

**LES CONSÉQUENCES DE LA CHASSE AU GROS GIBIER CHEZ DEUX
OMNIVORES OPPORTUNISTES**

par

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Thèse présentée au Département de biologie en vue
de l'obtention du grade de docteur ès sciences (Ph.D.)

FACULTÉ DES SCIENCES
UNIVERSITÉ DE SHERBROOKE

Sherbrooke, Québec, Canada, mars 2023

Le 22 mars 2023

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REMERCIEMENTS

Dans un premier temps, j'aimerais remercier ma directrice Fanie Pelletier de m'avoir fait confiance et d'avoir cru en mes idées. Je m'estime chanceux d'avoir pu faire partie de ton laboratoire et d'avoir eu la chance de bénéficier de tes conseils durant les quatre dernières années. Je voudrais aussi remercier mon codirecteur, Andreas Zedrosser, de m'avoir accueilli en Norvège et de m'avoir aidé à mieux comprendre le système d'étude ainsi que pour toutes les discussions enrichissantes sur les ours et la chasse en Scandinavie. Merci à vous deux pour la liberté académique et l'encadrement dont j'ai bénéficié; et de m'avoir aidé à développer ce projet.

J'aimerais remercier Jon Arnemo, membre de mon comité de conseillers, d'avoir rendu ce projet possible grâce à son expertise et en me permettant d'utiliser les données de plomb; et aussi de m'avoir invité à assister aux captures d'ours en Suède. Sans cette expérience immortalisée par la photo de terrain la plus épique de tous les temps, mon projet de doctorat n'aurait pas été le même. Merci à Boris Fuchs et Jonas Kindberg pour vos contributions à la majorité de mes chapitres et les nombreux échanges qui m'ont permis de mieux comprendre le système de chasse scandinave. Merci à Maikel Rosabal et Christian Dussault d'avoir accepté de m'aider à développer le chapitre sur l'ours noir; sans vous, il aurait été impossible de réaliser cette étude. À tous mes coauteurs, j'espère avoir la chance de collaborer avec vous à nouveau. Je voudrais aussi prendre le temps de remercier Marco Festa-Bianchet, membre de mon comité de conseillers, de m'avoir poussé à développer mes connaissances à propos des fondements théoriques sur lesquelles reposait mon projet. Je crois que cela a grandement contribué à améliorer la qualité de mes publications.

Pour terminer, je voudrais remercier Carole d'avoir été à mes côtés (et de m'avoir supporté...) tout au long de mes études graduées. Mon passage au doctorat aurait été beaucoup plus difficile sans ton support et tes encouragements.

SOMMAIRE

La chasse peut entraîner plusieurs conséquences chez les populations animales exploitées, incluant la sélection de certains traits comportementaux et des changements de comportement induits par un paysage de la peur. Les activités de chasse peuvent être perçues comme une menace par les animaux qui ne sont pas ciblés et ces derniers modifient leur comportement de façon à moduler leur exposition au risque perçu. Les conséquences de la chasse ne se limitent donc pas qu'aux espèces ou groupes démographiques ciblés par les activités de chasse; cependant, peu d'études ont réellement tenté de documenter les effets de la chasse sur les espèces non ciblées et, plus particulièrement, chez les carnivores qui peuvent autant percevoir les chasseurs comme une menace qu'une source d'accès à la nourriture. En effet, une pratique courante chez les chasseurs est d'éviscérer le gibier sur le site d'abattage, ce qui augmente considérablement la quantité de biomasse disponible pour les charognards. Toutefois, consommer cette ressource pourrait être désavantageux sur le long terme. La chasse est une importante source d'émission de pollution puisque la majorité des chasseurs de gros gibier utilisent des munitions en plomb. Ces munitions se fragmentent après avoir atteint leur cible et incrustent des millions de fragments de plomb qui peuvent ensuite être ingérés par des charognards qui se nourrissent des restes d'abattage jetés par les chasseurs. En temps normal, il est avantageux d'adopter des comportements charognards, mais cela devient inadapté durant la période de chasse puisqu'une grande quantité de plomb se retrouve dans les restes d'abattage et que les charognards n'ont aucun moyen d'évaluer ce risque.

L'objectif de ma thèse de doctorat était de documenter les conséquences de la chasse au gros gibier chez deux omnivores opportunistes. Mes travaux peuvent être divisés en deux grandes sections: une première sur les effets de la chasse sur le comportement de l'ours brun (*Ursus arctos*) Scandinave et une deuxième sur le lien entre la distribution des sites d'abattage de gros gibier et le risque d'exposition au plomb chez l'ours brun Scandinave en Suède et l'ours noir d'Amérique (*Ursus americanus*) au Québec. Les différents chapitres de cette thèse ont pu être

réalisés grâce à des collaborations avec le Scandinavian Brown Bear Research Project (SBBRP) et le ministère des forêts, de la faune et des parcs du Québec. Le SBBRP réalise un suivi longitudinal de la population suédoise d'ours bruns depuis 1985 et plusieurs individus sont munis d'un collier GPS permettant de suivre leurs mouvements.

Dans le chapitre 2, j'ai documenté la réponse des ours bruns face à la chasse à l'orignal (*Alces alces*) en Suède. J'ai montré que les ours évitent les sites d'abattage d'orignaux tant durant le jour que durant la nuit et qu'ils augmentent la sélection d'habitats moins favorables aux chasseurs durant les périodes de chasse à l'ours et à l'orignal. Cela suggère que les restes d'abattage n'ont pas un effet attractif chez les ours en Suède et que ces derniers ne font pas la différence entre les chasseurs d'ours et les chasseurs d'orignaux, puisqu'ils adoptent des tactiques d'anti-prédation similaires durant les deux périodes de chasse. Dans le chapitre 3, j'ai montré que la protection légale contre la récolte n'avait pas d'impact au niveau de la perception du risque chez les groupes protégés. Cela n'est pas surprenant en soi, mais mes résultats montrent que les femelles avec des jeunes dépendants se déplacent plus rapidement lorsqu'elles sont près des routes durant les heures légales de chasse. Cette réponse pourrait augmenter les coûts de locomotion chez les femelles avec des jeunes dépendants, et ce, malgré la protection dont elles bénéficient.

Dans les chapitres 4 et 5, j'ai montré que les concentrations de plomb dans les tissus de deux espèces d'ours varient en fonction de la distribution des sites d'abattage. Ces résultats indiquent que les ours sont plus exposés au plomb dans les zones où il y a plus de chasse. Pour le moment, nous ne savons pas si les augmentations observées sont suffisantes pour induire des effets délétères chez les ours, mais les effets néfastes du plomb peuvent être observés à de très faibles concentrations. Il est donc possible que les chasseurs de gros gibier créent un piège évolutif pour les mammifères charognards comme c'est le cas pour les charognards aviaires. Dans le chapitre 5, j'ai aussi utilisé une fonction de sélection de ressources afin de prédire la distribution des sites d'abattage d'orignaux à l'intérieur de notre aire d'étude en Suède. Cette utilisation novatrice de la fonction de sélection de ressources pourrait être aisément répliquée dans d'autres systèmes

d'étude et ainsi améliorer nos connaissances sur le lien entre la distribution des sites d'abattage et le risque d'exposition au plomb provenant des munitions chez les charognards.

À travers les différents chapitres de cette thèse, j'ai montré que la chasse pouvait entraîner des conséquences variées chez les espèces ou les groupes démographiques qui ne sont pas convoités durant les activités de chasse. Les chasseurs peuvent induire des réponses anti-prédatrices chez plusieurs espèces; ces réponses peuvent être associées à des coûts nutritionnels ou une augmentation des dépenses énergétiques durant une période critique juste avant l'hiver. Les chasseurs sont aussi d'importants émetteurs de plomb dans l'environnement, ce qui pose un risque pour la santé des charognards qui se nourrissent des restes d'abattage jetés durant la période de chasse. L'exposition au plomb provenant de la chasse est un piège évolutif bien documenté chez les charognards aviaires et j'ai montré que les mammifères pouvaient aussi s'exposer au plomb de la même façon. Si des effets délétères de cette exposition venaient à être détectés chez les mammifères, le piège évolutif pourrait s'étendre à d'autres groupes de charognards.

Mots clés : paysage de la peur, piège évolutif, plomb, chasse, écotoxicologie, sélection de ressources

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LISTE DES ABRÉVIATIONS ET DES SIGLES

AICc	Critère d'information d'Akaike corrigé pour faible taille d'échantillon / <i>Akaike Information Criterion corrected for small sample size</i>
ALAD	Acide delta-aminolévulinique / <i>Aminolevulinic acid dehydratase</i>
Ca	Calcium / <i>Calcium</i>
GPS	Système mondial de positionnement / <i>Global positioning system</i>
ICP-MS	Spectrométrie de masse par plasma à couplage inductif / <i>Inductively coupled plasma mass spectrometry</i>
iSSF	Fonction de sélection de pas intégrée / <i>Integrated step-selection function</i>
MFFP	Ministère des forêts, de la faune et des parcs du Québec / Quebec Minsitry of Forests, Wildlife and Parks
mg/kg	Milligramme par kilogramme / <i>Milligram per kilogram</i>
µg/kg	Microgramme par kilogramme / <i>Microgram per kilogram</i>
µg/dL	Microgramme par décilitre / <i>Microgram per decilitre</i>
µg/L	Microgramme par litre / <i>Microgram per litre</i>
Pb	Plomb / <i>Lead</i>
ppm	Partie par million / <i>Parts per million</i>
ppb	Partie par milliard / <i>Parts per billion</i>
RSF	Fonction de sélection de ressources / <i>Resource selection function</i>
Th	Thorium / <i>Thorium</i>
U	Uranium / <i>Uranium</i>

CHAPITRE 1

INTRODUCTION

1.1 Paysage de la peur

Le paysage de la peur est un concept utilisé par les écologistes pour décrire les variations spatio-temporelles du risque perçu chez une proie (Gaynor et al. 2019). Ces variations sont notamment susceptibles d’entraîner des changements de comportement chez les proies, ce qui peut entraîner des conséquences au niveau de la survie et la reproduction, ou au niveau des écosystèmes (Fortin et al. 2005, Palmer et al. 2022). Par exemple, chez les troglodytes familiers (*Troglodytes aedon*) la peur des prédateurs peut conduire certains individus à réduire le temps alloué aux comportements de quête alimentaire, au détriment de la qualité des soins parentaux, nuisant ainsi à la condition physique de leurs oisillons (Grade et al. 2021). De façon similaire, lorsque le risque de prédation est élevé, la baleine boréale (*Balaena mysticetus*) passe plus de temps près des côtes et dans des endroits avec un important couvert de glace au détriment du temps passé en eaux libres où la nourriture est plus abondante, entraînant ainsi d’importants coûts nutritionnels (Matthews et al. 2020). Bien que ce type de comportement permette de diminuer le risque de mortalité lié à la prédation, il peut devenir couteux pour un animal d’allouer trop de ressources aux comportements anti-prédation puisque cela se fait généralement au détriment de l’acquisition de nourriture (Hertel et al. 2016, Dwinnell et al. 2019). Les organismes doivent donc prendre un certain niveau de risque et balancer celui-ci avec les bénéfices associés à l’acquisition de ressources.

Selon l’hypothèse de l’allocation du risque, les animaux doivent préféablement allouer des comportements anti-prédation aux situations où le risque de prédation est élevé et mettre l’emphase sur l’acquisition de ressources dans les situations où ce risque est faible (Lima et Bednekoff 1999). La réponse des proies sera aussi plus grande dans les situations où le risque de prédation est élevé et prévisible, mais de courte durée (Lima et Bednekoff 1999). À l’inverse,

de longues périodes durant lesquelles le risque est élevé pourraient forcer les organismes à abandonner leurs tactiques anti-prédation afin d'acquérir des ressources essentielles (Lima et Dill 1990, Lima et Bednekoff 1999). Ce phénomène est bien illustré dans l'étude de Blecha et al. (2018), laquelle montre que les cougars (*Puma concolor*) évitent généralement les milieux urbains et périurbains; cependant après une longue période sans repas, ces derniers sont plus susceptibles de s'aventurer en milieux urbains afin d'accéder aux proies qui s'y trouvent. Ces résultats n'ont rien de surprenant étant donné que, dans ce cas-ci, le manque de nourriture devient plus désavantageux à court terme que les risques associés à de possibles interactions avec les humains. Il est aussi important de souligner que la prise de risque varie en fonction de l'abondance de ressource dans l'environnement. En effet, les animaux pourraient devoir s'exposer à de plus grands risques lorsque les ressources sont limitées (effet de rareté) et, à l'inverse, la prise de risque devient moins nécessaire dans un contexte où les ressources sont abondantes puisque les animaux peuvent acquérir suffisamment de ressource dans les zones à faibles risques (Olsson et al. 2002). La réponse au risque peut aussi varier selon le groupe démographique, puisque certains individus pourraient devoir prendre plus de risque afin de maintenir une alimentation optimale (Stewart et al. 2022). La balance entre les risques et les bénéfices associés à l'acquisition de ressources est donc dynamique et dépendante de son contexte.

1.2 Les conséquences de la chasse sur le comportement

Tout comme les prédateurs « naturels », les humains peuvent causer des changements de comportement chez la faune; toutefois, le risque de prédation par les humains diffère de la prédation naturelle. Que ce soit à cause de restrictions légales ou de préférences personnelles, le risque de prédation par les humains est souvent dirigé vers des groupes démographiques ou des individus affichant des traits spécifiques, ce qui peut entraîner la disparition ou la modification de ces traits au sein des populations exploitées (Pigeon et al. 2016, Campbell-Staton et al. 2021). Ce type de sélection artificielle peut avoir lieu au niveau des traits comportementaux (Ciuti et al. 2012, Leclerc et al. 2017, 2019). Les proies peuvent aussi

apprendre à moduler leur exposition au risque en modifiant leur comportement de façon à réduire les interactions avec les prédateurs (Thurfjell et al. 2017, Lamb et al. 2020). De plus, les humains peuvent altérer le comportement de certaines espèces en modifiant la disponibilité des ressources au niveau du paysage (Wilson et al. 2020), par exemple, avec le déploiement de sites appâtés (Penteriani et al. 2021) ou en rejetant des carcasses de gibier dans l'environnement (Haroldson et al. 2004, Cozzi et al. 2015, Déaux et al. 2018). Il y a donc trois principaux mécanismes par lesquels la récolte d'individus par les humains peut entraîner des changements de comportement chez la faune, incluant la sélection de traits comportementaux, en créant un paysage de la peur ou en modifiant la disponibilité des ressources au niveau du paysage.

1.2.1. Patrons d'activité

Une façon pour les animaux d'éviter les perturbations associées aux humains est de modifier proactivement leurs patrons d'activités puisque le risque de prédation par les humains n'est pas uniforme dans l'espace et le temps (Palmer et al. 2022). L'Homme étant un prédateur principalement diurne, les risques de mortalité liés à la chasse sont donc plus importants pendant la journée. L'activité humaine a d'ailleurs conduit plusieurs espèces de grands mammifères à devenir plus actifs pendant la nuit afin d'éviter les perturbations liées aux activités humaines (Gaynor et al. 2018). Par exemple, l'ours noir d'Amérique (*Ursus americanus*) est plus susceptible d'utiliser les zones développées pendant la nuit lorsque le niveau d'activité humaine est faible (Zeller et al. 2019). De façon similaire, les ours bruns (*U. arctos*) deviennent plus nocturnes dans les zones où l'activité humaine est plus intense, et cette adaptation leur confère un avantage au niveau de la survie (Lamb et al. 2020).

1.2.2. Sélection de ressources

Avant de discuter des conséquences de la chasse sur la sélection de ressources, nous devons préalablement définir ce qu'est la sélection de ressources. Tout dépendant du contexte, le terme ressource peut être défini comme un habitat ou de la nourriture. La sélection de ressources est

un processus hiérarchique qui se fait simultanément à plusieurs échelles spatiales communément appelées ordres de sélection (Johnson 1980, Boyce et McDonald 1999, Boyce et al. 2003). Selon la définition de Johnson (1980), il y a quatre ordres de sélection : 1) l'aire de distribution d'une espèce, 2) le domaine vital d'un individu ou d'un groupe, 3) la sélection d'habitats à l'intérieur du domaine vital et 4) la sélection de ressources à l'intérieur du domaine vital, par exemple de la nourriture ou des micro-habitats. Il est aussi important de souligner que les phénomènes observés à ces différents ordres sont indépendants les uns des autres. Ainsi ce qui est observable à un ordre de sélection ne peut pas être généralisé aux autres ordres (Boyce et al. 2003). Il est donc primordial de bien définir l'ordre de sélection étudié lorsque nous tentons de documenter les conséquences des activités humaines sur la sélection de ressources chez la faune.

Le risque de prédation par les humains est très prévisible tant spatialement que temporellement (Gaynor et al. 2018, 2022) et, une fois perçu par une proie, ce risque peut entraîner des changements au niveau de la sélection de ressources chez cette dernière. Les chasseurs pratiquent généralement leurs activités près du réseau routier et dans des zones caractérisées par une bonne visibilité latérale (Lebel et al. 2012, Gaynor et al. 2022). Ces endroits peuvent donc être évités par les animaux qui perçoivent les chasseurs comme une menace durant la période de chasse (Thurfjell et al. 2013, Paton et al. 2017). Stewart et al. (2022) ont montré que les cerfs de Virginie (*O. virginianus*) évitent généralement les parcelles de nourriture (c.-à-d., champs nourriciers) durant la journée et utilisent plus ces sites durant la nuit en dehors des heures légales de chasse. Il est également important de souligner que ce risque de prédation par les humains peut être perçu par des organismes qui ne sont pas ciblés par les chasseurs (Grignolio et al. 2011, Dobbins et al. 2020). La chasse peut donc induire un paysage de la peur chez un large groupe d'organismes indépendamment du fait qu'ils soient ciblés ou non durant lesdites activités de chasse.

La dynamique entre la chasse aux ongulés et le comportement des grands carnivores est peu documentée et particulièrement intéressante puisque, pour les carnivores, les chasseurs d'ongulés représentent tant une menace qu'une source d'accès à la nourriture. En effet, les

chasseurs peuvent aussi avoir un impact sur le comportement des prédateurs qui les perçoivent aussi comme une menace (Gaynor et al. 2022); cependant, la chasse récréative est aussi une importante source de nourriture pour plusieurs espèces (Mateo-Tomás et Olea 2010, Mateo-Tomás et al. 2015). Plusieurs études montrent qu'une multitude d'espèces se nourrissent des carcasses et viscères jetés par les chasseurs (Legagneux et al. 2014, Lafferty et al. 2016, Gomo et al. 2017). La chasse augmente considérablement la quantité de biomasse disponible pour les charognards et entre 57% et 86% de cette biomasse peut provenir des carcasses jetées par les chasseurs durant l'automne (Wikenros et al. 2013). Des études ont montré que des activités comme la chasse et la pêche pouvaient altérer le comportement de prédateurs ou charognards opportunistes (Haroldson et al. 2004, Cozzi et al. 2015, Déaux et al. 2018).

Une importante question demeure toutefois sans réponse: que se passe-t-il au niveau des compromis entre la prise de risque et l'acquisition de ressources lorsqu'un organisme est à la fois un charognard opportuniste et une proie potentielle? Cette question sera abordée au cours du chapitre 2.

1.3 Les pièges évolutifs

Les animaux utilisent souvent des indices indirects pour évaluer les bénéfices associés à l'acquisition de ressources; cependant, l'Homme, un important vecteur de changements (Maxwell et al. 2016), peut rapidement altérer la qualité des indices ou en introduire de nouveaux qui ressemblent aux originaux, pouvant ainsi conduire à la prise de décisions inadaptées à l'environnement dans lequel se retrouvent les animaux (Schlaepfer et al. 2002). Ce phénomène est connu sous le nom de piège évolutif dans sa forme généralisée ou piège écologique lorsque la décision inadaptée est liée à un choix d'habitat (Schlaepfer et al. 2002). Par exemple, certains insectes aquatiques confondent les panneaux solaires avec la surface des plans d'eau et y pondent leurs œufs, ce qui peut ainsi nuire à leur succès reproducteur (Horváth et al. 2010). Dans d'autres cas, les animaux ne sont simplement pas en mesure de bien évaluer la qualité d'une ressource à la suite d'un changement drastique dans la qualité de celle-ci.

L'effondrement du barrage Fundão au Brésil en 2015 illustre un autre exemple de piège écologique. Ce barrage retenait plusieurs tonnes de résidus miniers contenant d'importantes quantités d'éléments, comme le plomb, le mercure, le cadmium et l'arsenic, qui à la suite de l'effondrement, se sont déversées dans un réseau de rivières (Nunes et al. 2022). Malgré une importante réduction dans la qualité des habitats contaminés par les résidus miniers, plusieurs espèces d'oiseaux aquatiques ont continué de s'y nourrir, s'exposant ainsi à des niveaux élevés d'éléments pouvant avoir des conséquences sur la survie et la reproduction (Nunes et al. 2022). Dans ce cas-ci, la décision inadaptée est liée au choix d'habitat d'alimentation, mais parfois les mauvaises décisions peuvent être plutôt liées au choix de nourriture. C'est notamment le cas chez la tortue luth (*Dermochelys coriacea*) qui confond les sacs de plastiques transparents qui se retrouvent en milieux marins avec des méduses qui font partie de son alimentation normale (Schlaepfer et al. 2002, Santos et al. 2021). Le concept de piège évolutif ne se limite évidemment pas qu'aux choix d'habitats et à l'alimentation et peut s'étendre à d'autres aspects comme le choix de partenaires et la période de reproduction (Schlaepfer et al. 2002).

Dans tous les cas, un piège évolutif est susceptible d'entraîner des effets délétères sur le *fitness* des organismes, menant ainsi à une diminution de la population et, dans les cas extrêmes, à l'extirpation de certaines populations (Robertson et Blumstein 2019). Les pièges évolutifs n'ont pas tous la même intensité et peuvent être classés en deux catégories selon leur gravité. Il y a 1) les pièges évolutifs sévères dans lesquelles les organismes affichent une préférence pour les nouveaux signaux de moindre qualité au détriment des signaux habituels et 2) nous avons les pièges évolutifs de préférence égale dans lesquels les organismes ne font pas la différence entre les signaux des bonnes et des mauvaises ressources sans toutefois afficher de préférence envers l'un ou l'autre (Santos et al. 2021).

1.4 Le plomb et la chasse

En plus d'entraîner des conséquences sur la sélection de traits morphologiques (Pigeon et al. 2016, Campbell-Staton et al. 2021) et le comportement (Leclerc et al. 2017) chez les populations

sauvages exploitées, la chasse est aussi une importante source d'émission de pollution dans l'environnement et a le potentiel de créer un piège évolutif chez les charognards (Singh et al. 2021). En effet, la chasse est une importante source d'émission de plomb et pose un risque pour la santé des écosystèmes, de la faune et des humains (Arnemo et al. 2022). Le problème réside dans l'utilisation par les chasseurs de munitions faites en plomb. L'usage de ces munitions est problématique pour deux raisons: d'une part, le plomb est une substance toxique à faibles concentrations et peut avoir des effets délétères chez les organismes qui y sont exposés (Pain et al. 2019). D'autre part, les munitions en plomb se fragmentent souvent après avoir atteint leur cible, incrustant ainsi des fragments de plomb dans les tissus du gibier récolté (Hunt et al. 2006, Hampton et al. 2021). Ces fragments peuvent être ingérés par les charognards qui se nourrissent des restes d'abattage jetés par les chasseurs.

