée pour n'estimer que 20 variables (voir l'annexe 2.6 du chapitre principal), ce qui est un indice encourageant concernant la qualité de mes estimés et suggère que j'ai bien fixé les paramètres les moins sensibles. Mes résultats offrent également une démonstration (et une opportunité

de réflexion) de la possibilité d'utiliser cette méthode de modélisation pour estimer plus de 20 paramètres à la fois, ce qui pourrait constituer un futur champ d'investigation.

Enfin, la validité des résultats issus de mes simulations semble intrinsèquement liée avec la précision dans la cueillette de données sous-jacentes aux patrons observés, soit, dans notre cas, les estimés d'abondance, de rapport des sexes et de recrutement, tous issus des inventaires aériens. Or il existe certains biais associés à la méthode d'inventaire traditionnellement utilisée (Rivest et al., 1995 ; Fleming & Tracey, 2008 ; Gagnon-Labrosse, 2022). J'ai tenté de corriger le plus possible certains estimés, notamment à travers la prise en compte du taux de visibilité des orignaux dans les intervalles de confiance autour de nos valeurs. Bien qu'imparfaits, ces estimés restent néanmoins des ordres de grandeur utiles à la modélisation et à la gestion des populations.

PERSPECTIVES

Les conflits entre la faune sauvage et les populations humaines sont variés et quelques fois inévitables (König et al., 2020 ; Hill, 2021), bien qu'ils soient susceptibles d'être exacerbés lorsque les populations animales atteignent de hautes densités (Messmer, 2009 ; Baldwin, 2017). Dans le cas des grands herbivores, les dommages aux cultures et les collisions avec des véhicules sont fréquents (Laforge et al., 2016 ; Laliberté & St-Laurent, 2020 ; Valente et al., 2020). De plus, le broutement par les ongulés pourrait diminuer le succès des stratégies de gestion destinées à adapter les forêts au changement climatique (Felton et al., 2020 ; Champagne et al., 2021a,b). On comprend ainsi aisément les enjeux qui poussent aujourd'hui scientifiques et gestionnaires à étudier ces populations afin d'élaborer des mesures de gestion permettant de limiter ces impacts négatifs. Les modèles sont des outils de choix pour cela, constituant un bon complément aux données de terrain et permettant de diminuer les coûts et le temps associés à leur récolte.

Mes résultats ont notamment mis en évidence l'importance de la prédation opportuniste pour la dynamique des populations d'orignaux vivant à haute densité en l'absence de loup. Les perspectives de recherche en aval de cette étude incluent donc un suivi

d'individus de chaque espèce dans un système ours noir-coyote-orignal, visant notamment à quantifier les taux de prédation et le pourcentage de veaux tués chaque année, cela en fonction de la densité des populations observées. Cela permettrait de disposer de données plus précises à intégrer aux modèles de dynamique des populations de l'orignal en l'absence du prédateur principal, et de mieux comprendre comment les prédateurs dits opportunistes peuvent interagir pour remplacer partiellement celui-ci en termes d'impact sur les populations de grands herbivores. Une autre étude pourrait s'intéresser aux différentes possibilités de régénération des forêts boréales suite aux épidémies de tordeuse des bourgeons d'épinette, avec pour but de projeter l'évolution de la capacité support pour l'orignal sous plusieurs scénarios de régénération. Enfin, l'utilisation de la méthode de modélisation orientée par patrons pourrait certainement être bonifiée et élargie si l'on investiguait davantage sur le nombre maximal de paramètres pouvant être intégrés dans un même modèle et estimés par cette méthode, afin d'éventuellement y ajouter des procédés permettant d'augmenter la complexité des modèles sans pour autant perdre en précision dans l'estimation des paramètres.

En conclusion, mon étude a contribué à combler les besoins actuels dans le domaine de l'écologie animale, en s'intéressant en particulier à l'un des contextes les plus favorables à la croissance rapide des populations de grands herbivores. En plus d'affiner notre compréhension des interactions entre les facteurs environnementaux à l'œuvre dans de tels cas, mon modèle fournit un outil pouvant être utilisé à des fins pratiques par les gestionnaires, ou à des fins théoriques par de futurs modélisateurs.

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