1.4.1. La fragmentation des munitions

Le plomb est souvent utilisé comme composante principale pour fabriquer des munitions puisqu'il s'agit d'un métal peu dispendieux, facile à raffiner et malléable (Santé Canada 2013, Stokke et al. 2017). Cette dernière caractéristique est particulièrement importante puisqu'elle permet aux munitions de se déformer après un impact, augmentant ainsi les dommages causés à leur cible (Stokke et al. 2018). En revanche, la puissance de certaines armes à feu modernes est telle que les munitions faites en plomb se fragmentent sous la force de l'impact (Hunt et al. 2006, Gremse et al. 2014, Stokke et al. 2017, Menozzi et al. 2019, Hampton et al. 2021).

La quantité de fragments dépend de plusieurs facteurs incluant notamment le type d'arme à feu, le calibre, la vitesse du projectile, la distance de tir et l'angle de pénétration (Stokke et al. 2017). La fragmentation est aussi plus importante lorsque le projectile frappe des os ou lorsque de plus gros animaux sont atteints (Stokke et al. 2017). Il existe différents types de projectiles qui peuvent être utilisés pour chasser la grande faune et ce facteur doit aussi être considéré. Mis à part la chevrotine et les balles rayées pouvant être utilisées dans les fusils de chasse, les munitions de chasse se divisent en trois grandes catégories: 1) les munitions à expansion rapide

dont le cœur est en plomb, 2) les munitions à expansion contrôlée dont le cœur est aussi en plomb, mais dont l'enveloppe de cuivre est liée au cœur de plomb et finalement 3) les munitions monolithiques en cuivre (Grund et al. 2010, Stokke et al. 2017). Évidemment les munitions à expansion rapide se déforment et se fragmentent rapidement après un impact et libèrent généralement le plus grand nombre de fragments, alors que les munitions à expansion contrôlée sont généralement conçues pour afficher une meilleure rétention de masse (Grund et al. 2010). Il existe toutefois des doutes concernant la capacité des munitions à expansion contrôlée de réellement résister à la fragmentation, tels que le montrent les résultats contradictoires rapportés dans plusieurs études (Grund et al. 2010, Cruz-Martinez et al. 2015, Stokke et al. 2017). Malgré cette variété de facteurs pouvant influencer la fragmentation des projectiles, plusieurs études montrent que les munitions en plomb déposent d'importantes quantités de fragments dans les tissus du gibier récolté.

Des radiographies de carcasses d'ongulés atteints par des projectiles en plomb ont permis de montrer l'étendue de leur fragmentation (Hunt et al. 2006, Menozzi et al. 2019, Hampton et al. 2021). Plusieurs centaines de fragments visibles à l'œil nu dispersés dans les muscles et les organes internes du gibier à l'intérieur d'une distance radiale pouvant atteindre jusqu'à 45 cm (Grund et al. 2010). À ces fragments visibles, doivent s'ajouter des milliers de nanoparticules qui, bien qu'invisibles à l'œil nu, contribuent à contaminer les tissus du gibier avec des concentrations de plomb anormalement élevées (Kollander et al. 2017, Leontowich et al. 2022). Des analyses chimiques par spectrométrie de masse ont aussi permis de montrer que les muscles de sangliers (*Sus scrofa*) récoltés par des chasseurs utilisant des munitions en plomb avaient une concentration de plomb moyenne (écart type) de 511 (130) mg/kg autour du point d'impact, alors que les concentrations moyennes rapportées dans les tissus échantillonnés à 20-25 cm et plus de 30 cm du point d'impact étaient de 1.65 (0.87) mg/kg et 0.10 (0.04) mg/kg, respectivement (Menozzi et al. 2019).

1.4.2. Exposition au plomb chez les charognards aviaires

Plusieurs charognards aviaires sont aux prises avec des niveaux de plomb et les augmentations dans les concentrations de plomb coïncident avec la période de chasse au gros gibier. Par exemple, les concentrations de plomb dans le sang de grands corbeaux (*Corvus corax*) augmentent avec la progression des périodes de chasse au Québec au Canada et dans l'État du Wyoming aux États-Unis (Craighead et Bedrosian 2008, Legagneux et al. 2014). Des phénomènes similaires sont observables chez le vautour africain (*Gyps africanus*) et l'aigle royal (*Aquila chrysaetos*) au Botswana et en Suède, respectivement (Ecke et al. 2017, Garbett et al. 2018). Nous observons donc une corrélation temporelle assez forte entre les niveaux de plomb dans les tissus des charognards et le début ou la progression des périodes de chasse et ce phénomène a été observé dans plusieurs systèmes d'étude.

Les niveaux de plomb dans les tissus des charognards sont aussi spatialement corrélés avec la densité de récolte ou l'intensité de chasse, renforçant ainsi le lien entre la chasse et le risque d'exposition au plomb. Par exemple, les concentrations de plomb chez l'urubu à tête rouge (*Carthartes aura*) en Californie, États-Unis, sont plus élevées dans les unités de gestion où l'intensité de chasse aux porcs sauvages (*Sus scrofa*) est plus élevée (Kelly et Johnson 2011). De façon similaire, Garbett et al. (2018) montrent que les niveaux de plomb chez le vautour africain sont aussi plus élevés dans les endroits où la chasse est permise comparativement aux endroits où cette activité est interdite. Une étude récente réalisée par Kelly et al. (2021) montre que les loups (*Canis lupus*) échantillonnés au Minnesota, États-Unis, ont des concentrations hépatiques de plomb plus élevées dans les unités de gestion avec un plus grand taux de récolte de cerfs. Le même phénomène est aussi observable chez les oiseaux de proie en Suède qui montrent une augmentation dans leurs niveaux de plomb en fonction de la récolte de sangliers (Helander et al. 2021). Il existe donc d'importantes variations spatiotemporelles dans le risque d'exposition au plomb chez les charognards en fonction des périodes et des zones de chasse.

En plus des corrélations temporelles et spatiales entre la chasse et le risque d'exposition, nous pouvons aussi nous baser sur l'analyse des ratios d'isotopes stables du plomb pour identifier la provenance du plomb dans un échantillon (Komárek et al. 2008). Cet aspect est plus complexe que ceux mentionnés dans les deux paragraphes précédents et ne sera pas abordé dans les chapitres subséquents de cette thèse; cependant, il est important de couvrir cet aspect dans la présente mise en contexte afin de renforcer le lien entre la chasse et le risque d'exposition au plomb provenant des munitions chez les charognards.

Le plomb est un élément qui est naturellement présent dans l'environnement. Le plomb peut être d'origine primordiale, c'est-à-dire sans parents radioactifs, ou être le produit d'une des chaînes de désintégration radioactive du thorium ou de l'uranium. Le plomb a quatre isotopes stables (^{204}Pb , ^{206}Pb , ^{207}Pb et ^{208}Pb) dont les concentrations dépendent de l'abondance de plomb primordial, des niveaux de thorium et d'uranium, ainsi que de la demi-vie de leurs isotopes radioactifs (^{232}Th , ^{235}U et ^{238}U) (Komárek et al. 2008). Les isotopes stables du plomb peuvent être exprimés sous forme de ratios, ce qui permet de déterminer la contribution de différentes sources de plomb dans un échantillon en faisant des comparaisons entre leurs ratios d'isotopes stables (Gulson 2008, Komárek et al. 2008). Bien que les ratios d'isotopes stables dans les munitions soient très variables d'un manufacturier à l'autre (Peters 2002, Sjåstad et al. 2014), les munitions possèdent généralement une signature distincte des ratios d'isotopes stables naturellement présents dans les sols ainsi que de ceux provenant des carburants (Scheuhammer et Templeton 1998). Cela fait en sorte que l'étude des ratios d'isotopes stables de plomb accumulés dans les tissus d'organismes nous permet de vérifier si leur signature est semblable à celle présente dans l'environnement. Il est aussi possible d'examiner les changements d'isotopes stables du plomb en fonction de la concentration de cet élément dans les tissus, ce qui permet de comparer la signature des individus ayant été moins exposés au plomb avec celle de ceux y ayant été plus exposés (Scheuhammer et al. 2003).

Les ratios d'isotopes stables du plomb peuvent donc nous permettre de différentier le plomb circulant de l'environnement et celui provenant des munitions utilisées par les chasseurs. Une

étude de Church et al. (2006) montre que les condors de la Californie (*Gymnogyps californianus*) élevés en captivité avaient de faibles concentrations sanguines de plomb avec des ratios d’isotopes stables correspondant à ceux du plomb circulant en Californie, alors que les individus en liberté avaient des concentrations de plomb environ neuf fois plus élevées avec des ratios d’isotopes stables se rapprochant de la signature isotopique des munitions. Plusieurs autres études présentent des résultats semblables (Scheuhammer et al. 2003, Legagneux et al. 2014, Helander et al. 2021). Le lien entre l’exposition au plomb provenant des munitions chez la faune est donc bien établi et l’état actuel de nos connaissances laisse donc peu de place au doute quant à la crédibilité de ce lien. Malgré cela, il n’y pas ou peu de restrictions encadrant l’usage des munitions en plomb pour la chasse au gros gibier et des sondages ont montré qu’une grande majorité de chasseurs utilisent encore des munitions faites en plomb (Fachehoun et al. 2015, Stokke et al. 2017).

1.4.3. Conséquences de l’exposition au plomb

Le plomb est une substance néfaste à faibles concentrations et peut entraîner des conséquences sur tous les systèmes des vertébrés. Les conséquences du plomb découlent principalement de ses ressemblances avec d’autres éléments essentiels tels que le fer, le zinc et le calcium avec lesquels il compétitionne dans divers processus physiologiques (Santé Canada 2013, Singh et al. 2018, ATSDR 2020). Par exemple, le plomb peut se lier à l’acide delta-aminolévulinique (ALAD), ce qui empêche le zinc de s’y lier, inhibant ainsi l’activité de cette importante enzyme impliquée dans la synthèse de l’hème (Rodríguez-Estival et al. 2012, Santé Canada 2013, ATSDR 2020). Cela peut affecter la morphologie et la longévité des globules rouges et peut éventuellement mener à l’anémie (Santé Canada 2013, Singh et al. 2018). Le plomb peut aussi causer du stress oxydatif et des dommages à l’ADN (Singh et al. 2018); ou causer des problèmes cognitifs et neurologiques en interférant avec les actions régulatrices du calcium dans le cerveau (Singh et al. 2018).

Le plomb peut causer des intoxications aiguës ou chroniques et peut entraîner plusieurs conséquences sous-cliniques (c.-à-d. des effets peu perceptibles dans un contexte clinique). Les effets néfastes du plomb peuvent être observés à des concentrations sanguines de moins de 100 µg/L chez les humains et les animaux (Santé Canada 2013, Ecke et al. 2017, Singh et al. 2021), mais les niveaux doivent être généralement beaucoup plus élevés pour être associés à un empoisonnement sévère. Les niveaux de références, c'est-à-dire, les concentrations de plomb dans les tissus à partir desquelles on considère qu'il y a empoisonnement varient selon le type de tissu ou d'organisme. Par exemple, des concentrations sanguines de 200 à 500 µg/L peuvent être considérées comme un empoisonnement sous-clinique, alors qu'à plus de 500 µg/L on considère qu'il y a empoisonnement clinique chez plusieurs espèces d'oiseaux (Pain et al. 2019); cependant, afin de parler d'empoisonnements sévères la concentration de plomb doit habituellement dépasser le seuil de 1000 µg/L (Pain et al. 2019). Chez les mammifères, une concentration sanguine de plomb supérieure à 300 µg/L est indicatrice d'un empoisonnement, mais un diagnostic peut être établi à 600 µg/L (Dalefield 2017). Il est toutefois possible que ces seuils soient conservateurs puisque d'autres études ont rapporté des seuils de toxicité plus faibles chez les mammifères que chez les oiseaux (Buekers et al. 2009). Même les seuils d'empoisonnement sous-clinique rapportés chez les oiseaux pourraient être considérés comme conservateurs puisque des effets sous-létaux ont été observés à des concentrations sanguines de plomb huit fois plus faibles (Ecke et al. 2017).

Une étude récente basée sur plus de 1200 aigles échantillonnés à travers 38 États américains a montré que l'empoisonnement au plomb pouvait avoir un impact au niveau de la dynamique de population chez les charognards (Slabe et al. 2022). En effet, l'exposition au plomb provenant des munitions diminue d'environ 4% le taux de croissance des populations de pygargues à tête blanche (*Haliaeetus leucocephalus*) à l'échelle des États-Unis (Slabe et al. 2022). Cela peut sembler faible à première vue; cependant, cette suppression est uniquement causée par l'empoisonnement au plomb (c.-à-d. mortalité directe) et n'inclut pas les effets sous-létaux pouvant être induits par de plus faibles concentrations de plomb. Une concentration de plomb aussi faible que 25 ppb peut réduire la vitesse de déplacement et l'altitude de vol chez l'aigle

royal en Suède, augmentant ainsi les risques de mortalité accidentelle (ex. collisions avec des lignes à haute tension) et nuire aux comportements de quête alimentaire (Ecke et al. 2017). En effet, le risque de mortalité est 4,2 fois plus élevé chez les individus dont la plombémie dépasse le seuil de 25 ppb (Singh et al. 2021). L'exposition au plomb provenant des munitions peut donc avoir un impact sur les individus et possiblement les populations de charognards, et ce, même à de faibles concentrations.

1.4.4. Plomb et mammifères

La majorité des études ayant documenté le lien entre le risque d'exposition au plomb chez les charognards et la chasse portent sur des oiseaux (Pain 2009, Golden et al. 2016). Malgré le fait que plusieurs espèces de mammifères incluant l'ours brun et l'ours noir d'Amérique se nourrissent fréquemment des carcasses et viscères jetés par les chasseurs de gros gibier (Ruth et al. 2003, Haroldson et al. 2004, Legagneux et al. 2014, Lafferty et al. 2016), peu d'études ont été dédiées à l'étude de l'exposition au plomb provenant de la chasse chez les mammifères charognards (Rogers et al. 2012, Kelly et al. 2021, Chiverton et al. 2022). L'étude de Haroldson et al. (2004) montre que les grizzlys du Parc National de Yellowstone aux États-Unis ont tendance à sortir du périmètre du parc durant la période de chasse aux wapitis (*Cervus canadensis*), présumément pour bénéficier des carcasses jetées par les chasseurs. Legagneux et al. (2014) ont aussi montré que l'ours noir est le mammifère le plus fréquemment observé aux sites d'abattage d'orignaux au Québec, Canada. Ces études suggèrent que les ours bruns et noirs sont de bonnes espèces modèles afin d'étudier les impacts de la chasse sur le comportement et les risques d'exposition au plomb chez les mammifères qui sont des charognards potentiels.

Les comportements charognards pourraient permettre aux ours d'obtenir une ressource nutritive et facilement digestible à moindres coûts puisque la consommation de carcasses ne nécessite généralement pas d'investissements en énergie aussi importants que la prédation qui implique une poursuite et la neutralisation d'une proie (DeVault et al. 2003). La consommation de carcasses pourrait être avantageuse pour les ours puisque les individus provenant de populations

ayant un plus grand accès aux protéines animales ont tendance à être plus imposants (Hilderbrand et al. 1999, Mangipane et al. 2018). La condition physique est aussi un important déterminant de la survie et du succès reproducteur chez les femelles (Schwartz et al. 2003, Hertel et al. 2018). Les comportements charognards présentent donc certains avantages, mais ces comportements peuvent aussi être associés à un risque accru d'exposition au plomb qui pourrait à long terme amoindrir les bénéfices associés à l'ingestion de carcasses durant la période de chasse.

1.5 Objectifs

L'objectif général de ma thèse de doctorat était de documenter les conséquences de la chasse au gros gibier chez deux omnivores opportunistes, l'ours brun Scandinave et l'ours noir d'Amérique. Cette thèse peut être divisée en deux grandes sections; une première portant sur les conséquences de la chasse sur le comportement de l'ours brun en Suède (chapitres 2 et 3) et une seconde section portant sur le lien entre la chasse au gros gibier et l'exposition au plomb provenant des munitions chez l'ours brun en Suède et l'ours noir d'Amérique au Québec (chapitres 4 et 5). Les objectifs spécifiques à chaque chapitre étaient de :

- 1- Déterminer si les ours bruns sont attirés par les carcasses d'orignaux abandonnées par les chasseurs durant l'automne et s'ils perçoivent les chasseurs d'orignaux comme une menace.
- 2- Évaluer comment la chasse à l'ours affecte les déplacements des ours bruns de différents groupes démographiques à l'intérieur d'un paysage de la peur.
- 3- Quantifier l'influence de la densité de récolte de gros gibiers sur l'exposition à long terme au plomb provenant des munitions chez l'ours noir d'Amérique.

- 4- Vérifier comment les concentrations sanguines de plomb chez l'ours brun varient en fonction des concentrations de plomb dans le sol et de la distribution des sites d'abattage d'orignaux en Suède.

Afin d'atteindre ces objectifs, j'ai eu la chance de pouvoir collaborer avec le Scandinavian Brown Research Project et le ministère des forêts, de la faune et des parcs du Québec (MFFP). Ces collaborations m'ont notamment permis d'avoir accès à une imposante base de données contenant plus de quatre millions de coordonnées GPS à haute résolution provenant d'ours bruns scandinaves munis de colliers émetteurs. Nous avons aussi eu accès à des échantillons de dents d'ours noirs d'Amérique et aux données du système d'enregistrement de la grande faune grâce au MFFP. À ces données doivent s'ajouter les données publiques provenant du système d'enregistrement des orignaux en Suède (Älgdata).

1.6 Méthode générale

1.6.1. Espèces étudiées

Dans le cadre de cette thèse, j'ai travaillé sur deux des huit espèces d'ours : l'ours brun en Suède et l'ours noir d'Amérique au Québec. Ces deux espèces occupent sensiblement la même niche écologique dans les deux systèmes d'étude, ce qui m'a permis de tester parallèlement des hypothèses similaires dans deux systèmes d'étude et de valider de façon indépendante les conclusions de mes chapitres sur le risque d'exposition au plomb provenant des munitions utilisées par les chasseurs de gros gibiers.

1.6.1.1 *Ours brun*

L'ours brun, aussi appelé grizzly en Amérique du Nord, est une espèce présente en Asie, en Europe et en Amérique du Nord. L'ours brun est un omnivore opportuniste qui se nourrit de ce qui est disponible, incluant plantes, champignons, invertébrés, poissons et mammifères

(Schwartz et al. 2003), ainsi que de la nourriture d'origine humaine (Oro et al. 2013, Krofel et al. 2017). La composition de sa diète varie selon sa localisation géographique et la période de l'année. Par exemple, des baies (*Vaccinium* sp.) sont présentes dans 21,7% des échantillons d'excréments d'ours bruns collectés au cours du printemps en Suède, mais cette fréquence augmente à 98,3% durant l'automne (Stenset et al. 2016). Les ours en Suède sont aussi très dépendants de la production de baies qui influence leur condition physique, mais ils ne modifient pas la taille de leur domaine vital en fonction de la disponibilité de cette ressource (Hertel et al. 2018, 2019). Généralement, les ours provenant de populations ayant un meilleur accès aux protéines animales atteignent des tailles plus imposantes (Robbins et al. 2007); toutefois, les individus d'une même population peuvent atteindre un pourcentage de gras similaire (une mesure de la condition physique) malgré différentes compositions alimentaires (Mangipane et al. 2018).

L'ours brun est inactif durant l'hiver et hiberne dans une tanière. En Suède, la majorité des ours entrent dans leur tanière vers la fin octobre et n'en ressortent que vers la mi-avril (Friebe et al. 2001). Les dates d'entrées et de sorties de la tanière varient en fonction de plusieurs facteurs comme le sexe, l'âge, l'état reproducteur et d'autres facteurs environnementaux comme la température ambiante et l'arrivée de la première neige (Friebe et al. 2001, Evans et al. 2016). Les ours peuvent aussi émerger de leur tanière en hiver s'ils sont dérangés et, pour cette raison, vont sélectionner des sites de tanière dans des endroits tranquilles et difficiles d'accès comme les pentes abruptes (Elfström et al. 2008), minimisant ainsi les perturbations durant l'hibernation.

L'ours brun affiche un patron d'activité bimodale et, étant principalement actif aux alentours du lever et du coucher du soleil, est donc considéré comme crépusculaire (Ordiz et al. 2012, Bogdanović et al. 2021). Le patron d'activité de l'ours brun varie selon le groupe démographique et les saisons; les déplacements sont généralement plus importants chez les jeunes mâles et plus particulièrement pendant la période de reproduction au début de l'été (Bogdanović et al. 2021). Les activités humaines peuvent aussi altérer le comportement de l'ours

brun. Par exemple, le développement de la nocturnité chez l'ours dans les endroits où les perturbations liées à l'activité humaine sont plus grandes (Ordiz et al. 2014, Lamb et al. 2020). Cette modification de leur comportement leur permet de réduire les interactions avec les humains et ainsi de réduire leur risque de mortalité (Lamb et al. 2020). Les perturbations liées à l'activité humaine peuvent aussi conduire les ours à abandonner d'importants sites d'alimentation (Rode et al. 2007), ce qui peut avoir un impact au niveau de leur condition physique.

L'ours brun occupe une grande variété d'habitats, mais les patrons d'utilisation de l'espace vont varier selon l'heure de la journée, les saisons, la disponibilité des ressources, le groupe démographique et les risques auxquels ils sont exposés. Selon les populations, les mâles occupent des domaines vitaux d'environ 100 à plus de 8000 km², alors que les domaines vitaux des femelles se situent plutôt entre 24 et 2500 km² (Schwartz et al. 2003). Les ours ne sont pas territoriaux, mais il est tout de même possible que les mâles de plus grandes tailles monopolisent certaines ressources et excluent les groupes plus vulnérables, comme les femelles avec des jeunes dépendants et les juvéniles, de ces sites (Ben-David et al. 2004). Les variations dans l'utilisation de l'espace sont aussi en partie liées à l'abondance de nourriture; les individus provenant de populations ayant accès à des sources d'approvisionnement abondantes et groupées ont généralement des domaines vitaux plus petits, alors que les individus qui dépendent de ressources dispersées doivent occuper de plus grands espaces (Schwartz et al. 2003). La dispersion du domaine vital natal peut aussi être responsable d'une augmentation de la taille des domaines vitaux chez les jeunes individus (Graham et Stenhouse 2014).

L'ours brun utilise plusieurs types d'habitat de façon à maximiser l'accès à la nourriture tout en minimisant l'exposition aux perturbations provenant de l'activité humaine (Martin et al. 2010). Par exemple, les ours sélectionnent généralement les forêts en régénération et les coupes forestières puisque ces habitats contiennent une grande quantité de nourriture (Nielsen et al. 2004, Martin et al. 2010, Frank et al. 2015), mais évitent les zones ouvertes pendant le jour (Moe et al. 2007). Durant les périodes à haut risque, les ours vont aussi fortement éviter les zones

perturbées par l'activité humaine et sélectionner des zones plus sécuritaires comme les pentes abruptes et les sites localisés loin des routes (Martin et al. 2010, Northrup et al. 2012). En plus des risques associés à l'activité humaine, certains groupes démographiques plus vulnérables comme les juvéniles et les femelles avec des jeunes dépendants, doivent aussi se soucier des risques découlant d'interactions avec leurs congénères. Ces interactions sociales font en sorte que les jeunes ours ont souvent tendance à éviter moins fortement les zones habitées comparativement aux adultes qui les évitent fortement (Nellemann et al. 2007). Le même phénomène a aussi été observé chez les femelles avec des jeunes dépendants qui sélectionnent des sites près des habitations, présumément pour réduire les interactions avec les mâles (Van de Walle et al. 2019). Cette ségrégation spatiale entre les mâles et les femelles accompagnées de jeunes dépendants est plus importante durant la période de reproduction et serait une tactique visant à réduire le risque d'infanticide (Steyaert et al. 2013).

1.6.1.2 *Ours noir d'Amérique*

L'ours noir d'Amérique est, comme son nom l'indique, seulement présent en Amérique du Nord. L'Asie abrite aussi des ours noirs, mais contrairement à l'ours brun qui est présent sur plusieurs continents, l'ours noir d'Amérique et l'ours noir d'Asie (*U. thibetanus*) sont deux espèces distinctes. L'ours noir d'Amérique est un omnivore opportuniste dont la diète est très similaire à celle de l'ours brun; cependant, l'ours noir occupe une niche trophique plus basse lorsque les deux espèces coexistent (Jacoby et al. 1999, Belant et al. 2006). L'ours noir se nourrit majoritairement de végétaux, mais consomme de la nourriture d'origine humaine et de jeunes ongulés lorsque disponibles (Bastille-Rousseau et al. 2011, Hopkins et al. 2014). L'ours noir est aussi un charognard notoire et est fréquemment observé aux sites d'abattage d'ongulés (Legagneux et al. 2014, Lafferty et al. 2016). Les mâles ont tendance à avoir un niveau trophique plus élevé que les femelles (Ditmer et al. 2016), alors que les ours occupant des latitudes élevées ont une aussi plus grande proportion de viande dans leur diète (Bonin et al. 2020).

Comme l'ours brun, l'ours noir affiche aussi un patron d'activité bimodal avec des pics d'activité aux alentours du lever et du coucher du soleil (Lewis et Rachlow 2011). Les ours noirs sont généralement plus actifs pendant le jour au début de l'été et deviennent plus actifs durant la nuit vers la fin de l'été et le début de l'automne (Lewis et Rachlow 2011). La taille des domaines vitaux chez les ours noirs est très variable et il existe d'importantes différences entre les mâles et les femelles. Les domaines vitaux des mâles sont généralement plus grands que ceux des femelles et peuvent atteindre plus de 100 km² (Koehler et Pierce 2003, Ditmer et al. 2018a). À l'inverse, le domaine vital des femelles se situe plutôt entre 30 à 75 km² (Koehler et Pierce 2003, Brodeur et al. 2008), mais peut être aussi petit que 5 km² (Moyer et al. 2007). Les différences intersexuelles sont plus importantes au printemps durant la période de reproduction (Ditmer et al. 2018a), puisque les mâles augmentent significativement leurs déplacements durant cette période afin d'augmenter la fréquence des rencontres avec les femelles (Gantchoff et al. 2018). La disponibilité des ressources peut aussi avoir un impact sur la taille des domaines vitaux chez les ours noirs comme montré dans l'étude de Massé et al. (2014) qui illustre que les ours ayant accès à des stations d'alimentation artificielles ont des domaines vitaux plus petits que ceux d'individus n'y ayant pas accès.

1.6.2. Aires d'étude

1.6.2.1 *Suède*

L'aire d'étude est située dans le centre-sud de la Suède dans les comtés de Dalarna, Gävleborg et la partie méridionale du comté de Jämtland. Le paysage est majoritairement occupé par la forêt boréale et caractérisé par des activités de foresterie intensive et un dense réseau de routes de gravier qui facilite l'accès au territoire (Martin et al. 2010, Ordiz et al. 2014). La densité d'habitants est relativement faible avec de quatre à sept habitants/km² (Martin et al. 2010, Ordiz et al. 2014). Les principales classes d'habitats sont les forêts de conifères et les forêts mixtes avec quelques parcelles d'arbres décidus à différents stades de succession, incluant des zones de coupes et des forêts en régénération entrecoupées de lacs et de tourbières (Martin et al. 2010).

Les principales espèces d’arbres sont le pin sylvestre (*Pinus sylvestris*), l’épinette de Norvège (*Picea abies*), des bouleaux (*Betula spp.*) et plusieurs arbustes à baies (*Vaccinium spp.*) (Elfström et al. 2008, Ordiz et al. 2013).

La période de chasse à l’ours débute le 21 août de chaque année et peut s’étendre jusqu’au 15 octobre; ou jusqu’à ce que les quotas régionaux soient atteints (Bischof et al. 2008). Dans les dernières années, les quotas de récolte ont été atteints dans les premières semaines de la période de chasse et parfois même avant le début du mois de septembre (voir Figure 2.1 pour les statistiques). Tous les individus peuvent être légalement récoltés avec une arme à feu, à l’exception des groupes familiaux qui bénéficient d’une protection légale (Van de Walle et al. 2018). Un groupe familial inclut une mère avec des jeunes dépendants et ce, peu importe leur âge (Van de Walle et al. 2018). En Suède, les ours bruns sont principalement chassés à l’aide de chiens de poursuite ou de chiens aboyants qui les pistent à partir des routes ou près de sites appâtés (Bischof et al. 2008).

Pour ce qui est de la chasse à l’orignal (*Alces alces*), la période de chasse débutait le premier lundi de septembre et peut s’étendre jusqu’à la fin du mois de janvier de l’année suivante ou jusqu’à l’atteinte des quotas régionaux. Il est aussi important de souligner que les chasseurs suédois prennent une pause entre la fin septembre et la mi-octobre afin de minimiser les perturbations durant le pic du rut chez l’orignal. Comme pour la chasse à l’ours, les orignaux sont chassés avec des chiens dont le rôle est de créer des perturbations et de diriger le gibier en direction de chasseurs positionnés stratégiquement dans des corridors de fuites potentiels (Sand et al. 2006, Liberg et al. 2010). Les chasseurs récoltent en moyenne 84 000 orignaux annuellement et environ 94% de ces orignaux sont récoltés entre septembre et novembre (Wikren et al. 2013). Tous les orignaux sont récoltés avec une arme à feu, puisque l’usage d’armes primitives telles que l’arc et l’arbalète est prohibé. La vaste majorité (98%) des chasseurs suédois utilisaient encore récemment des munitions en plomb pour chasser l’orignal (Stokke et al. 2017).

1.6.2.2 Québec

Le Québec est divisé en plusieurs écorégions (ou biomes): les forêts décidues, mixtes et boréales ainsi que la toundra. Le sud de la province est dominé par les terres agricoles, les forêts décidues et les forêts mixtes. La forêt boréale occupe les latitudes moyennes et la toundra est localisée dans le nord de la province. Au Québec, il y a principalement trois espèces de gros gibiers qui peuvent être chassées: l'ours noir d'Amérique, le cerf de Virginie (*Odocoileus virginianus*) et l'orignal. L'ours noir est présent dans toutes les régions du Québec et peut être chassé avec des armes primitives ou des armes à feu ou trappé de la mi-mai à la fin juin et à l'automne dans certaines régions. Le cerf de Virginie est majoritairement présent dans les forêts décidues et mixtes du sud de la province et peut être chassé d'octobre à novembre avec des périodes spécifiques pour les armes primitives et les armes à feu (Huot et Lebel 2012). La chasse à l'orignal, quant à elle, se déroule entre septembre et octobre dans les forêts mixtes et boréales avec des périodes spécifiques pour les armes primitives et les armes à feu (Lefort et Massé 2015).

Dans tous les cas, les chasseurs doivent avoir un permis de chasse valide et un coupon de transport. Contrairement à la Suède, il est illégal d'utiliser des chiens de poursuite pour chasser le gros gibier au Québec. Les chasseurs peuvent utiliser des armes « primitives » telles que l'arc, l'arbalète et l'arme à chargement par la bouche ou des armes à feu modernes comme les carabines et les fusils de chasse à percussion centrale. La grande majorité (~75 %) des chasseurs de gros gibiers au Québec utilisent des munitions en plomb, mais ce nombre est probablement une sous-estimation puisqu'environ 10 % des chasseurs admettent ne pas savoir quel type de munitions ils utilisent (Fachehoun et al. 2015). Il est raisonnable de présumer que ce 10 % de chasseurs utilisent aussi des munitions en plomb, puisqu'il est peu probable qu'ils utilisent des munitions en cuivre sans le savoir.

CHAPITRE 2

LES CONSÉQUENCES DE LA CHASSE À L'ORIGNAL SUR LA SÉLECTION DE RESSOURCES CHEZ L'OURS BRUN SCANDINAVE

2.1 Description de l'article et contribution

La chasse peut grandement affecter le comportement des animaux en instaurant un paysage de la peur, en sélectionnant des individus avec des traits comportementaux spécifiques ou en altérant la distribution des ressources au niveau du paysage. Plusieurs études ayant documenté les conséquences de la chasse chez la faune se sont concentrées sur les espèces ciblées durant les activités de chasse et peu d'attention a été dédiée aux espèces non ciblées. Dans cet article, j'ai voulu déterminer comment les ours réagissent à l'augmentation de la disponibilité d'une ressource nutritive durant la période de chasse. Les ours sont chassés en Suède, mais ce sont aussi des charognards potentiels. Les ours peuvent donc percevoir les chasseurs d'orignaux autant comme une menace que comme une source d'accès à la nourriture. J'ai estimé la distribution des sites d'abattages d'orignaux à l'aide d'une fonction de sélection de ressources et j'ai utilisé des fonctions de sélection de pas afin de déterminer quelle est la réponse des ours face à la chasse à l'orignal. Les résultats montrent que les ours en Suède évitent les sites d'abattage d'orignaux, ce qui suggère que les restes d'abattage jetés par les chasseurs n'ont peu ou pas d'effet attractif. Les résultats montrent plutôt que les ours semblent percevoir les chasseurs d'orignaux, comme une menace et qu'ils évitent fortement les endroits fréquentés par ces derniers durant la saison de chasse. Cette étude suggère que les chasseurs d'orignaux et les chasseurs d'ours ont un effet similaire sur la sélection de ressources chez les ours. J'ai élaboré l'idée initiale qui a ensuite été raffinée en collaboration avec Fanie Pelletier et Andreas Zedrosser. J'ai construit les bases de données, réalisé les analyses statistiques et rédigé la version initiale de ce manuscrit. Tous les auteurs ont contribué à améliorer la méthodologie et à l'interprétation des résultats en commentant les versions préliminaires de ce manuscrit. Ce manuscrit est publié à *Ecological Applications*. <https://doi.org/10.1002/eap.2840>

Landscape of fear or landscape of food? Moose hunting triggers an antipredator response in brown bears

Ecological Applications (2023), e2840

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<https://doi.org/10.1002/eap.2840>

2.2 Abstract

Hunters can affect the behavior of wildlife by inducing a landscape of fear, selecting individuals with specific traits, or by altering resource availability across the landscape. Most research investigating the influence of hunting on wildlife resource selection has focused on target species and less attention has been devoted to non-target species, such as scavengers that can be both attracted or repelled by hunting activities. We used resource selection functions to identify areas where hunters were most likely to kill moose (*Alces alces*) in south-central Sweden during the fall. Then, we used step-selection functions to determine whether female brown bears (*Ursus arctos*) selected or avoided these areas and specific resources during the moose hunting season. We found that, during both day and nighttime, female brown bears avoided areas where hunters were more likely to kill moose. We found evidence that resource selection by brown bears varied substantially during the fall and that some behavioral changes were consistent with disturbance associated with moose hunters. Brown bears were more likely to select concealed locations in young (i.e., regenerating) and coniferous forests and areas further away from roads during the moose hunting season. Our results suggest that brown bears react to both spatial and temporal variations in apparent risk during the fall: moose hunters create a landscape of fear and trigger an antipredator response in a large carnivore even if bears are not specifically targeted during the moose hunting season. Such antipredator responses might lead to indirect habitat loss and

lower foraging efficiency and the resulting consequences should be considered when planning hunting seasons.

Keywords: behavior, disturbance, human-wildlife interactions, step-selection function, risk perception, scavenger, *Ursus arctos*

2.3 Introduction

Animals select resources based on a trade-off between fear and fitness (Lima and Bednekoff 1999). Predators, including humans, commonly create a landscape of fear, and potential prey adapt their behavior to modulate their exposure to the perceived risks (Lima and Dill 1990, Brown et al. 1999, Lima and Bednekoff 1999). For example, elk (*Cervus elaphus*) in Alberta, Canada, tend to increase their use of concealed areas and move further away from roads during the hunting season compared to the non-hunting season (Paton et al. 2017). Studies on multiple taxa, including fish and mammals, have also reported that artificial removal may apply a demographic filter to a population by selectively harvesting individuals with specific behavioral traits (Leclerc et al. 2017). Ciuti et al. (2012) showed that hunters from south-west Alberta, Canada, harvested elk that were bolder, used open areas more often and had higher movement rates. Hunting can also affect the behavior of non-target species, e.g. opportunistic scavengers, by altering resource availability across the landscape and providing essential resources (Cozzi et al. 2015, Lafferty et al. 2016, Wilson et al. 2017, Gomo et al. 2017). In this study, we determined the response of an opportunistic omnivore to landscape variations in scavenging opportunities and perceived mortality risk from ungulate harvest.

Hunters are not randomly distributed on the landscape and generally use areas based on accessibility [e.g., road access and topography (Diefenbach et al. 2005)] and visibility [e.g., open areas (Lebel et al. 2012)]. For example, Lebel et al. (2012) found that the probability of hunters killing a white-tailed deer (*Odocoileus virginianus*) on Anticosti Island (Québec, Canada) increased with visibility and decreased with increasing distance from roads. Also,

harvest sites of brown bear (*Ursus arctos*) and moose (*Alces alces*) are found in close association with roads in both Canada and Sweden (Boer 1990, Steyaert et al. 2016). Therefore, disturbances or attractants resulting from hunting activities, such as ungulate slaughter remains (i.e., gut piles, bone and hide dumps; or carcasses of wounded animals that were not found) are also concentrated around areas preferentially used by hunters. Scavengers should be attracted to those areas during the ungulate hunting season.

Brown bears are large opportunistic omnivores that are hunted in Sweden. Previous studies have shown that individuals adjust their behavior in response to the bear hunting season by changing their activity pattern and by avoiding areas with high levels of human activities (Ordiz et al. 2011, Hertel et al. 2016b). The bear hunting season in Sweden generally starts around two weeks prior to the moose hunting season in the fall; however, we do not know if and how bears react to moose hunting activities. There are two alternative hypotheses predicting behavioral changes in bears in response to moose hunting. First, moose hunters could be perceived as a threat, due to the high amount of human activity on the landscape and therefore brown bears could avoid the areas used by moose hunters due to the perceived risk. Alternatively, moose hunters and their activities could attract bears through the provision of slaughter remains. Swedish hunters harvest ~84,000 moose each year during the fall, which represents approximately 26% of the population at the national level (Kälén et al. 2022). Thus, large amounts of slaughter remains are available to scavengers during the hunting season. Bears commonly scavenge on slaughter remains discarded by hunters (Friebe et al. 2001, Elfström et al. 2014, Lafferty et al. 2016), and dietary analyses in Scandinavian brown bears showed that ~14% of scats collected during the fall contained vertebrate materials (Stenset et al. 2016). Scandinavian brown bears rely mostly on berries (e.g., *Vaccinium* spp., *Empetrum* spp.) during hyperphagia in the fall (Stenset et al. 2016), but consume meat when available (Dahle et al. 1998, Persson et al. 2001, Elfström et al. 2014). Therefore, we can expect brown bears to scavenge on slaughter remains discarded by moose hunter during the fall.

The goal of this study was to determine if hunting activities affect the behavior of a non-target species. We used data from Sweden to evaluate if and how brown bears react to moose hunting because they could perceive this activity as both a threat and a food source. First, we estimated resource selection by moose hunters and determined the relative probability of moose kills across our study area. Second, we evaluated the impact of moose hunting on brown bear habitat selection. We hypothesized that bear habitat selection should vary with hunting activities shifting from bear to moose hunting because the trade-off between increased mortality risk corresponds with a pulse in resource availability and accessibility. In addition, human activities strongly influence the behavior of bears (Stillfried et al. 2015, Hertel et al. 2016b, Lamb et al. 2020). We predicted that during the moose hunting season, bears should reduce the use of areas with higher probability of moose kills during the day (i.e., the legal hunting hours for moose in Sweden); and that they should increase the use of those areas at night to access slaughter remains when humans are inactive on the landscape and because mammals in general shift to nocturnality to avoid interactions with humans (Gaynor et al. 2018).

2.4 Materials and Methods

2.4.1. Study area

The study area was in Dalarna, Gävleborg and the southern part of Jämtland counties in south-central Sweden (~61°N, 15°E). The landscape is covered with a highly managed boreal forest with low human density (4-7 inhabitants/km²) and a dense network of forest roads (0.7 km/km²) (Martin et al. 2010, Ordiz et al. 2013). Main habitat types are coniferous and mixed forests with deciduous stands of different age classes (including clearcuts) interspersed by lakes and bogs (Martin et al. 2010). The main tree species are Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and birch (*Betula* spp.) with an abundant underlayer of berry shrubs, especially *Vaccinium* spp. (Elfström et al. 2008, Ordiz et al. 2013).

The bear hunting season in Sweden starts on August 21 and lasts until October 15 or until the regional quotas are filled, whichever comes first (Bischof et al. 2008), but most bears are shot within the first three days of the hunting period (Figure 2.1). Brown bears are hunted mainly by using baying or pursuing dogs that pick up scent trails on roads or near bait sites (Le Grand et al. 2019). All bears can be legally shot with the exception of family groups, i.e. a female accompanied by dependent offspring of any age (Van de Walle et al. 2018).

The moose hunting season in our study area starts on the first Monday of September and lasts until February the next year; however, 94% of the moose harvest occurs from September through November (Wikrenros et al. 2013). Between 2016 and 2019, only 6% of the 351 legally killed bears were harvested after the onset of moose hunting in our study area, indicating little overlap between bear and moose hunting seasons. In Sweden, moose are usually hunted with baying dogs that push them towards the locations of still hunters (Sand et al. 2006, Liberg et al. 2010). Our study area is divided into 17 moose management units (Figure S2.1) and the Swedish County Administrations compile daily moose harvest data (number of harvested moose/day) during the hunting season for each unit. Moose hunting generally starts slowly in September and stops completely from the end of September to mid-October to minimize disturbance during the peak of the moose rut (Figure 2.1). Then, moose hunting resumes at high intensity from mid-October to early November (Figure 2.1). Based on the dates of the bear and moose hunting seasons, we split the fall into five periods for each year between 2016-2019: 1) we defined the period between August 10 and August 20 as “before hunting”, 2) the period between August 21 and the first Monday of September as “bear hunt”, 3) the period between the first Monday of September and the day of the last moose harvest in September as “low intensity moose hunt”, 4) the period between the day of last moose harvest in September and day of the first moose harvest in October as “moose hunt pause”, and 5) the day of the first moose harvest in October until October 21 as the period of “high intensity moose hunt” (see also Figure 2.1).

We used October 21 as the final cut off because most bears start to hibernate at this time (Friebe et al. 2014).

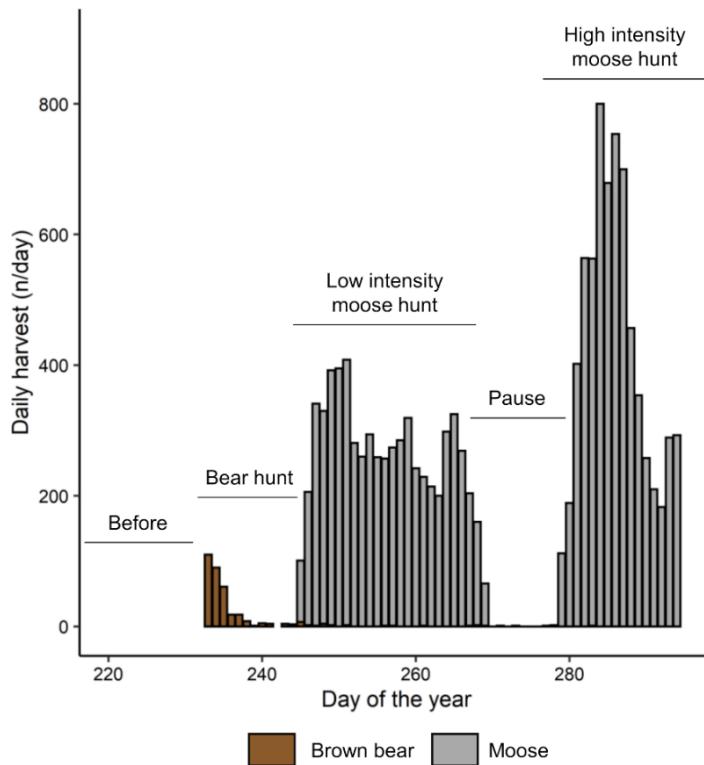


Figure 2.1 Number of moose and brown bears harvested per day of the year within moose management units that could have been used by GPS-collared brown bears in south-central Sweden, 2016-2019.

Labels indicate how the fall was split into five periods based on bear and moose hunting patterns.

2.4.2. Capture and handling

Between 2016 and 2019, female brown bears ($n = 30$ different bears; $n = 53$ bear-years) were darted from a helicopter with a remote drug delivery system (Dan-Inject, Børkop, Denmark). In this study, we excluded males because only two individuals were monitored. See Arnemo and

Evans (2017) for more details on the capture protocol. Brown bears were equipped with GPS-GSM collars (GPS Plus; Vectronic Aerospace, Berlin, Germany). All capture and handling protocols were approved by the Swedish Ethical Committee on Animal Research, Uppsala (C18/15) and the Swedish Environmental Protection Agency (NV-00741-18, NV-01758-14).

2.4.3. Resource selection by moose hunters

Between 2016-2019, we obtained 3,136 moose harvest locations from four moose management areas (Söder-Voxnan, Voxna, Härjedalen and Ljusnan-Voxnan) located in south-central Sweden (Figure S2.1). These locations were voluntarily provided by hunters, while registering killed moose on the official database of the Swedish county administrations (Älgdata, <https://algdata-apps.lansstyrelsen.se/algdata-apps-stat>). Other management areas within our study area were either not used by brown bears or few hunters disclosed moose harvest locations (resulting in poor coverage) and were therefore excluded from further analyses.

We used resource selection functions (RSF) to predict resource selection in moose hunters (Manly et al. 2002). We generated the same number of random positions (coded 0) as used moose harvest locations (coded 1) within each management area (in yellow; Figure S2.1). We extracted the percentages of landcover types within buffers of 65 m radius centered on both moose harvest and random locations, which corresponds approximatively to the average distance moose are shot in Scandinavia (Stokke et al. 2017). Landcover types were extracted from a reclassified 10 x 10 m landcover map of the Swedish Environmental Protection Agency (Naturvårdsverket 2018). Clearcut data were obtained from the Swedish Forestry Agency (Skogsstyrelsen 2020) by entering “Utförda avverkningar” in the search box. We extracted the distance to the closest road (in meters) from a distance raster (10 x 10 m) based on the National Road Data Base of the Swedish Transport Administration (Trafikverket 2019), which can be obtained by searching “Nationell väg databas” in the search box. Elevation was extracted from a digital elevation model (Lantmäteriet 2004), which can be obtained by entering “Terrain Model Download, grid 50+” in the search box.

The terrain ruggedness index (TRI) was derived from the digital elevation model by using the TRI tool in QGIS version 3.14.0 (QGIS Development Team 2020).

We built the RSF by using a generalized linear model with a binomial family and a logit link function [*glm* function, *stats* package; (R Core Team 2021)]. The model included variables known to influence visibility and accessibility within the landscape. We included the distance to the closest road, terrain ruggedness (with a quadratic term), elevation (with a quadratic term), proportion of human infrastructure, proportion of open bogs and clearcut and forest composition (young forest, 5-15 m conifer forest, 5-15 m mixed forest and 5-15 m deciduous forest). We used Akaike information criterion (AICc) to validate the choice of model (Appendix 2: Section S3). We used k-fold cross validation to assess the predictive ability of our model (Boyce et al. 2002).

2.4.4. Brown bear response to moose hunting

Our dataset contained a total of 82,042 bear locations recorded at 1-hour intervals between August 10 and October 21, 2016-2019. We filtered the data to only include locations with dilution of precision < 10 (D'Eon and Delparte 2005) and removed lines with missing observations. For each location, we noted the moose management unit as well as the hunting period during which it was recorded: before hunting, bear hunt, low intensity moose hunt, moose hunt pause, or high intensity moose hunt.

We first used integrated step-selection functions (iSSF) to determine how brown bears responded to moose hunting. The purpose of this analysis was not to build a model predicting resource selection in brown bears during the fall, but rather use iSSF to directly model the bears' response to moose hunting. The iSSF approach consists in comparing a pair of consecutive GPS positions, referred to as a step (coded as 1), to a series of available steps (coded as 0) that are randomly generated around the starting location of the observed steps (Thurfjell et al. 2014, Avgar et al. 2016). We used the *amt* package (Signer et al. 2019) to generate 10 available steps

for each observed step. The step length (m) and turning angle (rad) of available steps were modelled from Gamma and von Mises distributions, respectively (Signer et al. 2019). We added 0.001 to all step lengths to avoid an error when log-transforming steps with no movement (step length = 0 m). We extracted the mean relative probability of moose kill within 50 m at the end of each used and available steps and we included this variable with its quadratic term, the log of step length and the cosine of the turning angle as variables in conditional logistic regressions. We used the Poisson formulation of conditional logistic regressions fitted with *glmmTMB* (Brooks et al. 2017) as suggested by Muff et al. (2020) to account for interindividual differences in behavior and functional response. This approach requires adding the step ID as a random intercept and fixing its variance to a large value (i.e., 10^6) and it allowed us to include random coefficients for all the variables in the models, thereby accounting for functional response and interindividual differences in resource selection (Muff et al. 2020).

We built separate models for each demographic group (females with dependent offspring, n = 18; lone females, n = 17; and subadult females, n = 18) because age and reproductive status are known for influencing the response to human disturbances in brown bears (Ordiz et al. 2012, Lamb et al. 2020). For each demographic group, we built two sets of models for steps recorded during the day and night based on the hours of sunrise and sunset (i.e., when the sun is 6 degrees above the horizon), because it is forbidden to hunt moose from sunset to 1h before sunrise in our study area. We adjusted sunrise/sunset times by ± 1 h to account for potential disturbance related to hunter travel in/out of posts, transportation, or search for wounded game, which may extent past legal hunting hours. We also modelled the bears' response to the probability of moose kill (by hunters) separately for each hunting period (Figure 2.1) because we expected the behavior of brown bears and their response to human disturbance to change over our study period, resulting in a total of 30 models. The effect of the probability of moose kill was modelled during the 'before hunting' and 'bear hunt' periods, even though moose hunting had not yet started, to provide contrast with the moose hunting periods. We also created post-hoc models to specifically investigate the movement response of brown bears to moose hunting. The movement parameters (log of step length and cos of turning angle) were added in the models

and interacted with the probability of moose kill and its quadratic term extracted at the start of each step with a random slope for all parameters, including interaction terms (Table 2.1). Due to convergence issue, we could not create separate models for each demographic group in the movement models and we have added the results of these models as supporting information (see Appendix 2: Section S2.5).

Table 2.1 Structure of models used to estimate moose hunter resource selection function (RSF) and the integrated step selection functions (iSSF) for brown bears in south-central Sweden, 2016-2019.

Models	Structure
Hunter RSF	Distance to road + Elevation + Elevation ² + Ruggedness + Ruggedness ² + Infrastructure + Clearcut + Open bog + Young forest + 5-15 m conifer forest + 5-15 m deciduous forest + 5-15 m mixed forest
Brown bear iSSF (RSFhunt selection)	RSFhunt + RSFhunt ² + log_sl + cos_ta
Brown bear iSSF (RSFhunt movement)	log_sl + cos_ta + log_sl:RSFhunt + log_sl:RSFhunt ² + cos_ta:RSFhunt + cos_ta:RSFhunt ²
Brown bear iSSF (Landscape)	Young forest + 5-15 m conifer forest + 5-15 m deciduous forest + 5-15 m mixed forest + Clearcut + Distance to road + Ruggedness + Open bog + log_sl + cos_ta

Notes: A random coefficient [e.g., (0 + Young forest | bear-year)] was added for each variable, including movement parameters, quadratic terms and interactions, listed in brown bear iSSF models. All bear models also included random intercept with fixed large variance (i.e., 10⁶) for step ID. The effects of time of day, demographic groups and hunting periods were accounted for in separate models, except in the iSSF movement models in which demographic groups were combined. The moose hunter RSF did not include random effects.

We used the relative selection strength (RSS) to visualize the bears' response to the relative probability of moose kill (Avgar et al. 2017). This method estimates how likely an animal is to select a location (x_1) relative to another location (x_2). It is calculated by generating predictions of the relative probability of use at the two locations (x_1 and x_2), while holding all other variables constant (e.g., at their mean) except the variable for which we aim to visualize the effect size. At the first location (x_1), movement parameters were held constant at their mean (Table 2.2), while the relative probability of moose kill varied across the range of possible values. At the second location (x_2), all variables were held at their mean value (See Table S2.1). The RSS was calculated during each hunting periods and time of the day, thereby allowing to visualize the effect of the relative probability of moose kill during each hunting period. The RSS was computed by using the calculations outlined in Avgar et al. (2017).

2.4.5. Brown bear habitat selection during moose hunting

We also modelled resource selection at fine temporal scale in brown bears by using iSSF. We extracted landcover types within circular buffers (radius = 50 m) centered at the end location of each step. We conducted a scaling experiment to determine the appropriate buffer size and concluded that buffers with a 50 m radius were the most suitable (Figure S2.2). We included most variables from the hunter RSF with movement parameters (i.e., log of step length and the cosine of the turning angle) to determine the influence of moose hunting on resource selection in brown bears. We added random coefficients for each variable and formulated mixed conditional logistic regressions for each period with *glmmTMB* (Brooks et al. 2017, Muff et al. 2020) as described in the previous section. We did not include the relative probability of moose kill in combination with other landscape covariates due to lack of independence between this variable and the others (i.e., $\rho_{\text{road}} = 0.58$).

All landscape covariates were scaled by subtracting their mean value and dividing the difference by their standard deviation (Table S2.1) to facilitate model convergence. We screened numerical variables with a Spearman correlation matrix [*cor* function; *stats* package (R Core Team 2021)]

and variance inflation factors [*vif* function; *car* package (Fox and Weisberg 2019)] to detect multicollinearity. All variables had low correlation coefficients ($\rho < 0.40$) and variance inflation factors were low ($VIF \leq 1.17$) indicating low multicollinearity within our set of variables. The distance to the closest road was multiplied by -1 in the iSSF models to facilitate result interpretation. The RSS was calculated as described above. We used AICc to validate the choice of model (Appendix 2: Section S3). All statistical analyses were conducted in R version 4.1.0 (R Core Team 2021) and maps were processed in QGIS version 3.14.0 (QGIS Development Team 2020).

2.5 Results

2.5.1. Resource selection by moose hunters

The hunter RSF showed that moose hunters in Sweden were more likely to shoot moose in areas closer to roads and with higher proportion of clearcuts (Table 2.2). Moose hunters were also more likely to shoot moose at intermediate elevation and terrain ruggedness values (Table 2.2). Moose were more likely to get shot in areas with lower proportion of human infrastructure (Table 2.2). Moose hunters were less likely to shoot moose in areas with higher proportions of mixed and coniferous forests (Table 2.2), whereas the proportion of young forests, deciduous forests and open bogs did not influence the relative probability of moose kill (Table 2.2).

We assessed the predictive ability of our model with k-fold cross validation by randomly dividing our dataset into five folds and ranking the RSF values within ten quantile bins (Boyce et al. 2002, Roberts et al. 2017). The mean correlation between bin ranks and the adjusted area frequencies was $r_s = 0.88$ and ranged from 0.72 to 0.97, thereby indicating high predictive power (Boyce et al. 2002). Therefore, we used this model to calculate the relative probability of hunters harvesting a moose at a 100 m resolution across our study area (Figure 2.2).

Table 2.2 Habitat selection coefficients (β) with standard error (SE) and lower and upper boundaries of 95% confidence intervals for moose harvest locations in south-central Sweden, 2016-2019.

Variable	β	SE	Lower	Upper
Intercept	0.062	0.036	-0.009	0.133
% Infrastructure	-0.530	0.128	-0.781	-0.280
% Young forest	-0.035	0.027	-0.089	0.018
% Open bog	0.032	0.031	-0.028	0.092
% Clearcut	0.106	0.028	0.052	0.160
Distance to road	-0.443	0.044	-0.530	-0.356
Elevation	0.274	0.035	0.206	0.342
Elevation²	-0.060	0.022	-0.103	-0.016
Terrain ruggedness	0.158	0.037	0.085	0.230
Terrain ruggedness²	-0.035	0.011	-0.056	-0.013
% 5-15 m Conifer	-0.115	0.028	-0.170	-0.061
% 5-15 m Deciduous	0.030	0.027	-0.022	0.082
% 5-15 m Mixed	-0.053	0.027	-0.105	0.000

Notes: % Infrastructure denotes the percentage of cover occupied by permanent artificial structures within the 65 m buffers centered on moose harvest and available locations. Bolded rows indicate significant effect on selection.

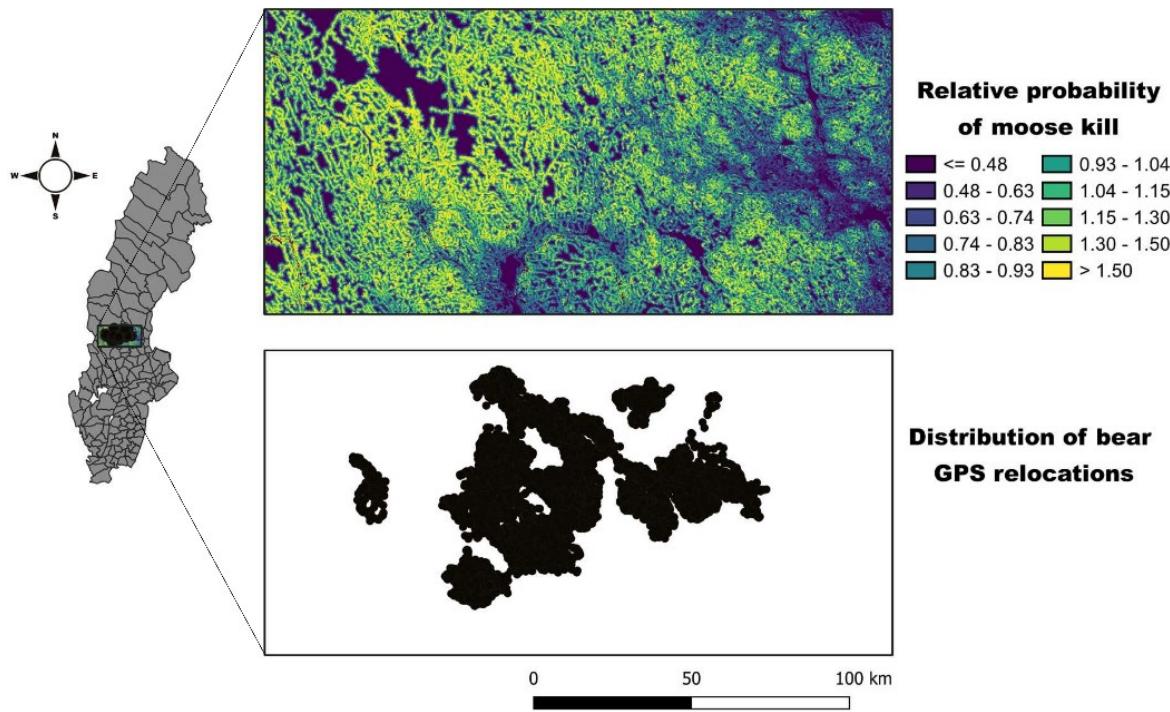


Figure 2.2 Relative probability of shooting a moose at a resolution of 100 m and the distribution of bear GPS relocations ($n = 82,042$ from 53 bear-years) in south-central Sweden during 2016-2019.

The relative probabilities of moose kills were estimated from an exponential equation: $w(x) = \exp(\beta_1x_1 + \beta_2x_2 + \dots + \beta_nx_n)$, where the β_i values were estimated from the full model (Table S2.5). The 10 bins are based on 10% quantiles.

2.5.2. Brown bear response to moose hunting

Brown bears generally avoided areas with higher probability of moose kills, especially during the day (Figure 2.3 and Figure 2.4). Females with dependent offspring weakly selected for areas with intermediate probability of moose kills at night during the the *low intensity moose hunt* and the *moose hunt pause* (Figure 2.3a and 2.3b; Figure 2.4). Solitary females were also more likely to select areas with intermediate probability of moose kills at night *before hunting* and during *bear hunt*, the *low intensity moose hunt*, and the *moose hunt pause* (Figure 2.3a and 2.3b; Figure

2.4). Subadult females selected for areas with intermediate probability of moose kills at night during all hunting periods (Figure 2.3a and 2.3b; Figure 2.4).

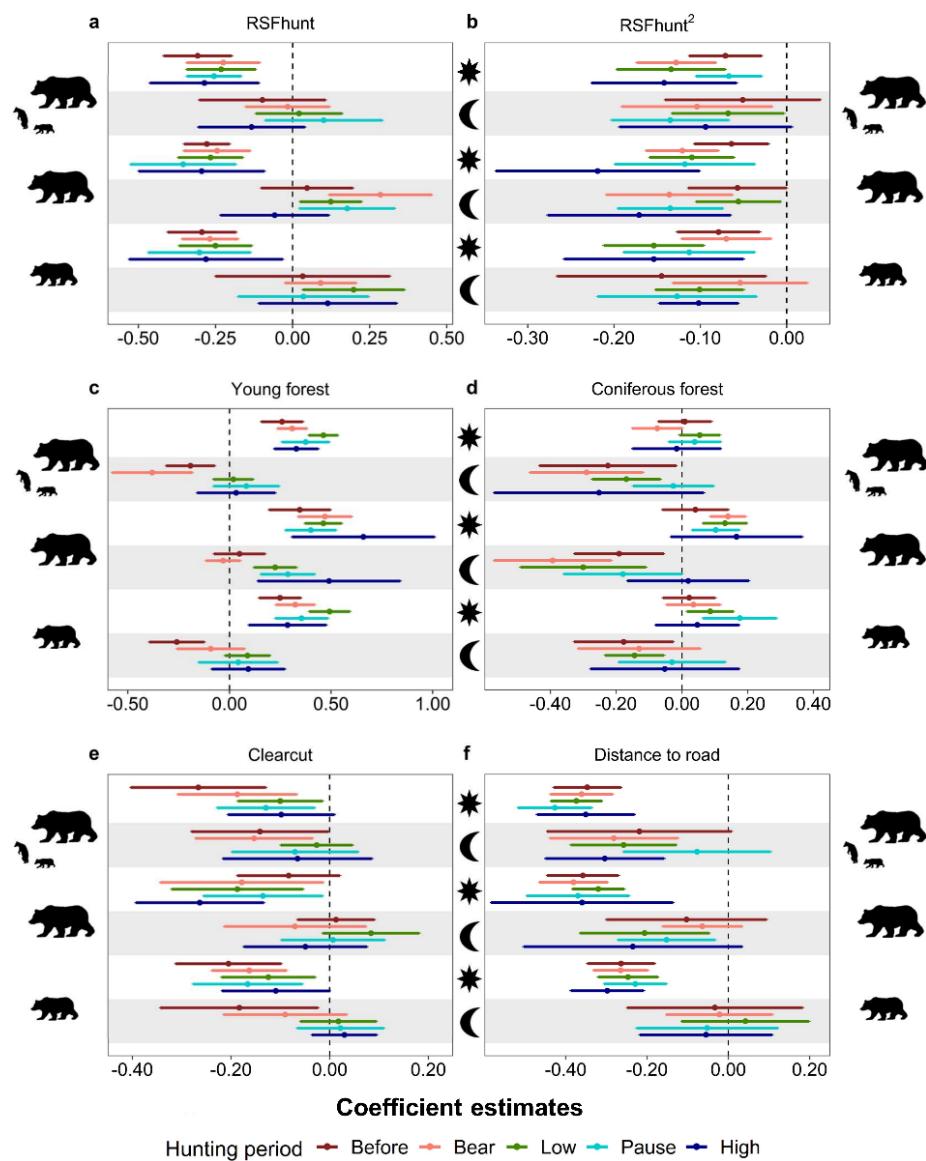


Figure 2.3 Coefficient estimates for the selection of probability of moose kill (RSFhunt), its quadratic term (RSFhunt²), young forest, coniferous forest, clearcut and the distance to the closest road with 95% confidence intervals.

The coefficients were estimated from integrated step-selection functions for female brown bears with dependent offspring ($n = 18$ bear-years), solitary

females ($n = 17$ bear-years) and subadult females ($n = 18$ bear-years) for day and night in south-central Sweden, 2016-2019. The coefficients were estimated for each hunting period: before hunting (red), bear hunt (pink), low intensity moose hunt (green), pause (cyan) and high intensity moose hunt (dark blue). Other parameters are presented in Figure S2.3, Figure S2.4 and Table S2.6.

Females with dependent offspring strongly avoided areas with higher probability of moose kills during the daylight hours of both bear and moose hunting periods (Figure 2.3b). Bears from all demographic groups became gradually less active as the fall progressed and took shorter steps (i.e., travelled shorter distances) that were less directional, except females with dependent offspring that took longer and more directional steps (i.e., straight movements) during the daylight hours of the bear hunt (Table S2.6 and Figure S2.4). Female brown bears also moved faster and more directionally when traveling in areas with higher probability of moose kills (Table S2.7 and Figure S2.5).

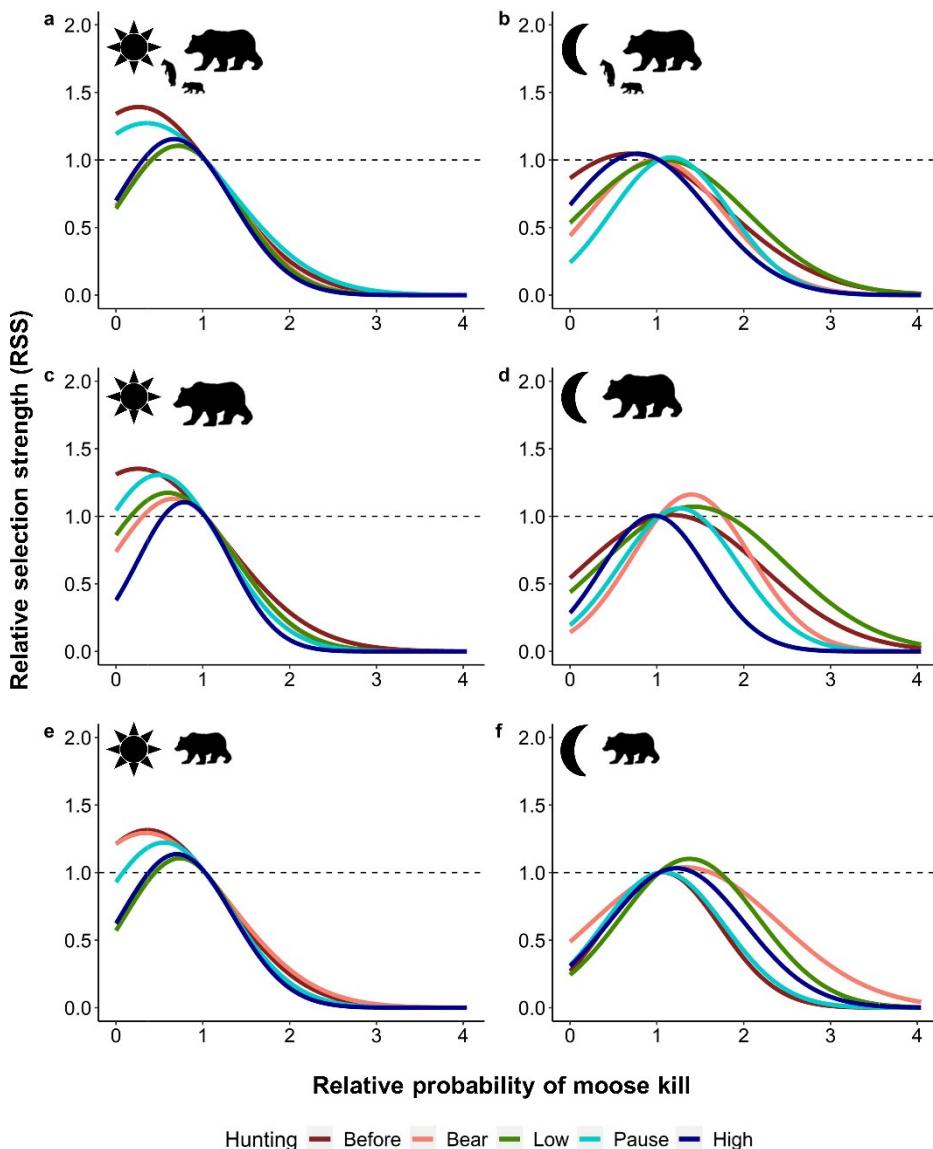


Figure 2.4 Relative selection strength (RSS) for the probability of moose kill (by hunters) in female brown bears with dependent offspring ($n = 18$ bear-years), solitary females ($n = 17$ bear-years) and subadult females ($n = 18$ bear-years) for day and night in south-central Sweden, 2016-2019.

The RSS shows how much likely a bear is to select a location relative to another location. An RSS of 1.5 at location x_1 indicates that brown bears were 1.5 more likely to use location x_1 relative to location x_2 . The RSS was calculated for each

hunting period: before hunting (red), bear hunt (pink), low intensity moose hunt (green), pause (cyan) and high intensity moose hunt (dark blue).

2.5.3. Brown bear habitat selection during moose hunting

Our results indicate that brown bear habitat selection varied substantially during the fall and some changes (i.e., selection of young forest, clearcuts and distance to the closest road) were consistent with disturbances associated with bear and moose hunting (Figure 2.3 and Figure 2.5). Brown bears selected for young forests during the day of all hunting periods (Figure 2.3c and Figure 2.5a). The diurnal use of young forests by females with dependent offspring and subadults peaked during the low intensity moose hunt, whereas it was highest during the bear hunt and both periods of moose hunting in solitary females (Figure 2.3c). Solitary females were also more likely to select for areas with higher proportions of coniferous forest during the days of the bear hunt and during low and high intensity moose hunt compared to the other periods (Figure 2.3d and Figure 2.5b).

Areas with higher proportions of clearcut were generally avoided during the day, whereas those areas were less strongly avoided or used in proportion of their availability at night (Figure 2.3e). Females with dependent offspring and subadults slightly increased the diurnal use of clearcuts during the periods of low and high intensity moose hunt, whereas solitary females showed the strongest avoidance of clearcuts during the bear hunt and both moose hunting periods (Figure 2.3e).

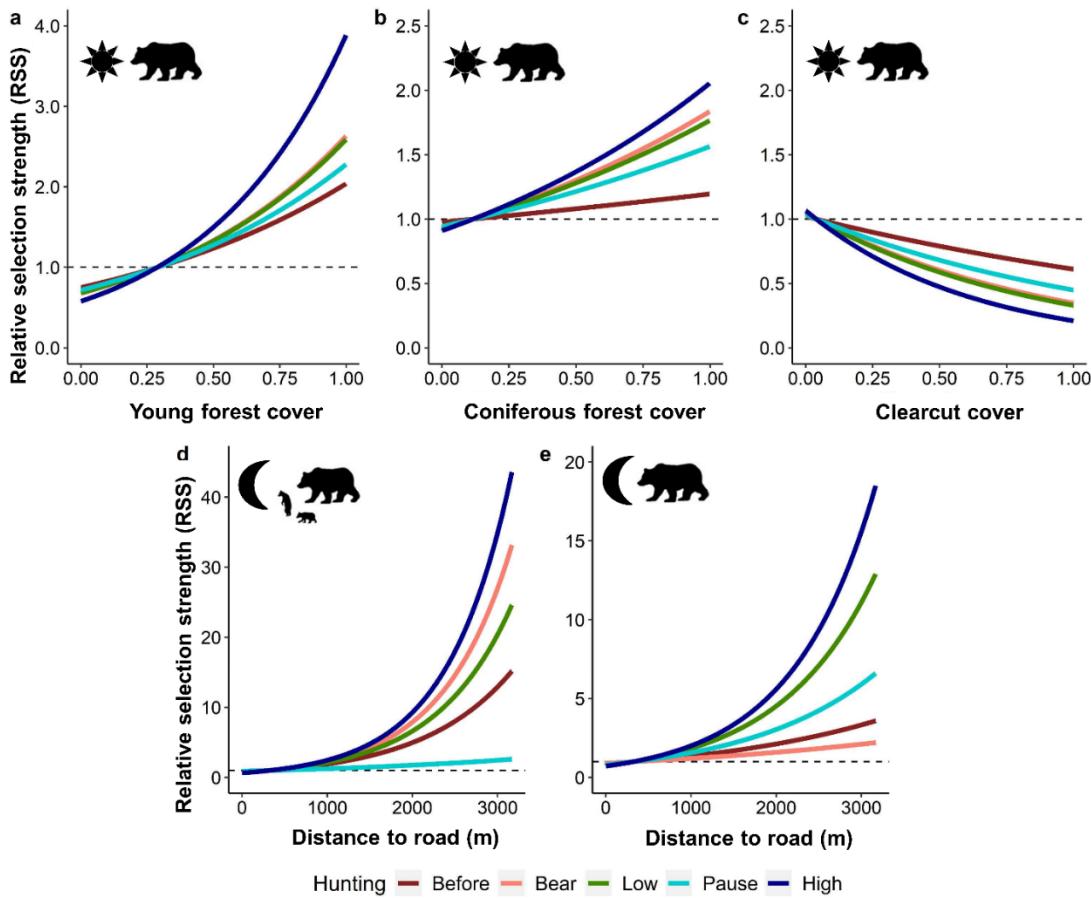


Figure 2.5 Relative selection strength (RSS) for a) young forest by solitary females ($n = 17$ bear-years) during the day, b) coniferous forest by solitary females during the day, c) clearcuts by solitary females during the day and d) and e) the distance to the closest road by females with dependent offspring ($n = 18$ bear-years) and solitary females during the night in south-central Sweden, 2016-2019.

The RSS shows how much likely a bear is to select a location relative to another location. An RSS of 1.5 at location x_1 indicates that brown bears were 1.5 more likely to use location x_1 relative to location x_2 . The RSS was calculated for each hunting period: before hunting (red), bear hunt (pink), low intensity moose hunt (green), pause (cyan) and high intensity moose hunt (dark blue). Note the scale difference between panels d and e.

Bears from all demographic groups avoided roads during the days of all periods, whereas roads were less strongly avoided during the night (Figure 2.3f). The selection coefficients for roads during the day did not vary much across hunting seasons in all demographic groups (Figure 2.3f). During the night of hunting periods the selection coefficient for adult females were closer to coefficient estimates during the day, whereas such changes were not evident in subadults (Figure 2.3f, Figure 2.5d and Figure 2.5e). Roads were avoided more strongly by solitary females at night during both periods of moose hunting. A similar pattern was observed in females with dependent offspring, but they also avoided roads more strongly at night during the bear hunt (Figure 2.3f, Figure 2.5d and Figure 2.5e). The other parameters did not show substantial variations according to hunting periods and are reported in the supporting information (Figure S2.3 and Table S2.6).

2.6 Discussion

In this study, we found that activity patterns of hunters and their use of the landscape influenced habitat selection by female brown bears. Specifically, we investigated if and how female brown bears react to moose hunting because moose hunters can alter the availability of food resources as well as create a landscape of fear. Our analyses supported our a priori hypothesis that moose kills are located closer to roads and in areas with good visibility. Our results also suggest that female brown bears perceive moose hunting activities as a threat because they generally avoided areas with high probability of moose kills. Solitary female bears increased the selection for better concealment during the day-time hours of both the bear and moose hunt. We additionally found that females avoided roads more strongly during the night in both the bear and the moose hunting periods. We did not find strong support for the prediction that, during the night, female brown bears were attracted to areas with high probability of moose kills. Overall, our results suggest that moose hunting was perceived as a threat and created a landscape of fear, and that slaughter remains were not strong attractants for female bears in south-central Sweden.

Moose harvest locations were not randomly distributed across the landscape and as expected, were concentrated around specific landscape features that favored accessibility and visibility such as proximity to a road, high proportions of clearcuts and intermediate values of elevation and terrain ruggedness. This pattern was expected since the road network allows hunters to easily move across the landscape and it has been documented in multiple systems regardless of the targeted species (Boer 1990, Lebel et al. 2012, Ciuti et al. 2012, Paton et al. 2017, Leclerc et al. 2019). Rugged terrain and/or high elevations may also impede movement of hunters across the landscape and restrict access (Diefenbach et al. 2005); however, slightly elevated and mid-slope locations could improve visibility by providing hunters with better vantage points and more open shooting lanes. Our study showed that visibility influenced the distribution of moose harvest locations, which is supported by moose harvest locations being disproportionately distributed in areas with higher proportions of clearcuts. The importance of visibility is more disputed in the literature (Perry et al. 2020) and ultimately depends on the hunting tactics (i.e., passive vs active) used by hunters (Norum et al. 2015). Animals can perceive predators as a threat and in response allocate more time to antipredator behaviors (Lima and Bednekoff 1999); however, spending more time hiding often comes at the expense of foraging opportunities and can carry substantial costs (Lima and Dill 1990, Hertel et al. 2016b). Solitary females responded to variations in perceived risk from moose hunting activities by increasing the selection of landcover classes with short to medium conifers (i.e., young and coniferous forests) that obstruct lateral visibility. Selection for better concealment during the hunting season is a common antipredator response that has been reported in bears and other game species (Ordiz et al. 2011, Thurfjell et al. 2013, Lone et al. 2015, Paton et al. 2017, Gaynor et al. 2022), but to our knowledge, such a response has rarely been documented in a large carnivore that is not specifically targeted by hunters (Dobbins et al. 2020). Previous work has shown that brown bears in Sweden forage less efficiently during the bear hunt, which may negatively affect their body condition (Hertel et al. 2016b). Our results suggest that bears were unable to differentiate bear and moose hunters, likely because they use similar hunting methods, and thus responded similarly during both hunting seasons. Therefore, we can expect the foraging efficiency of bears to be negatively affected during the moose hunting season. Consecutive and partially overlapping hunting seasons in the fall likely introduce continuous disturbance during the last

weeks of hyperphagia in bears. It is important to consider that our analyses were based on successful moose harvest locations and that all other hunting activities were not included in the model, which suggests that we likely underestimated the disturbance associated with moose hunting.

The disturbances induced by human activities are heterogeneously distributed in space and time (Gaynor et al. 2022). For instance, humans tend to concentrate their activities in areas closer to roads and stronger avoidance of these areas has been documented in several large mammals (Ciuti et al. 2012, Bonnot et al. 2013, Paton et al. 2017, Ladle et al. 2019). Our results show that brown bears in Sweden have a similar response. We observed the largest differences in selection for areas close to roads between hunting periods in females with offspring and solitary females during the night; however, we expected for such behavioral changes to occur during the day when hunters are active (Paton et al. 2017, Gaynor et al. 2018, Brown et al. 2020). Brown bears already avoided roads during the day before the onset of hunting and since roads are a network of interconnected linear features at relatively high density in our study area, it might be impossible for bears to move further away from a road without moving closer to another one, thereby explaining the lack of variation in road selection across hunting periods during the day. Following an encounter with humans, bears change both their day and nighttime movement behavior and activity pattern for up to two days after the disturbance (Ordiz et al. 2013). Thus, the pronounced changes in road selection during the night could be carry-over effects from daytime disturbances. This suggests that the effects of human disturbances are long-lasting in bears, and it would also explain why slaughter remains discarded by hunters did not seem to be strong attractants in our study. Long-lasting effects of bear hunting during the moose hunting periods cannot be completely excluded but are unlikely a limitation in this study because experimental approaches simulating human disturbance have shown that the behavior of Scandinavian brown bears returns to normal within three days following the disturbance (Ordiz et al. 2013). Therefore, it is unlikely that a short period of intensive hunting caused behavioral changes over several months. Disturbances from bear hunting or seasonal variations would also not account for changes in resource selection that occurred during the moose hunt pause as the

habitat selection coefficients for this period were similar to those estimated for before hunting, which suggests that moose hunting indeed caused some of the observed changes.

There is no selective advantage for an opportunistic scavenger to avoid a highly nutritious food resources such as slaughter remains (DeVault et al. 2003), which suggests that this response is likely related to fear induced by human activities. Animals develop stronger antipredator responses when exposed to higher levels of human activity (Lamb et al. 2020, Dobbins et al. 2020). Thus, we can expect that bears in hunted population living in an anthropized landscape to become wary of humans and avoid high-risk areas. Previous studies showed that bears are able to identify low risk-high reward areas (Lodberg-Holm et al. 2019), while feeding on berries to build up fat reserves (Hertel et al. 2018). Consequently, we expect bears in Sweden to feed sufficiently without the need to take additional risks to obtain slaughter remains; however, other carnivores that are more reliant on animal proteins could take more risks and approach humans to access food resources (Blecha et al. 2018). If a similar study was conducted across a gradient of anthropogenic disturbances, we would expect individuals from less disturbed landscapes to be less afraid of hunters, thereby affecting the balance of perceived risks and benefits.

Brown bears exhibited changes in resource selection during the fall that could not be easily attributed to moose hunting and we also observed marked differences across demographic groups. For example, the pattern of young forest selection in solitary females differed from that of subadults and females with dependent offspring. The reason for these different patterns of resource selection is unclear, but family groups are protected in Sweden (Van de Walle et al. 2018), which may alter their perception of potential risk. However, it may be an unlikely explanation because risk perception is similar in bears from all demographic groups when experimentally approached by humans (Ordiz et al. 2013). Alternatively, we would expect females with dependent offspring and subadults to take more risk later during the fall to maintain optimal foraging efficiency due to higher energy requirements during lactation (López-Alfaro et al. 2013) and greater thermoregulatory costs in smaller individuals (Humphries et al. 2003, Manchi and Swenson 2005). As berry patches become more depleted during the fall (Hertel et

al. 2016a), females with dependent offspring and subadults may also search for alternative food sources such as ants (Frank et al. 2015) or slaughter remains in clearcuts, resulting in resource selection patterns that differ from that of solitary females. Another explanation and potential limitation of our study is that the presence of large males around slaughter remains could deter females from using these locations, but we could not investigate this aspect due to low sample size of males. There is evidence from Sweden that females with dependent offspring avoid slaughter remains due to the presence of dominant conspecifics at these sites (Elfström et al. 2014). The results of our study, however, suggest that all three female demographic groups avoided areas with higher probability of moose kills. Data from camera trap surveys also showed that brown bears, in general, were not commonly observed at hunter kill sites in Scandinavia (Wikenros et al. 2013, Gomo et al. 2017). Although, these surveys were conducted in areas with low bear densities, they support the contention that bears generally perceive moose hunters as a threat because if slaughter remains were strong attractants, we would expect bears to scavenge on them even at low bear densities.

2.7 Conclusion

Our study found within-season variation in brown bear habitat selection and showed that this variation is affected by the activity patterns of hunters and their use of the landscape. Ultimately, predation as well as human harvest has a multitude of effects on the behavior of targeted prey species [e.g., increased vigilance (Paton et al. 2017), indirect habitat loss (Dwinnell et al. 2019), nutritional costs (Hertel et al. 2016b)]; however, our results show that hunting also can trigger antipredator responses in non-target species. The potential consequences of ungulate hunting on the behavior of bears may have remained unnoticed if our analyses had not accounted for temporal variations in ungulate hunting intensity. The costs associated with a landscape of fear can be substantial for wildlife (Hertel et al. 2016b, Dwinnell et al. 2019) and they should be considered when planning and managing hunting seasons. Managers may wish to plan different hunting season simultaneously to concentrate the disturbance induced by hunting activities within a shorter timeframe. Our study also highlights the importance of collecting both temporal

and spatial data on harvested wildlife as they can be used to model a landscape of fear, thereby providing valuable insights into the effects of human activities on wildlife. We recommend that future studies investigating the effects of human disturbances consider carrying out their analyses at scales reflecting temporal changes in risk.

2.8 Acknowledgements

The long-term funding of the Scandinavian Brown Bear Research Project (SBBRP) has come primarily from the Swedish Environmental Protection Agency, the Norwegian Environment Agency, the Austrian Science Fund, and the Swedish Association for Hunting and Wildlife Management. LB received financial support from the Canadian Wildlife Federation, the Natural Sciences and Engineering Research Council of Canada (grants 355492 and 05405 to FP) and the Canada Research Chair in Evolutionary Demography and Conservation (grant 229221 to FP 2009 and 2014). We are grateful to the many field workers and volunteers of the SBBRP that have contributed to the data collection for this study. We especially acknowledge the help of Dr. honoris causa S. Brunberg. LB, AZ and FP conceived the original methodology. LB conducted statistical analyses and wrote the first draft of the manuscript. All co-authors contributed to improve methodology, to result interpretation and gave final approval for publication.

2.9 Open research statement

The data used in habitat selection analyses (hunters and bears) can be found on Dryad (Brown et al. 2023), <https://doi.org/10.5061/dryad.sxksn037d>.

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CHAPITRE 3 COÛTS COMPORTEMENTAUX ASSOCIÉS À LA PROTECTION LÉGALE EN CONTEXTE DE CHASSE

3.1 Description de l'article et contribution

Les restrictions de chasse visent généralement à protéger certains segments plus vulnérables au sein des populations exploitées tout en dirigeant les efforts de chasse vers des groupes démographiques spécifiques; cependant, ces mêmes restrictions peuvent tout de même entraîner des conséquences pour les individus qui bénéficient d'une protection légale contre la récolte. L'objectif de ce chapitre était de comparer les patrons de mouvement chez les ours en fonction des variations spatiotemporelles dans le niveau de risque perçu. Les résultats de ce chapitre montrent que les femelles avec des jeunes dépendants augmentent leur taux de mouvement lorsqu'elles sont près des routes tôt le matin pendant la période de chasse à l'ours. Cela suggère une réponse anti-prédatrice de la part des femelles avec des jeunes dépendants et que la protection légale dont elles bénéficient n'affecte pas leur perception du risque. Cette réponse pourrait mener à des coûts comportementaux et contribuer à l'augmentation des coûts de locomotion chez les ours. Une augmentation significative des coûts de locomotion durant une période critique pourrait entraîner des conséquences au niveau de la survie et de la reproduction chez les groupes démographiques protégés. Les gestionnaires de la faune devraient mesurer et considérer ces coûts lors de l'élaboration des stratégies de gestion. Ce chapitre souligne aussi l'importance d'évaluer les conséquences de la chasse chez les groupes démographiques qui ne sont pas ciblés durant les activités de chasse.

J'ai développé l'idée originale pour cet article en collaboration avec Fanie Pelletier et Andreas Zedrosser. J'ai construit la base de données, réalisé les analyses statistiques et rédigé la première version de ce chapitre. Tous les auteurs ont contribué à l'interprétation des résultats et à améliorer la qualité de ce manuscrit en commentant le texte et la méthodologie. Ce manuscrit est maintenant en préparation pour *Ecology and Evolution*.

Legal protection from harvest does not shield against the cost of hunting disturbance

En préparation pour Ecology and Evolution

Ludovick Brown, Andreas Zedrosser, Jonas Kindberg and Fanie Pelletier

3.2 Abstract

Harvest regulations commonly attenuate the consequences of hunting on specific segments of a population; however, such regulations may still carry indirect costs due to perceived risk by non-target individuals. We compared the movement rates and behavioral responses of Scandinavian brown bears across spatiotemporal variations in risk in relation to onset of bear hunting in Sweden. Although females with dependent offspring are legally protected, they increased their movement rate after the start of legal hunting hours during bear hunting, especially in areas close to roads where hunting risk is higher. Our results suggest that legal protection from harvest have no influence on risk perception and may induce indirect behavioural costs in the protected segments of a population.

Keywords: *Ursus arctos*, movement rate, hunting, risk perception, disturbance, landscape of fear

3.3 Introduction

Recreational hunting has well documented consequences on wildlife, including behavioural changes, reductions in body size in the exploited segments of populations, altered population structure, and increased mortality rates (Fenberg and Roy 2008; Darimont et al. 2009; Leclerc et al. 2017). Wildlife managers typically implement regulations to reduce the risk of mortality in specific segments of exploited populations. For instance, antler point restrictions are often implemented to reduce the harvest rate of subadult males in hunted deer populations (Wallingford et al. 2017; Kellner et al. 2021). Harvest regulations commonly direct mortality toward specific demographic groups; however, the same regulations may carry indirect costs for the protected segments of a population due to perceived predation risk (Brown et al. 2020). Hunting can cause behavioural changes in legally protected demographic groups (Van de Walle et al. 2018; Brown et al. 2020), but the consequences remain poorly explored (Leclerc et al. 2017).

The spatiotemporal variations in perceived predation risk, commonly referred to as a landscape of fear (Gaynor et al. 2019), may cause animals to alter their behaviour, which in turn may induce trophic cascades and can alter ecosystem structure (Schmitz et al. 2004). Animals adopt anti-predatory tactics in response to perceived risks and may avoid areas that contain essential resources to minimize risk exposure (Hertel et al. 2016; Dwinnell et al. 2019). Such behavioural responses due to anthropogenic activities have been reported even when humans pose little to no risk (Rode et al. 2007; Gaynor et al. 2018), suggesting that legal protection may have limited impact on risk perception and may cause indirect energetic costs through behavioural changes.

We used the brown bear (*Ursus arctos*) as a model species to evaluate the movement response of an intensively hunted species across small-scale spatiotemporal variations in perceived risk. In Sweden, all brown bears can be harvested during the legal hunting period, except members of family groups (i.e., females accompanied by dependent offspring of any age) which are legally protected (Van de Walle et al. 2018). Swedish hunters are generally law-abiding and

only very few bears from family groups are killed during the hunting season. However, hunters in Sweden commonly use baying dogs to trail and drive bears (Bischof et al. 2008), which also results in pursuits of family groups because dogs do not discriminate between lone bears and family groups. Therefore, we could expect a similar behavioural response to hunting in unprotected bears and family groups. Previous work has shown that brown bears respond to hourly variations in risk by reducing foraging activities and movements during times of the day when the risk of hunter-caused mortality is highest (Ordiz et al. 2012; Hertel et al. 2016). Here, we build on these results and specifically investigate the movement rates and activity patterns of the protected segments of the bear population, i.e., family groups, during the hunting season in comparison to groups that can be legally hunted to better understand the indirect effects of hunting in wildlife populations.

The predation risk from hunters is heterogeneously distributed across space and time, but it is also highly predictable because it is restricted to legal hunting hours during daytime and generally occurs in areas close to roads (Steyaert et al. 2016; Perry et al. 2020; Gaynor et al. 2022). Since the strength of a behavioural response is highly dependent on the intensity of the disturbance (Le Grand et al. 2019; Gaynor et al. 2022), we can expect bears to show varying levels of behavioural responses to human activities when moving across heterogeneous landscapes. We hypothesized that brown bears change their behaviour after the onset of the hunting season to minimize the time spent in high-risk areas. As hunting activities are mainly distributed around roads, we expect bears to increase their movement rate when located close to roads during legal hunting hours, especially during the morning when most hunting-caused mortalities occur (Hertel et al. 2016).

3.4 Method

Our study area was located in south-central Sweden (~61°N, 15°E) during 2016-2019. The landscape contains a highly managed boreal forest with a dense network of forest roads and low human density (Martin et al. 2010; Ordiz et al. 2013). Bear hunting in Sweden starts on August

21 and lasts until October 15 or until the regional quota has been filled, whichever comes first (Bischof et al. 2008). Bears are almost exclusively hunted with baying or pursuit dogs that pick-up scent trails and drive bears towards hunters (Leclerc et al. 2019). All bears can be legally harvested except members of family groups, which are protected year-round (Van de Walle et al. 2018).

3.4.1. Bear capture and telemetric survey

Brown bears ($n = 47$ individuals; $n = 92$ bear-years) were darted from a helicopter with a remote drug-delivery system (Dan-Inject, Børkop, Denmark) and equipped with GPS-GMS collars (GPS Plus; Vectronic Aerospace, Berlin, Germany). See Arnemo and Evans (2017) for more details about the capture protocol. All capture and handling protocols were approved by the Swedish Ethical Committee on Animal Research, Uppsala (C18/15) and the Swedish Environmental Protection Agency (NV-00741-18, NV-01758-14).

3.4.2. Data handling

We only used data from individuals that survived the hunting season ($n = 35$ bear-years were discarded beforehand) and relocation data with dilution of precision < 10 (D'Eon and Delparte 2005). Our final data set contained 39,559 GPS locations from 92 bear-years collected at 1h intervals between August 10 and 31, during 2016-2019. We defined the period 'before hunting' as the 11 days (August 10-20) before the onset of the bear hunt and used August 31 as a cut-off for the 'bear hunt' (August 21-31) to avoid any interference with the onset of moose hunting on the first Monday of September. GPS locations were converted to animal tracks with the package *amt* (Signer et al. 2019), which calculates the distance travelled in 1h as a straight line between consecutive locations. The distance to the closest road (in meters) was extracted from a distance raster (10 m resolution) based on the National Road Data Base of the Swedish Transport Administration (Trafikverket, <https://www.trafikverket.se>).

3.4.3. Statistical analyses

We modelled the distance travelled between two consecutive relocations (i.e., step length) in bears with linear mixed effect models in the *nlme* package (Pinheiro et al. 2021), which allowed us to include a corCAR1 structure and account for temporal autocorrelation. The model included the distance to the closest road as a proxy for risk, the season (i.e., before hunting versus bear hunting), and the time of day. We converted clock time into solar time (hereafter referred to as suntime) in radians with sunrise and sunset standardized at $\pi/2$ and $3\pi/2$, respectively (*overlap* package; (Ridout and Linkie 2009)). We used the structure described in Richter et al. (2020) to model the effect of suntime with trigonometric functions [i.e., $(\sin(\text{suntime}) + \cos(\text{suntime}) + 2 \cdot \sin(\text{suntime}) + 2 \cdot \cos(\text{suntime}))$]. We added nine two-way interactions and four three-way interactions between the variables distance to road, suntime, and period. We used separate models for each demographic group [i.e., females with dependent offspring, $n = 19$ bear-years; lone females, $n = 32$ bear-years; subadult females (< 4 years old), $n = 32$ bear-years; males, $n = 9$ bear-years] to facilitate the interpretation of the results. Subadult and adult males were pooled into a single group due to the low sample size. We also added random slopes for suntime by bear-year, thereby accounting for interindividual behavioural differences, and added a random intercept for the date. We removed random slopes from the male model due to convergence issues and only kept the random intercept. We used diagnostic plots to ensure that model assumptions were met. The response variable was log-transformed to achieve normality of the residuals and we added 1 to all observations to facilitate log-transformation of steps with no movement (i.e., 0 m). The distance to the closest road was standardized to facilitate model convergence. We set α at 0.05 and all statistical analyses were carried out in R 4.1.0 (R Core Team 2021).

3.5 Results

Bear movement rates followed a bimodal pattern with peaks around sunrise and sunset in all demographic groups (Figure 3.1). The movement rate of females with dependent offspring

increased around the start of legal hunting hours during bear hunting in areas close to roads (Figure 3.1a), but this effect dissipated with increasing distance from roads (Figure 3.1b). The movement rate of females with dependent offspring generally increased during the bear hunting season ($\beta_{\text{hunting}} = 0.12$, $p = 0.01$), whereas it decreased in lone females ($\beta_{\text{hunting}} = -0.15$, $p < 0.001$) and remained the same in subadult females ($\beta_{\text{hunting}} = 0.02$, $p = 0.56$) and males ($\beta_{\text{hunting}} = -0.05$, $p = 0.69$). There was also an interaction between the hunting period and the effect of roads on the movement rate of females with dependent offspring ($\beta_{\text{road}} \times \text{hunting} = -0.07$, $p = 0.06$), suggesting that females with dependent offspring moved faster when close to roads during the hunting season compared to before hunting, whereas such effect was not evident in other demographic groups ($p > 0.05$; Table S3.1). We also obtained similar results when modeling the movement rate with an alternative approach based on generalized additive mixed effect models (Figure S3.1).

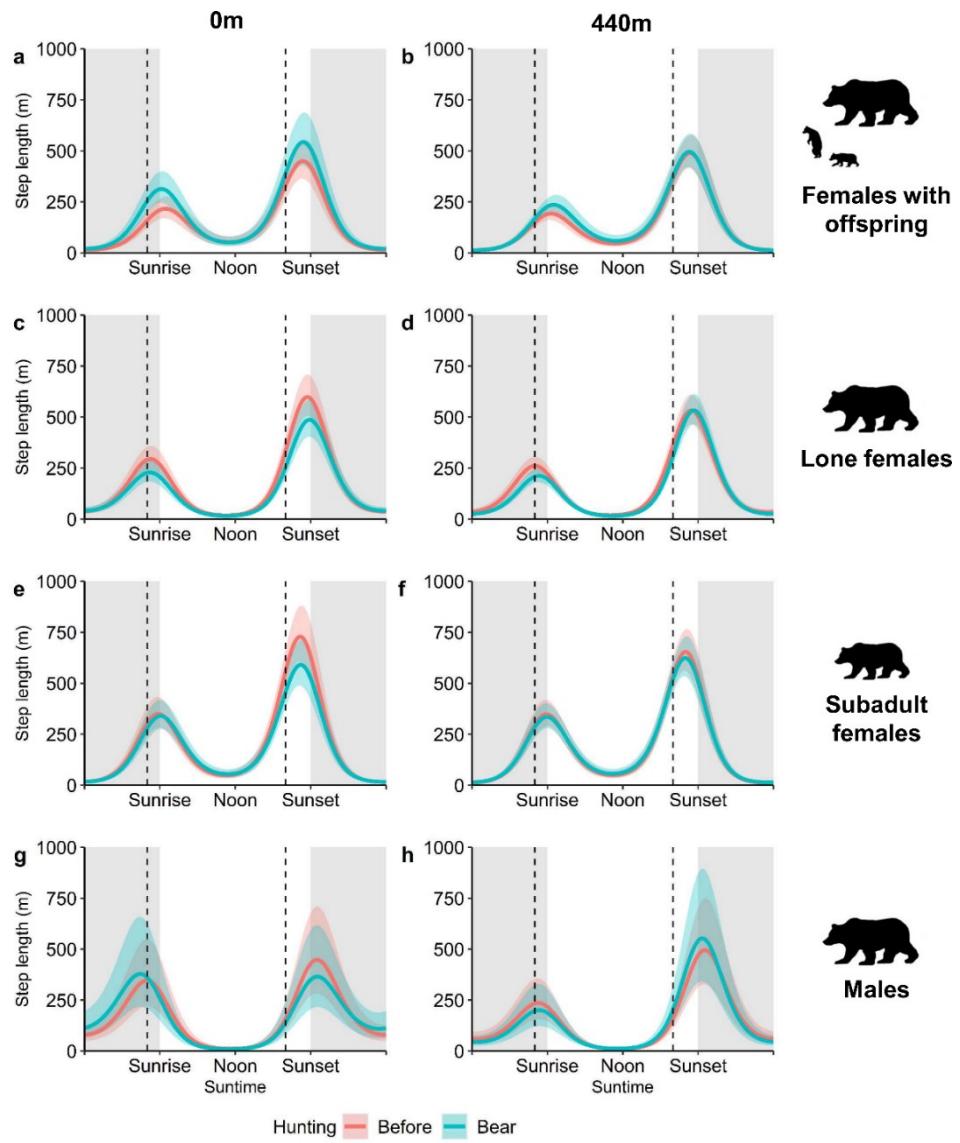


Figure 3.1 Predicted step length (m) with 95% confidence intervals for brown bears according to time of day during each season (before hunting and bear hunting) for females with dependent offspring ($n = 19$ bear-years), lone females ($n = 32$ bear-years), subadult females ($n = 32$ bear-years), and males ($n = 9$ bear-years) in south-central Sweden, during 2016–2019.

Step length was predicted at 0 m and 440 m (0 and 75% quantiles) from the closest road and during each season (red = before hunting, blue = bear hunting). The vertical dashed lines show the start (left) and end (right) of legal hunting

hours. Shaded areas represent nighttime, whereas the white areas represent daytime.

3.6 Discussion

We found partial support for our hypothesis that bears change their movement rates in response to spatiotemporal variations in risk from hunting. Our prediction was supported by an increased movement rate of females with dependent offspring in areas close to roads during the bear hunt and it also suggests that legal protection from harvest did not influence their movement response to perceived threat from hunters. In contrast to our prediction, we found a decreased movement rate in lone females during the bear hunt, whereas no effects of hunting were found in males and subadult females.

Our results suggest that the increased movement rate during the bear hunt in females with dependent offspring was likely an anti-predator response because it was more pronounced closer to roads, where most bear mortalities occur in our study area (Steyaert et al. 2016). Increased movement rate in response to hunting has been observed in moose (*Alces alces*) from Alaska, USA, where individuals living in areas accessible by hunters have higher movement rates during the hunting period compared to individuals located in areas with poor road access (Brown et al. 2018). A similar pattern was reported in mule deer (*Odocoileus hemionus*) from Oregon, USA, that also increased movement rates during the hunting season (Brown et al. 2020). Increased movement rates in areas close to roads during the bear hunt may be a way for females with dependent offspring to reduce the amount of time spent in areas where perceived risk is high.

We observed a decreased movement rate in lone females during the bear hunt and this response has also been associated with anti-predatory tactics used to prevent detection from predators (Ordiz et al. 2012; Marantz et al. 2016; Paton et al. 2017); however, the decreased movement rate in lone females is unlikely a response to hunting because their movement rate was similar in areas close to roads and those located further away during the bear hunt. A general decrease

in movement is likely more consistent with a seasonal pattern. Alternatively, it may also indicate that female bears adopt different anti-predatory tactics when accompanied by dependent offspring. Previous studies have shown that white-tailed deer (*O. virginianus*) and caribou (*Rangifer tarandus*) have different responses to risk when accompanied by fawns or calves (Viejou et al. 2018; Higdon et al. 2019). Higher energy requirement from rearing offspring may also prevent females from foregoing foraging during the bear hunt resulting in a stronger flight response when a threat is perceived, whereas lone females may react differently and hide in concealed locations to avoid detection during the bear hunt (Brown et al. 2023).

Members of family groups are protected and cannot be legally harvested by hunters in Sweden; however, they are still chased by hunting dogs that have been released to search and follow scent trails from bears. The death rate of bears once dogs have engaged in a pursuit is unknown, but the risk of mortality from hunting is low in the protected demographic groups (Van de Walle et al. 2018). This also suggests the possibility that legal protection from harvest does not prevent repeated harassment of the protected segment of the population, which may carry significant energetic costs. Simulated hunts with dogs have shown that both bears and moose increase movement speed on the day the disturbance had occurred, followed by a reduction in movement during the days after a disturbance had occurred (Ordiz et al. 2013; Le Grand et al. 2019; Græsli et al. 2020). This implies that females with dependent offspring initially spend more energy to leave high-risk areas after an encounter with hunters.

We showed that females with dependent offspring increase their movement rate in response to hunting, which could lead to increased energy expenditure during a critical time of the year. Although we did not measure energy expenditures in bears, the link between increased energetic costs due to higher speed in mammals is well established (Pagano et al. 2018). The disturbance caused by hunting coupled with a lower foraging efficiency during the hunting season could have consequences on survival and reproductive success in brown bears (Hertel et al. 2016) and other non-target species (Brown et al. 2020). Legal protection from harvest does not prevent repeated harassment during the hunting period, which could increase energetic costs in

individuals that are protected from harvest. Wildlife managers should be aware that hunting may still induce indirect behavioural costs in species or individuals that are legally protected from harvest.

3.7 Data accessibility

Data and codes to replicate statistical analyses are provided as electronic supporting information.

3.8 Author contributions

L.B.: conceptualization, formal analyses, investigation, methodology, writing—original draft; A.Z.: conceptualization, supervision, writing—review and editing; J.K.: project administration, funding acquisition, writing—review and editing; F.P.: conceptualization, supervision, funding acquisition, writing—review and editing. All co-authors gave final approval for publication.

3.9 Competing interest

None to declare

3.10 Acknowledgements

The Norwegian Environment Agency, the Swedish Environmental Protection Agency, the Research Council of Norway and the Austrian Science fund are the primary funders of the Scandinavian Brown Bear Research Project. FP was supported by NSERC Discovery grant (2018-05405) and E.W.R. Steacie Memorial Fellowship (549146-2020). We thank the field crew who took part in the bear captures, especially David Ahlqvist and Andrea Fribe. We also thank Martin Leclerc, Shane Frank and Anne Hertel for consultation regarding the design of statistical analyses.

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CHAPITRE 4

INFLUENCE DE LA DENSITÉ DE RÉCOLTE DE GROS GIBIER SUR L'EXPOSITION AU PLOMB CHEZ L'OURS NOIR

4.1 Description de l'article et contribution

Le lien entre la chasse au gros gibier et l'exposition au plomb chez les charognards est bien établi dans la littérature. Chez les charognards aviaires, la densité de récolte de gros gibiers est reconnue pour influencer le risque d'exposition au plomb; cependant, peu d'études ont tenté de documenter le lien entre la densité de récolte de gros gibiers et l'exposition au plomb chez les mammifères charognards, malgré le fait que plusieurs espèces de mammifères soient couramment observées aux sites d'abattage de gros gibiers. L'objectif de ce chapitre était de déterminer si la densité de récolte de gros gibier affecte l'exposition au plomb chez un grand omnivore opportuniste, l'ours noir d'Amérique (*Ursus americanus*). Les résultats de ce chapitre montrent qu'il y a un lien entre la densité de récolte de gros gibiers par arme à feu et les concentrations de plomb dans les dents d'ours noirs au Québec et qu'il y a aussi une importante bioaccumulation de plomb avec l'âge chez cette espèce. Cela suggère que la chasse récréative augmente le risque d'exposition au plomb chez l'ours noir au Québec et que ces derniers accumulent de plus grandes concentrations de plomb au cours de leur vie dans les endroits où la densité de récolte de gros gibiers par arme à feu est plus élevée. Globalement, les résultats obtenus lors de ce chapitre montrent que les mammifères opportunistes qui consomment les restes d'abattage contaminés par des fragments de plomb peuvent s'exposer au plomb au même titre que les charognards aviaires durant la période de chasse.

J'ai développé l'idée originale pour cet article en collaboration avec Fanie Pelletier et Andreas Zedrosser. J'ai conditionné les échantillons pour les analyses chimiques, construit la banque de données, réalisé les analyses statistiques et rédigé la première version de ce chapitre. Maikel Rosabal a coordonné les analyses de laboratoire et fourni du matériel lors des analyses préliminaires. Christian Dussault a coordonné l'envoi des échantillons et a fourni les données

d'âge et de chasse provenant du Ministère des Forêts, de la Faune et des Parcs du Québec. Tous les auteurs ont contribué à l'interprétation des résultats et à améliorer la qualité de ce manuscrit en commentant le texte et la méthodologie. Cet article est publié dans le journal *Environmental Pollution*. <https://doi.org/10.1016/j.envpol.2022.120427>.

Lead exposure in American black bears increases with age and big game harvest density

Environmental Pollution (2022) 315, 120427

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<https://doi.org/10.1016/j.envpol.2022.120427>

4.2 Abstract

Hunting has multiple consequences for wildlife, and it can be an important source of environmental pollution. Most big game hunters use lead (Pb) ammunition that shed metal fragments in the tissues of harvested animals. These Pb fragments become available to scavengers when hunters discard contaminated slaughter remains in the environment. This exposure route has been extensively studied in avian scavengers, but few studies have investigated Pb exposure from ammunition in mammals. Mammalian scavengers, including American black bears (*Ursus americanus*), frequently use slaughter remains discarded by hunters. The objective of this study was to investigate whether big game harvest density influenced long-term Pb exposure in American black bears from Quebec, Canada. Our results showed that female black bears had higher tooth Pb concentrations in areas with higher big game harvest densities, but such relationship was not evident in males. We also showed that older bears had higher tooth Pb concentrations compared to younger ones. Overall, our study showed that Pb exposure increases with age in black bears and that some of that Pb likely comes from bullet fragments embedded in slaughter remains discarded by hunters. These results suggest that hunters may drive mammalian scavengers into an evolutionary trap, whereby the long-term benefits of consuming slaughter remains could be negated due to increased Pb exposure.

Keywords: *Ursus americanus*, scavenger, Pb, ammunition, bioaccumulation, hunting

4.3 Introduction

Recreational hunting has well documented consequences on wildlife behavior and populations (Frank et al., 2017; Gaynor et al., 2018; Leclerc et al., 2017), while also being an important source of environmental pollution (Arnemo et al., 2022). The use of lead (Pb) ammunition for hunting is an important source of Pb emissions and poses a threat to both humans and wildlife (Arnemo et al., 2022; Fachehoun et al., 2015; Fisher et al., 2006; Hampton et al., 2018; Heier et al., 2009). In addition to the toxicity of their principal component, another concern regarding the use of Pb ammunition is their propensity to fragment upon impact. Bullets used for hunting medium to large game animals must expand when penetrating tissues to increase damage (Stokke et al., 2018). Consequently, Pb bullets shed metal fragments along the wound channel (Gremse et al., 2014; Kollander et al., 2017; Menozzi et al., 2019; Stokke et al., 2017). X-rays of carcasses have shown that animals shot with Pb bullets had signs of metal (i.e., Pb) depositions in several tissues and organs in a radius of up to 45 cm around the wound channel (Grund et al., 2010; Hampton et al., 2021; Hunt et al., 2006; Menozzi et al., 2019).

Multiple species of obligate and facultative scavengers feed on slaughter remains (Finkelstein et al., 2012; Gomo et al., 2017; Lafferty et al., 2016; Legagneux et al., 2014; Wikenros et al., 2013) and are at greater risk of Pb exposure. This risk is also proportional to the number of carcasses contaminated with Pb bullets within an area, and thus harvest density is generally an important predictor of Pb levels in scavengers (Helander et al., 2021; Kelly et al., 2021; Kelly and Johnson, 2011; Wayland and Bollinger, 1999). Most species for which Pb exposure from ammunition has been documented are birds (Golden et al., 2016; Pain et al., 2019), but several mammal species also consume slaughter remains (Lafferty et al., 2016; Legagneux et al., 2014); however, little attention has been devoted to Pb exposure from ammunition sources in mammalian scavengers (Kelly et al., 2021; Rogers et al., 2012).

Anecdotal evidence suggests that mammals are also at risk of Pb exposure by ingesting bullet fragments embedded in the carcasses of shot animals (Chiverton et al., 2022). Any intake of Pb

is toxic and affects all systems of all vertebrates by, for example, inducing oxidative stress or substituting essential ions (e.g., Ca^{+2}), thereby disrupting physiological processes (Pain et al., 2019; Singh et al., 2018). Pb exposure translates into increased mortality rates and altered movement patterns in avian scavengers (Ecke et al., 2017; Singh et al., 2021). Therefore, the risk of Pb exposure from spent ammunition needs to be evaluated in mammals. In this study, we used the American black bear (*Ursus americanus*) as a model for mammalian scavengers to investigate Pb exposure from recreational hunting. The American black bear is an opportunistic omnivore (Bastille-Rousseau et al., 2011; Popp et al., 2018) that is commonly observed scavenging on slaughter remains discarded by hunters (Lafferty et al., 2016). Legagneux et al. (2014) showed that they were the most abundant mammalian scavenger at moose (*Alces alces*) kill sites in Quebec, Canada, suggesting that they are at risk of Pb exposure. This risk is further exacerbated because most big game hunters in Quebec (~ 75%) still use Pb ammunition (Fachehoun et al., 2015), which indicates that most slaughter remains discarded by hunters contain Pb fragments.

The risk of Pb exposure can be assessed by determining the concentrations in specific tissues. For instance, teeth are known for accumulating high Pb levels and are a reliable tool for monitoring long-term Pb exposure in humans (Barbosa et al., 2005). Teeth are composed of different calcified tissues (enamel, dentin and cementum) that incorporate the Pb that was absorbed at the time of their formation (Barbosa et al., 2005). The cementum forms continuously and Pb accumulates in this tissue over lifetime (Clark et al., 2021). The accumulation of Pb in teeth is thus age- and dose-dependent (Arora and Hare, 2015; Steenhout and Pourtois, 1981).

The objective of this study was to investigate whether big game hunting influences the long-term Pb exposure in a large facultative scavenger, the American black bear. We hypothesized that harvest density (number of large animals killed/km²) affects the Pb concentration in black bears because individuals living in areas with higher harvest density have greater access to slaughter remains with embedded Pb fragments. We also hypothesized that Pb levels in bears vary by age. We predicted 1) that the Pb concentrations in black bear teeth are positively related

to harvest density around the sampling locations, and 2) that older bears have higher tooth Pb concentrations compared to younger bears.

4.4 Materials and Methods

4.4.1. Study area

Our study was carried out in the province of Quebec, Canada. The province is divided into several ecoregions with deciduous and mixed forests in the south, boreal forests at mid-latitudes and tundra in northernmost areas (Figure S4.1). American black bears (from now on referred to as black bears) occur in all regions of the province and can either be trapped or hunted from mid-May to the end of June. In some management units, bears can also be hunted during the fall, but the fall hunt is much less popular than the spring hunt. White-tailed deer (*Odocoileus virginianus*) are mainly present in deciduous and mixed forests in the south of the province and can be hunted with either primitive weapons or modern firearms from October to November (Huot and Lebel, 2012). Moose are more abundant in mixed and boreal forests. Moose hunting takes place between September and October with specific seasons for primitive weapons and modern firearms (Lefort and Massé, 2015).

4.4.2. Sample collection and chemical analyses

We obtained black bear teeth ($n = 80$ females; $n = 115$ males) collected from individuals that were legally harvested in 22 management units during the annual bear hunt in 2017 and 2018. Two vestigial premolars (PM1) were extracted; one was sent to Matson's Laboratory (Manhattan, Montana; matsonslab.com) for age determination by counting cementum growth layers (Matson et al., 1993), and the second tooth was used for chemical analyses.

The teeth used for chemical analyses were cleaned with a scalpel to remove any trace of soft tissues and soaked in a solution of 3 mM EDTA (MB Grade, Ultrapure, Thermo Scientific,

Ottawa, Ontario, Canada) to remove the trace elements on their surface. We rinsed the teeth under milli-Q water to make sure no EDTA was left on the samples, and then stored them in metal-free tubes (Metal-Free Centrifuge Tubes, VWR International, Mississauga, Ontario, Canada) at room temperature until digestion procedures. The samples were digested overnight in 2 ml of 65% (v/v) nitric acid (HNO₃; Optima grade, Fisher Scientific, Whitby, Ontario, Canada). Then, the digestion procedure was completed by heating the samples at 65°C for 2 hours before completing the volume to 15 ml with milli-Q water. The Pb concentrations were determined by inductively coupled plasma mass spectrometry (ICP-MS; Thermo Elemental X Series, Winsford, England, UK). We used Bone Meal (SRM 1486, National Institute of Standards and Technology, Gaithersburg, MD, USA) as a certified reference material, which yielded an average recovery rate of 95 ± 6 % (mean ± s.d.; n = 6). The Pb concentrations for digestion blanks were higher than the method detection limits (0.003 ± 0.003 µg/g), but negligible in comparison to metal concentrations measured in our samples [on average less than 1% of the minimum Pb concentration (0.39 µg/g) measured in black bear teeth].

4.4.3. Big game harvest density

By regulation, big game hunters in Quebec must register all harvested black bears, moose, and white-tailed deer with the Quebec Ministry of Forests, Wildlife and Parks, and provide information on the kill location and the type of weapon used (i.e., bow, crossbow, muzzleloader, shotgun, or rifle). To estimate fine-scale harvest density, we generated a grid of 25 km² cells across the province and counted the number of big game animals harvested within each cell. We defined harvest density as the number of white-tailed deer (n = 252,470), black bears (n = 21,719) and moose (n = 126,881) harvested with a firearm within each 25 km² grid cell during 2013-2018 (Figure 4.1). We extracted the average big game harvest density within buffers of 2 to 12 km (i.e., in 1 km increments) centered around each bear harvest locations.

We selected those buffer sizes because they represent realistic home range sizes for black bears (Ditmer et al., 2018) and they adequately represent areas that could have been used by black bears before their death.

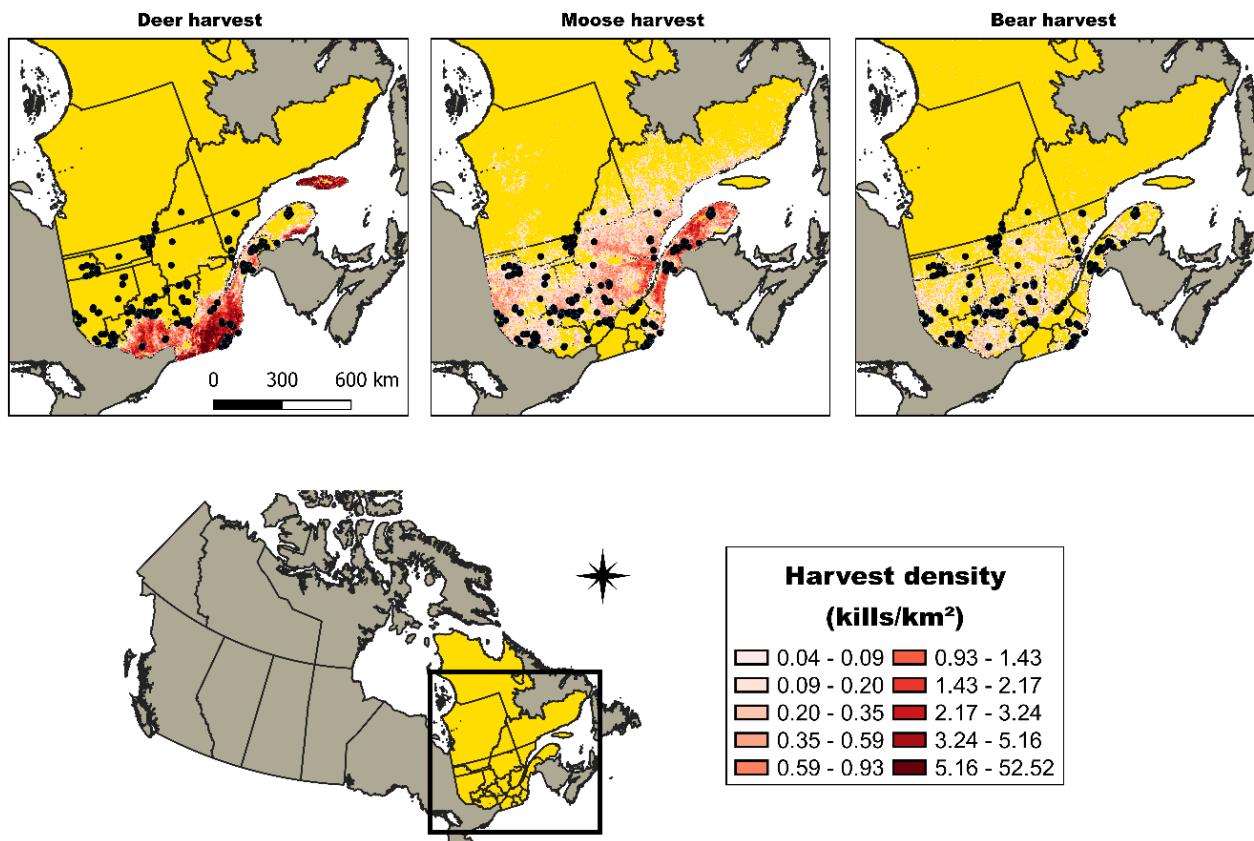


Figure 4.1 Big game harvest density (kills/km²) in Quebec, Canada.

Harvest density is defined as the number of white-tailed deer, moose, and American black bears harvested with a firearm per km² during 2013-2018. The black dots indicate the black bear harvest locations ($n = 195$). Yellow areas indicate that harvest density was 0.

4.4.4. Statistical analyses

We build a set of thirteen candidate linear mixed effect models predicting the Pb concentrations in black bear teeth by using the lme4 package (Bates et al., 2015). We analyzed males and females separately because there are intersexual differences in space use and foraging behavior (Ditmer et al., 2018, 2016), which could affect the potential of Pb exposure. This approach allowed us to select the most appropriate scale for males and females. Male bears typically have larger home ranges than females (Ditmer et al., 2018) and that could affect the scale at which harvest density affects Pb exposure in both sexes. The model set included a Null model, an age only model, and one measure of harvest density, i.e., the number big game killed at one of 2 to 12 km (Table 4.1). All models included a random intercept for the management unit in which the bears were killed, which controlled for potential variations in background Pb levels and other emission sources across our study area. Model selection was conducted by Akaike Information Criterion corrected for small sample size (AICc) with the AICcmodavg package (Mazerolle, 2020). We considered models with $\Delta\text{AICc} < 2$ to be equivalent but only discussed the top model. We used the r^2 function from the *performance* package (Lüdecke et al., 2021) to obtain the conditional and marginal R² of the top models.

We investigated spatial autocorrelation within our dataset with the Moran.I function [ape package; (Paradis and Schliep, 2019)]. The tooth Pb concentrations were not spatially correlated in females (Moran's I = 0.05, p = 0.35) nor in males (Moran's I = 0.06, p = 0.23) and thus we did not include a spatial autocorrelation structure in subsequent analyses. We used diagnostic plots to ensure that model assumptions were respected, and we log-transformed the Pb concentrations to achieve normality and homoscedasticity of residuals. All statistical analyses were carried out in R version 4.1.0 (R Core Team, 2021).

Table 4.1 Candidate linear mixed effect models used to predict log-transformed tooth lead (Pb) concentrations ($\mu\text{g/g}$) in hunted female ($n = 80$) and male ($n = 115$) American black bears in Quebec, Canada, during 2017-2018. All models included the management unit (i.e., MU) in which the bears were killed as a random intercept. Harvest density was measured in buffers with a radius of 2 to 12 km in 1 km increments.

	Model structure	Biological hypotheses
Null	$\log(\text{Pb}) \sim 1 + (1 \text{MU})$	Pb is constant
Age	$\log(\text{Pb}) \sim \text{Age} + (1 \text{MU})$	Pb is influenced by age
2 – 12 km	$\log(\text{Pb}) \sim \text{Harvest density} + \text{Age} + (1 \text{MU})$	Pb is influenced by age and harvest density within one of 2 to 12 km buffer

4.5 Results

White-tailed deer harvest density ranged from 0 to 52 kills/km² (0.08 ± 0.70 kills/km²), whereas moose harvest density ranged from 0 to 5.48 kills/km² (0.04 ± 0.20 kills/km²), and bear harvest density from 0 to 2.88 kills/km² (0.01 ± 0.04 kills/km²) (Figure 4.1). Deer harvest density was highest in the South of the province and contrasted with moose harvest density which was highest at mid-latitudes and towards the East, whereas bear harvest density was generally low and scattered across the province (Figure 4.1). The Pb concentrations in black bear teeth ranged from 0.39 to 8.89 $\mu\text{g/g}$ (Figure 4.2). The average Pb concentrations were 2.01 ± 1.61 $\mu\text{g/g}$ in females and 1.62 ± 0.93 $\mu\text{g/g}$ in males. The bear age ranged from < 1 to 16.5 years old. Females and males were on average 5.11 ± 3.21 years old and 4.26 ± 2.25 years old, respectively.

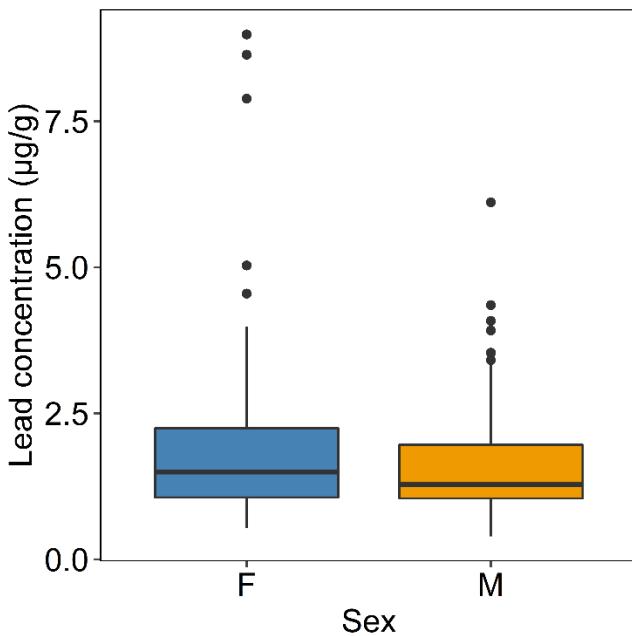


Figure 4.2 Tooth lead (Pb) concentrations ($\mu\text{g/g}$) measured in hunted female ($n = 80$) and male ($n = 115$) American black bears from Quebec, Canada, during 2017-2018.

Boxes represent the interquartile range, and the horizontal lines represent the median value of each group. Blue = females, orange = males.

The model that performed best at explaining tooth Pb concentration in female black bears was attributed 0.26 of the weight within the set of models and included the explanatory variables age and big game harvest density within 2 km (Table 4.2). The second-best model, including age and harvest density at 3 km, had a ΔAICc of 0.49 and was attributed 0.21 of the weight (Table 4.2). The third-best model that included an effect of age and harvest density at 4 km had a ΔAICc of 1.32 with a weight of 0.14 (Table 4.2). The top ranked model for males only included the effect of age and was attributed 0.19 of the weight within the set (Table 4.2). The models including the effect of harvest density at 2 to 6 km had $\Delta\text{AICc} < 2$ with top-ranked models and were each attributed between 0.07 to 0.09 of the weight (Table 4.2). These results suggest that adding harvest density did not contribute to better explain the tooth Pb concentrations in male bears compared to the model that only included an effect of age.

Table 4.2 Model selection by Akaike's Information Criterion corrected for small sample sizes (AICc). The models were used to predict log-transformed tooth lead (Pb) concentrations in hunted female ($n = 80$) and male ($n = 115$) American black bears from Quebec, Canada, during 2017-2018. K = number of parameters, AICc = AICc value, ΔAICc = delta AICc, w = model weight.

	K	AICc	ΔAICc	w
<i>Females</i>				
2 km	5	100.61	0.00	0.26
3 km	5	101.10	0.49	0.21
4 km	5	101.93	1.32	0.14
5 km	5	102.71	2.10	0.09
6 km	5	103.48	2.87	0.06
7 km	5	104.11	3.50	0.05
8 km	5	104.52	3.91	0.04
12 km	5	104.72	4.11	0.03
9 km	5	104.76	4.15	0.03
11 km	5	104.85	4.24	0.03
Age	4	104.85	4.24	0.03
10 km	5	104.89	4.27	0.03
Null	3	148.50	47.89	0.00
<i>Males</i>				
Age	4	159.37	0.00	0.19
2 km	5	160.85	1.48	0.09
3 km	5	160.95	1.58	0.09
4 km	5	161.07	1.70	0.08
5 km	5	161.19	1.82	0.08
6 km	5	161.31	1.94	0.07
7 km	5	161.42	2.05	0.07
8 km	5	161.48	2.11	0.07
9 km	5	161.51	2.14	0.07
10 km	5	161.53	2.16	0.07
11 km	5	161.54	2.17	0.06
12 km	5	161.54	2.17	0.06
Null	3	179.14	19.77	0.00

Our analyses suggest that harvest density within a buffer of 2 km centered on bear kill locations influenced the tooth Pb concentrations in female black bears (Table 4.3; Figure 4.3a), but this effect was only marginal in males (Table 4.2). For each increase of 1 kill/km² within a 2 km buffer, the tooth Pb concentrations in females increased by 11% (95% CI = 3-21%). To ensure that the relationship between big game harvest density and tooth Pb concentrations in female black bears was not driven by an outlier, we re-estimated the models after removing the observation with the highest harvest density and obtained similar results (Table S4.1).

Our results also indicate that age was an important predictor of tooth Pb concentrations in both males and females (Figure 4.3b & 4.3d). The Pb concentrations in bear teeth increased by 14% (95% CI = 10-17%) and 11% (95% CI = 6-15%) for every increase in one year in age in females and males, respectively. We also added a post-hoc analysis with the effect of big game harvest density (within a radius of 2 km) broken down by game species to determine whether the effect that we observed in females was constant across different hunts. The parameter estimates of this post-hoc analysis are presented as supporting information and showed that the observed effect was mainly driven by white-tailed deer harvest (Table S4.2).

Table 4.3 Estimates from the top-ranked linear mixed effect models used to predict log-transformed tooth lead (Pb) concentrations ($\mu\text{g/g}$) in hunted female ($n = 80$) and male ($n = 115$) American black bears in Quebec, Canada, during 2017-2018. Conditional R^2 represents the proportion of variance explained by both fixed and random effects, whereas marginal R^2 represents the proportion of variance explained by fixed effects only.

	Estimate	95% confidence intervals		Variance	s.d.			
		Lower	Upper					
Females								
<i>Fixed effects:</i>								
Intercept	-0.318	-0.552	-0.084	Management unit	0.043 0.207			
Harvest density (2 km)	0.108	0.028	0.187	Residuals	0.158 0.398			
Age	0.129	0.098	0.158					
Conditional $R^2 = 0.58$, Marginal $R^2 = 0.46$								
Males								
<i>Fixed effects:</i>								
Intercept	-0.107	-0.319	0.106	Management unit	0.037 0.193			
Age	0.102	0.060	0.142	Residuals	0.196 0.443			
Conditional $R^2 = 0.31$, Marginal $R^2 = 0.18$								

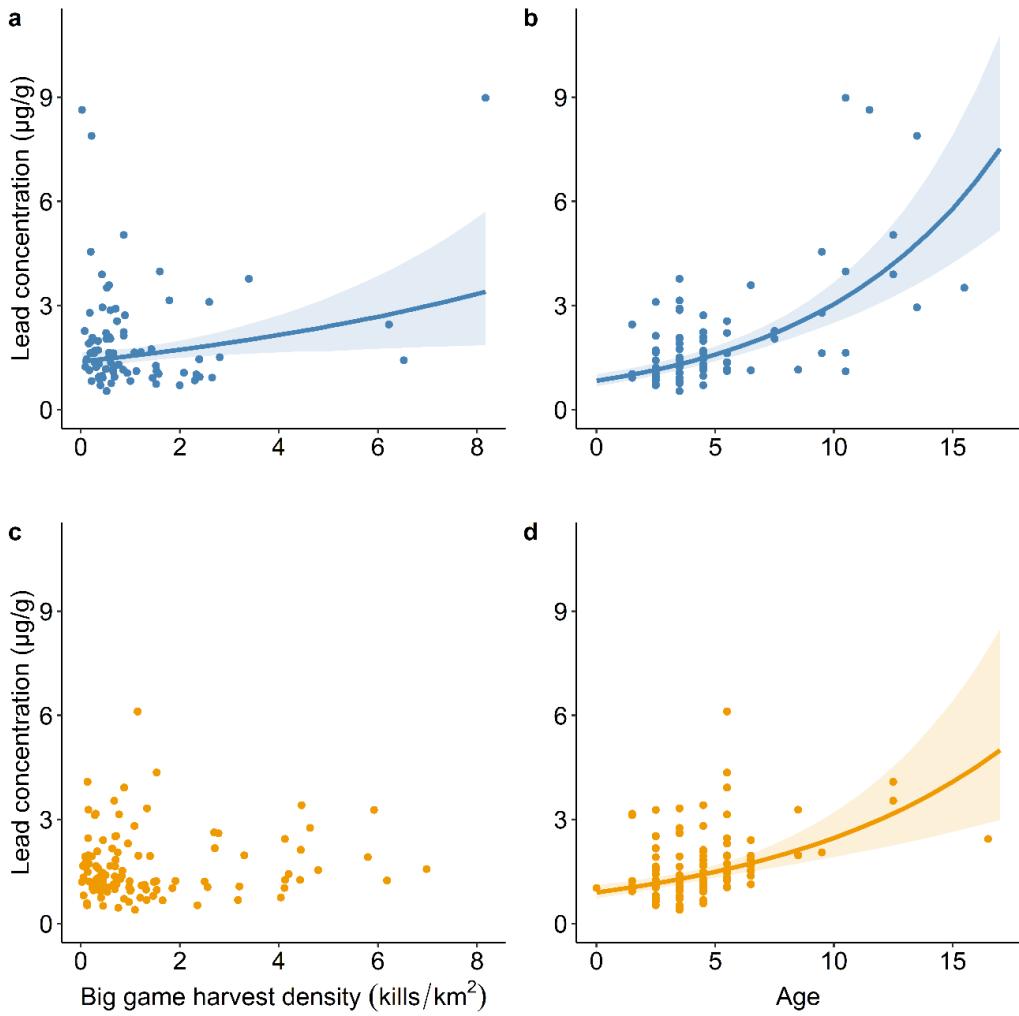


Figure 4.3 Predicted tooth lead (Pb) concentrations ($\mu\text{g/g}$) in hunted female ($n = 80$) and male ($n = 115$) American black bears from Quebec, Canada, during 2017-2018.

Panels a & c) predicted Pb concentrations across values of big game harvest density (kills/km^2) with age fixed at 5 years old and panels b & d) predicted Pb concentrations across the age of the individuals (years) with harvest density fixed at $1.24 \text{ kills}/\text{km}^2$. Lines show predictions with 95% confidence intervals, whereas points represent the raw data used to estimate the models. Blue = females, orange = males. Harvest density was not retained in the top-ranked model for males.

4.6 Discussion

We found that Pb exposure in black bears increased with harvest density, but this effect was only present in females and this effect was mainly driven by white-tailed deer harvest density, which was on average twice as high as the average moose harvest density. We also found that tooth Pb concentrations increased with age in both males and females. Overall, our results suggest that big game harvest density has the potential to influence the long-term risk of Pb exposure in a facultative scavenger and that bears accumulate Pb in their teeth over their lifetime.

Harvest density has been identified as an important predictor of Pb levels in the tissues of avian scavengers (Helander et al., 2021; Kelly and Johnson, 2011; Wayland and Bollinger, 1999). Here, we found a similar result in a large facultative mammalian scavenger. As harvest density, and by extension slaughter remain density increases, the Pb fragments from bullets become increasingly available to scavengers, which is reflected in the Pb concentrations of the dental tissues of black bears. Bears likely accumulate Pb from multiple sources, including emissions from fossil fuel combustion (Chételat et al., 2022) and by ingesting soil while foraging (Gall et al., 2015); however, our study suggests that recreational hunting can be an additional source of Pb exposure in mammalian scavengers over their lifetime, even if slaughter remains are only available during a relatively short period (i.e., a few weeks) each year (Gomo et al., 2017). Considering that Pb ammunitions increases Pb exposure in scavengers, big game hunters could drive bears and possibly other mammalian scavengers into an evolutionary trap, whereby they make maladaptive decisions based on cues that have been altered by human activities (Schlaepfer et al., 2002).

It is advantageous for scavengers to feed on slaughter remains as it allows them to gain access to animal proteins at minimal costs (DeVault et al., 2003); however, scavenging on slaughter remains discarded by hunters can be a maladaptive decision because this resource likely contain Pb fragments from bullets. Over the long-term, hunting with Pb ammunition may negate the

short-term benefits associated with consuming fresh slaughter remains by exposing scavengers to high Pb levels. Previous studies showed that avian scavengers exposed to Pb from bullet fragments have decreased survival and population growth rates, even at low levels of exposure (Green et al., 2022; Singh et al., 2021; Slabe et al., 2022). It was also shown that blood Pb concentrations of 25 ppb was sufficient to alter the flight behavior in golden eagles (*Aquila chrysaetos*) (Ecke et al., 2017) and that individuals with blood Pb concentrations above this value were 4.2 more likely to die compared to eagles below this threshold (Singh et al., 2021). Although these results in golden eagles cannot be directly compared to black bears in our study, they suggest that deleterious effects of Pb can occur at levels of exposure that are well below commonly reported guidelines (Ecke et al., 2017). Considering that toxicity thresholds are generally lower in mammals compared to birds (Buekers et al., 2009), we could expect sublethal effects in mammalian scavengers that are exposed to low Pb levels, but whether such consequences occur in black bears remains to be determined.

The Pb concentrations in black bear teeth are difficult to contextualize in relation to physiological consequences because toxicity thresholds in bears are unknown and only a few other studies are available to make comparisons. A previous study reported Pb concentrations of 1.32 ± 0.27 ppm and 15.08 ± 4.05 ppm in the dentine and enamel of black bear teeth, respectively (Kohn et al., 2013). Although the concentrations that we reported in our study appear in the middle of this range, we could not make direct comparison because we determined Pb concentrations in whole teeth instead of tissue-specific concentrations with laser ablation. The Pb concentrations reported in our study were lower than those previously reported in bank voles ($11.5\text{--}80.2\text{ }\mu\text{g/g}$) (*Clethrionomys glareolus*) from contaminated areas in Poland (Appleton et al., 2000). Some of our samples had Pb concentrations that were consistent with those reported in the enamel of humans that grew up during the leaded gasoline era [peak value of $4.94\text{ }\mu\text{g/g}$; (Robbins et al., 2010)], thereby suggesting that some black bears were exposed to abnormally high Pb levels at least at some point over their lifetime.

We also found that age was an important predictor of Pb levels in bear teeth, which is in accordance with multiple studies that showed a similar effect of age on Pb levels in the tissues of both birds and mammals (Clark et al., 2021; Gall et al., 2015; Lazarus et al., 2018; Slabe et al., 2022). For instance, a similar relationship between age and tooth Pb burden has been reported in humans (Steenhout and Pourtois, 1981). Pb kinetic is unknown in bears, but we can assume that as in humans, it follows a three-compartment model (i.e., blood-organ-bones) and that total body concentrations increase with time (regardless of exposure rate) due to the long half-life (i.e., 10-30 years) of elimination in bones (Arnemo et al., 2022). Increasing tooth Pb concentrations with age was expected because the elimination rate of Pb in teeth is negligible (Steenhout, 1982) and the concentrations measured in whole-teeth represent cumulative life-time exposure.

It is unclear why big game harvest density only affected Pb exposure in females and not in males. This result was unexpected since gut piles should be available to both sexes and males are in general more carnivorous than females (Ditmer et al., 2016). Part of the explanation may reside in behavioral differences between males and females; males typically have much larger home ranges ($>100 \text{ km}^2$) compared to females ($\sim 30 \text{ km}^2$) during the mating season in June and July (Brodeur et al., 2008; Ditmer et al., 2018; Koehler and Pierce, 2003), which partially overlap with the bear hunting season in Quebec. Thus, it is possible that the buffers centered on harvest locations may not be as representative of the feeding areas used by males during the fall when most carcasses and gut piles are available and could explain the lack of relationship between harvest density and Pb levels in males. Physiological differences between males and females, especially during lactation, could alternatively explain the intersexual differences that we observed. Maternal transfer of Pb during gestation is unlikely to be an important factor because this period lasts for about two months during hibernation in bears (Clamon Schulz et al., 2003); however, lactation can last more than a year and peaks between June and July, which also correspond to the period of fastest growth in cubs (Arnould and Ramsay, 1994; Farley and Robbins, 1995). During lactation, there is remobilization of Pb stored in bones, which increases

blood Pb concentrations (Fuchs et al., 2021) and possibly increase the amount of Pb that can be deposited in dental tissues during their formation.

Increased Pb absorption during lactation could also explain intersexual differences in tooth Pb concentrations. Although lactation decreases during late summer and fall, females with cubs still lactate during the fall hunting season (Farley and Robbins, 1995). Intestinal Pb absorption from food increases from 10% to approximatively 20% during lactation (Maldonado-Vega et al., 1996), resulting in lactating females absorbing higher proportions of ingested Pb compared to non-lactating females and males. Overall higher Pb absorption in females due to years of lactation could have allowed our models to detect the effect of big game harvest density and would explain the male and female differences. Males scavenging on gut piles and carcasses may absorb a smaller portion of ingested Pb and, when coupled with the relatively short-term availability of slaughter remains (Gomo et al., 2017), it may be insufficient to cause significant increase in whole-tooth Pb concentrations, which reflect cumulative life-time exposure.

4.7 Conclusion

Our study provides evidence that big game harvest density influences tooth Pb concentrations in female black bears, and that tooth Pb concentrations increased with age in both male and female bears. Overall, these results suggest that bears living in areas with high big game harvest density may face increased long-term Pb exposure and ultimately a higher risk of Pb poisoning. It is currently unknown whether the observed increase in tooth Pb concentrations has deleterious effects on black bears at the individual or population level and additional studies are needed to provide insight into this aspect. Laser ablation (e.g., LA-ICP-MS) may be useful for reconstructing the history of Pb exposure by measuring concentrations in cementum layers of teeth (Clark et al., 2021). Blood samples collected shortly after the hunting season could provide information on short-term exposure during this period and facilitate comparisons with reference levels associated to deleterious effects in other mammals. If such consequences occur, hunters

could create an evolutionary trap for black bears and possibly other mammals that scavenge on slaughter remains that are discarded during the hunting season.

4.8 Declaration of interest

The authors declare no conflict of interest.

4.9 Credit author statement

Ludovick Brown: Conceptualization, Methodology, Formal analyses, Investigation, Writing — original draft; **Maikel Rosabal:** Methodology, Investigation , Resources, Writing — review & editing, Project administration; **Christian Dussault:** Investigation, Resources, Writing — review & editing, Funding acquisition, Project administration; **Jon M. Arnemo:** Writing — review & editing; **Boris Fuchs:** Writing — review & editing; **Andreas Zedrosser:** Conceptualization, Supervision, Writing — review & editing; **Fanie Pelletier:** Conceptualization, Supervision, Writing — review & editing, Funding acquisition, Project administration.

4.10 Funding

This study was funded by NSERC Discovery grant (2018-05405), E.W.R. Steacie Memorial Fellowship (549146-2020) and the Quebec Ministry of Forests, Wildlife and Parks.

4.11 Acknowledgement

We thank the Quebec Ministry of Forests, Wildlife and Parks for providing the black bear teeth and age data, as well as harvest locations of big game.

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CHAPITRE 5

LIEN ENTRE LA DISTRIBUTION DES SITES D'ABATTAGE D'ORIGNAUX ET L'EXPOSITION AU PLOMB CHEZ L'OURS BRUN

5.1 Description de l'article et contribution

Dans ce chapitre, j'ai vérifié comment les concentrations de plomb dans le sang des ours bruns en Suède varient en fonction de la distribution des sites d'abattage d'orignaux et des variations dans les concentrations de plomb dans le sol. Mes travaux montrent que les concentrations de plomb dans le sang des ours sont positivement corrélées avec la probabilité de sites d'abattage d'orignaux et avec les concentrations de plomb dans le sol autour du site de capture des ours. De façon plus générale, mes résultats montrent que les fonctions de sélection de ressources basées sur un échantillon de sites d'abattage de gros gibiers pourraient être utiles afin de prédire la distribution de sites d'abattage à fine échelle à l'intérieur d'une région et cela devient particulièrement utile dans les endroits où nous n'avons pas accès aux coordonnées GPS de tous les sites d'abattage comme c'est le cas en Suède. Cette approche pourrait permettre de raffiner certaines analyses en incorporant les variations spatiales à fine échelle dans la disponibilité des carcasses et ainsi mieux prédire le risque d'exposition au plomb provenant des munitions. Cela est particulièrement important lorsque l'espèce modèle est un mammifère dont les mouvements sont plus restreints que ceux des oiseaux. J'ai élaboré l'idée et la méthodologie initiale. J'ai aussi réalisé les analyses statistiques et spatiales en plus d'écrire la version initiale de ce manuscrit. Boris Fuchs a construit la base de données contenant les données de plomb et celles sur les ours. Jon Arnemo et Boris Fuchs ont capturé les ours et collecté les échantillons de sang. Ils ont aussi fourni les données de plomb dans le sang des ours. Ilia Rodushkin a réalisé les analyses chimiques. Tous les auteurs ont contribué à améliorer la méthodologie et le texte en commentant la version initiale. Cet article est publié dans le journal *Science of the Total Environment*, <https://doi.org/10.1016/j.scitotenv.2023.162099>.

Lead exposure in brown bears is linked to environmental levels and the distribution of moose kills

Science of the Total Environment (2023) 873, 162099

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<https://doi.org/10.1016/j.scitotenv.2023.162099>

5.2 Abstract

Lead (Pb) is heterogeneously distributed in the environment and multiple sources like Pb ammunition and fossil fuel combustion can increase the risk of exposure in wildlife. Brown bears (*Ursus arctos*) in Sweden have higher blood Pb levels compared to bears from other populations, but the sources and routes of exposure are unknown. The objective of this study was to quantify the contribution of two potential sources of Pb exposure in female brown bears (n = 34 individuals; n = 61 samples). We used multiple linear regressions to determine the contribution of both environmental Pb levels estimated from plant roots and moose (*Alces alces*) kills to blood Pb concentrations in female brown bears. We found positive relationships between blood Pb concentrations in bears and both the distribution of moose kills by hunters and environmental Pb levels around capture locations. Our results suggest that the consumption of slaughter remains discarded by moose hunters is a likely significant pathway of Pb exposure and this exposure is additive to environmental Pb exposure in female brown bears in Sweden. We suggest that spatially explicit models, incorporating habitat selection analyses of harvest data, may prove useful in predicting Pb exposure in scavengers.

Keywords: *Ursus arctos*, Pb, scavenger, slaughter remain, resource selection function

5.3 Introduction

Lead (Pb) is a naturally occurring trace element that is heterogeneously distributed in the environment and its geochemical cycle has been affected by human activities (Arnemo et al., 2022; Komárek et al., 2008). Atmospheric Pb emissions declined in most countries following the ban on leaded gasoline during the late-20th century (Danielsson and Karlsson, 2015; Nriagu, 1990; Strömberg et al., 2008), but unleaded gasoline and smelter emissions may still influence environmental Pb levels (Chételat et al., 2022; Chrastný et al., 2018; Widory et al., 2018). Pb also has a long residence time in soils and certain areas with high historic Pb depositions still contain high levels (Berglund et al., 2009). Thus, organisms inhabiting areas with high Pb levels are at greater risk of Pb exposure either by direct soil ingestion or by foraging on soil organisms or plants (Berglund et al., 2009; Scheifler et al., 2006). For instance, passerines sampled in urban environments, where the soils were contaminated by vehicle emissions, have higher blood Pb concentrations when compared to birds sampled in rural environments (Chatelain et al., 2021; McClelland et al., 2019; Roux and Marra, 2007).

Several types of human activities, such as hunting with Pb-based ammunition, can increase the level of Pb found in the environment. Bullets used in hunting rifles are designed to expand upon penetration and shed metal fragments in tissues (Green et al., 2022; Hunt et al., 2006; Kollander et al., 2017; Leontowich et al., 2022; Menozzi et al., 2019; Stokke et al., 2017). Carcasses and gut piles discarded during the hunting season have high numbers of embedded bullet fragments and animals that scavenge on this food resource can be exposed to high Pb levels (Fisher et al., 2006; Helander et al., 2021; Legagneux et al., 2014); and the resulting risk is not uniform in space because it is intrinsically linked to the distribution of hunters on the landscape.

Spatially explicit models can be used to predict the risk of Pb exposure from multiple sources in wildlife (Mateo-Tomás et al., 2016). These models are known for being sensitive to scale (Johnson et al., 2021); yet we are currently lacking information on the fine-scale variations in risk of Pb exposure from bullet fragments embedded in discarded slaughter remains. Many

studies have investigated the relationship between hunting and Pb exposure in scavengers without considering the spatial variation (Craighead and Bedrosian, 2008; Ecke et al., 2017; Legagneux et al., 2014), or only consider this aspect at coarser spatial scales (Kelly and Johnson, 2011; Singh et al., 2021), which may limit the identification of exposure sources, especially when the variations in environmental Pb levels are recorded at scales larger than the area used by model organisms (Johnson et al., 2021). In this study, we first modelled the fine-scale distribution of moose (*Alces alces*) harvest in Sweden by analysing moose harvest locations with habitat selection analysis, which originally has been developed to analyse data from GPS-collared animals (Northrup et al. 2022). Second, we determined whether variations in blood Pb levels in brown bears (*Ursus arctos*) were related to the distribution of harvested moose. Most studies that have investigated Pb exposure from bullet fragments embedded in slaughter remains in scavengers were on birds, but mammalian scavengers are also likely at risk of increased Pb exposure when feeding on slaughter remains (Brown et al., 2022; Chiverton et al., 2022; Kelly et al., 2021).

As model organism, we used the brown bear, an opportunistic omnivore that occupies large home ranges (Dahle and Swenson, 2003; Graham and Stenhouse, 2014; Schwartz et al., 2003) and feeds across trophic levels. In Sweden, brown bears feed mostly on berries, invertebrates, such as ants, as well as vertebrates, including moose calves and ungulate carcasses when available (Bojarska and Selva, 2012; Schwartz et al., 2003; Stenset et al., 2016). Due to their habitat use and foraging behaviors, brown bears could be exposed to multiple potential sources of Pb, including fossil fuel combustion and ammunition. Brown bears in Sweden are exposed to Pb from unconfirmed sources (Fuchs et al., 2021). The mean (SD) blood Pb level of 96.6 (35.6) µg/L reported by Fuchs et al. (2021) are higher than levels reported in North American [55 (40) µg/L] and other European [58.0 (34.7) µg/L] brown bears (Lazarus et al., 2018; Rogers et al., 2012). However, none of these studies have identified sources of Pb exposure in brown bears. Due to the high toxicity of Pb for vertebrates at low concentrations (Pain et al., 2019), it is important to identify the sources and understand the route of exposure in vertebrate scavengers to implement efficient management actions aiming at reducing Pb exposure in wildlife.

The aim of this study is to build a spatially explicit model to quantify the contribution of two potential sources of Pb to the blood Pb concentrations measured in Scandinavian brown bears: Pb from plant roots (hereafter refer to environmental Pb level) and Pb from ammunition used by moose hunters. We hypothesised that the environmental Pb levels, and the distribution of moose kills influence blood Pb concentrations in brown bears. We predicted that blood Pb concentrations in Scandinavian brown bears would be positively related to both environmental Pb levels, and the probability of moose kill.

5.4 Materials and Methods

5.4.1. Study area

The study area was in Dalarna and Gävleborg counties, south-central Sweden (~61°N, 15°E). The landscape mainly consists of a highly managed boreal forest with stands of different age classes and interspersed by lakes and bogs (Martin et al., 2010). The canopy is mainly composed of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and birch (*Betula* spp.), whereas the underlayer mainly consists of berry shrubs (*Vaccinium* spp.), heather (*Calluna vulgaris*) and grasses with mosses and lichens covering the ground (Elfström et al., 2008; Ordiz et al., 2013; Swenson et al., 1999). The area is also characterized by a dense network of forest roads (0.7 km/km²) and low human density (4-7 inhabitants/km²) (Martin et al., 2010; Ordiz et al., 2013).

Moose hunting in Sweden during the study period was allowed from the first Monday of September to the end of January and, on average, 84,000 moose are harvested annually during this period. Most moose (~75%) are harvested between September and the end of October (Wikrenos et al., 2013). Brown bears in Sweden typically enter their den towards the end of October (Evans et al., 2016; Friebe et al., 2014, 2001) and thus have access to the slaughter remains discarded by hunters. Those slaughter remains likely contain Pb fragments because most hunters in Scandinavia use Pb ammunition (Stokke et al., 2017).

5.4.2. Environmental Pb concentrations and hunting variables

We obtained a biogeochemistry (Biogeokemi) database from the Geological Survey of Sweden (© Sveriges Geologiska Undersökning) that contains the concentrations of trace elements, including Pb, of plant roots (*Carex* spp., *Fontinalis antipyretica* or *Filipendula ulmaria*) collected in or near small streams in Sweden between 1982 and 1996. The methods used for sampling and conducting chemical analyses are described in Lax and Selinus (2005). The trace element concentrations in plant roots reflect the concentrations in the water as well as those of the surrounding soil and bedrock and thus represent reliable estimates of the amount of trace elements circulating in the environment (Lax and Selinus, 2005). Our study area in south-central Sweden was represented by a total of 2,264 samples of plant roots in this database. We used these samples to predict environmental Pb concentrations on a dry weight basis across our study area by using ordinary kriging. We fitted a Matern variogram with Stein's parameterization (nugget = 0.224, psill = 0.366, kappa = 0.3, range = 0 – 23,594 m) with the *fit.variogram* function [*gstat* package (Gräler et al., 2016)] to predict Pb concentrations across our study area with a resolution of 500 m. The interpolated surface was generated with the *krige* function [*gstat* package, (Gräler et al., 2016)]. We log-transformed Pb concentrations and added a constant (C = 2.5) to all observations to obtain normally distributed data ($W = 0.99$, $p = 0.06$). We then back-transformed the predicted values to the original scale to obtain a map with predicted Pb concentrations across our study area. We used five-fold cross validation [*krige.cv* function; *gstat* package, (Gräler et al., 2016)] to assess the predictive power of the variogram.

The distribution of moose kills in south-central Sweden was estimated following the approach in Brown et al. (2023) by applying resource selection functions (RSF) to moose harvest locations during 2017-2019. Briefly, the RSF was estimated by using a logistic regression that contrasted the landscape characteristics at used (i.e., moose harvest locations provided by hunters) and available (i.e., random) locations (Fieberg et al., 2021; Manly et al., 2002). Hunters typically use areas that are located closer to roads and that have good lateral visibility (e.g., clearcuts), but avoid rugged terrain with poor visibility. The RSF included landcover types (i.e., forest

composition, clearcut and bogs), distance to closest road and other variables such as elevation, and terrain ruggedness index, which may impede the movement of hunters across the landscape. The values produced by an RSF are proportional to the probability of selection (Johnson et al., 2006; Manly et al., 2002) or, in this specific example, they are proportional to the probability of hunters killing a moose at any location within our study area. The relative probability of moose kill was estimated for each year based on moose harvest locations from the previous fall_{t-1}. The RSF model is described and validated in Brown et al. (2023).

5.4.3. Capture, sample collection and chemical analyses

We carried out a total of 61 captures of adult female brown bears ($n = 34$ individuals), during 2017-2020. The captures were carried out as part of the Scandinavian Brown Bear Research Project, which mainly focuses on the demography of female brown bears. A total of 34 samples were collected from lactating females, whereas 27 samples were collected from females that were not lactating. Some individuals ($n = 16$) were captured and sampled more than once. Bears were darted from a helicopter with a remote drug delivery system (Dan-Inject, Børkop, Denmark) during the spring (April to June). See Arnemo and Evans (2017) for more details on the capture protocol. The capture location was recorded with a hand-held GPS. At each capture, 4 or 6 mL of blood were collected from the jugular vein with evacuated K3EDTA tubes ($n = 26$) (Vacuette, Greiner Bio-One International GmbH, Kremsmünster, Austria) or evacuated heparin trace element tubes ($n = 35$) (Vacuette), respectively. The samples were first stored in a cooler in the field and then frozen at -20 °C until they were processed in the lab. The Pb concentrations was measured by inductively coupled plasma sector field mass spectrometry (ICP-SFMS, ELEMENT XR, Thermo-Scientific, Bremen, Germany). The blood samples collected during 2017-2019 ($n = 42$) were part of a previous study (Fuchs et al., 2021), which mainly aimed at determining whether blood Pb concentrations were correlated to life history traits. The Pb concentrations in digestion blanks were low (< 2µg/L) compared with sample results and the difference between measured and expected Pb concentration in the certified reference material (Seronorm Trace Elements Whole Blood Levels 1 and 2 from SERO AS,

Norway) was < 6% (Fuchs et al. 2021). See Fuchs et al. (2021) for further details about sample collections and Rodushkin et al. (2000) for further details about chemical analyses.

5.4.4. Statistical analyses

We calculated the mean environmental Pb concentrations, and the mean relative probability of moose kill (fall_{t-1}) within circular buffers with a radius of 2, 4 and 6 km around the capture locations. We used multiple linear regressions [*lm* function; *stats* package (R Core Team, 2021)] to determine if the environmental Pb concentrations and the probability of moose kill around the capture locations influenced blood Pb concentrations in brown bears. We started by building a set of six candidate models (Table 5.1). This set contained a null model, a model in which Pb concentrations only changed according to sampling year, and another model in which blood Pb concentration in female brown bears was affected by their lactation status (Table 5.1). Other models within that set contained either the relative probability of moose kill, or the environmental Pb concentrations. The last model contained a combination of all the variables (Table 5.1). All the models (except the null model) included the year of sample collection as a variable to control for potential differences between years. We did not include the age of bears because it was previously shown that this variable was not related to blood Pb concentrations in Scandinavian brown bears (Fuchs et al., 2021).

Table 5.1 The structure and biological hypotheses of candidate linear models used to predict the main source of lead (Pb) exposure in female brown bears (n = 34 individuals; n = 61 samples) from south-central Sweden, during 2017-2020.

	Model structure	Biological hypotheses
Null	$\log(\text{Pb}) \sim 1$	Pb is constant
Year	$\log(\text{Pb}) \sim \text{Year}$	Pb is influenced by year only
Lactation	$\log(\text{Pb}) \sim \text{Lactation}$	Pb is influenced by lactation only
RSF hunt	$\log(\text{Pb}) \sim \text{Probability of moose kill} + \text{Lactation} + \text{Year}$	Pb is influenced by probability of moose kill, lactation and year
Background Pb	$\log(\text{Pb}) \sim \text{Background Pb} + \text{Lactation} + \text{Year}$	Pb is influenced by background Pb, lactation and year
Full	$\log(\text{Pb}) \sim \text{Background Pb} + \text{Probability of moose kill} + \text{Lactation} + \text{Year}$	Pb is influenced by background Pb, probability of moose kill, lactation and year

Although our dataset contained 16 females sampled more than one year, we could not use mixed effect models with a random intercept with bear ID due to insufficient replication (bears were sampled 1.79 times on average over the study period). Model selection was conducted by Akaike's Information Criterion corrected for small sample size (AICc) by using the *aicmodavg* package (Mazerolle, 2020) in R. We considered models with a $\Delta\text{AICc} < 2$ to be equivalent. We first conducted the model selection for each scale (2, 4 and 6 km) separately and then carried out a second AICc with the top-ranked model of each scale to determine the best performing model. We used diagnostic plots to ensure that model assumptions were fulfilled. We had to log-transform the response variable (i.e., blood Pb concentrations) to achieve normality of residuals.

The environmental Pb concentration was not correlated to the probability of moose kill within buffers at the three scales (2 km, rho = 0.03, p = 0.79; 4 km, rho = -0.04, p = 0.76; 6 km, rho = -0.02, p = 0.87). All statistical analyses were conducted in R version 4.1.0 (R Core Team, 2021).

5.5 Results

Female brown bears had a mean blood concentration of 91 (36) µg/L. Lactating females (n = 34) had a mean blood Pb concentration of 104 (36) µg/L (range: 56-221 µg/L), whereas this value was 73 (36) µg/L (range: 25-155 µg/L) in non-lactating females (n = 27). Our kriging model predicted environmental Pb concentrations ranging from 4.6 to 95 mg/kg (dry weight) on the measured scale (i.e., back-transformed; $\exp(x)-2.5$) and showed large spatial variations with the highest Pb concentrations being in the west of the study area (Figure 5.1a). The cross-validation procedure revealed that observed and predicted values of environmental Pb concentrations were positively correlated ($\rho = 0.60$, $p < 0.001$), indicating that the model indeed predicted environmental Pb concentrations. Residuals were uncorrelated to predicted values ($\rho = 0.02$, $p = 0.45$). The mean of residuals was < 0.01, which also indicates that the prediction errors were small relative to predicted values.

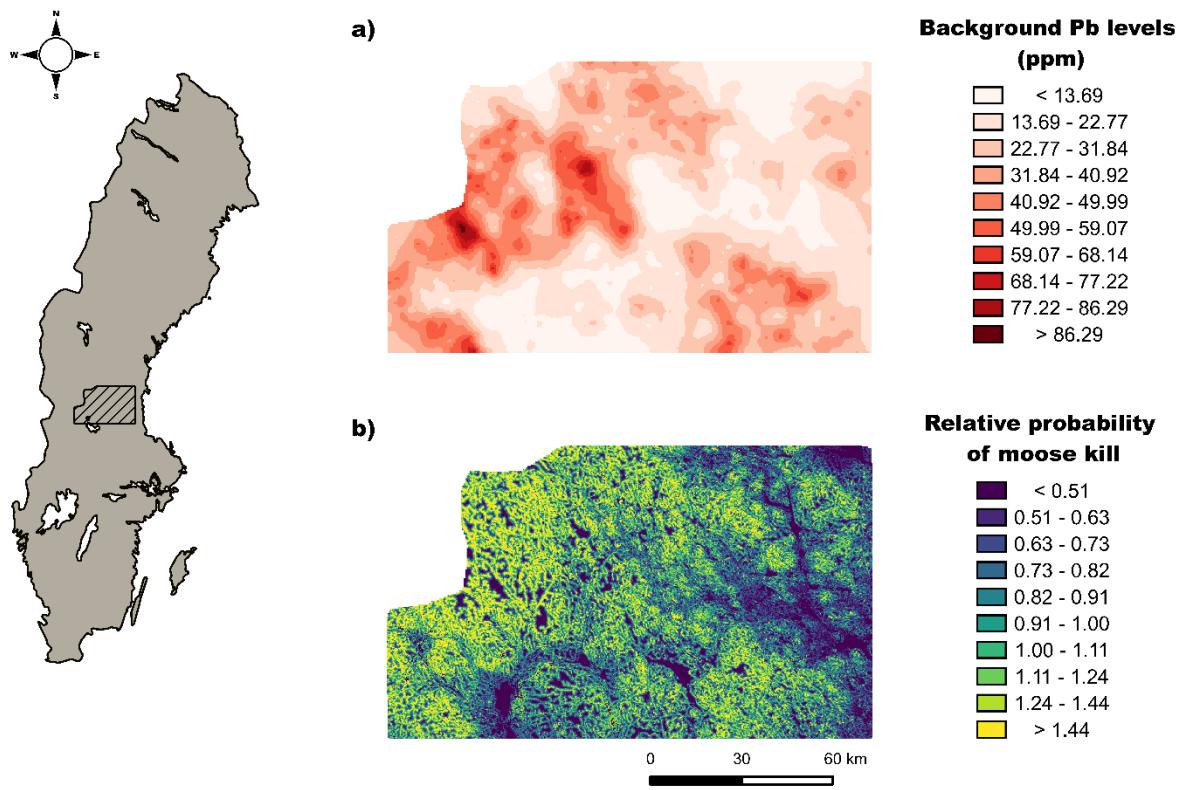


Figure 5.1 a) Predicted background lead (Pb) concentration (ppm) at a 500m resolution within our study area in south-central Sweden. The interpolated surface was generated by using ordinary kriging on Pb concentrations measured in plant roots. Data extracted from the biogeochemistry database of the Geological Survey of Sweden (© Sveriges Geologiska Undersökning). b) Predicted probability of moose kill at a 100m resolution within our study area. The probabilities were calculated from a resource selection function based on moose harvest locations that were provided by hunters [modified from Brown et al. (2023)]. See Brown et al. (2023) for more details about the resource selection function.

The model that performed best at explaining blood Pb concentrations in bears was the Full model (Akaike weight = 0.86) that included effects of the lactation status, the sampling year, the environmental Pb concentration and the relative probability of moose kill (fall_{t-1}) extracted within 2 km buffers around the capture locations (Table 5.2). The second-best performing model was the Environmental Pb models (Akaike weight = 0.14), which had a ΔAICc of 3.69 with the best model (Table 5.2). The other models received considerably less support as their ΔAICc were > 19 with the top-ranked model (Table 5.2). The results were similar across scales (Table S5.1), but the 2 km-scale performed best (Table S5.2). Thus, we only discuss the results with variables extracted at 2 km and present the other results as supporting information (Table S5.3).

Table 5.2 Model selection by Akaike information criterion corrected for small sample size (AICc). The model set was used to identify potential sources of Pb exposure in female brown bears ($n = 34$ individuals; $n = 61$ samples) with variables extracted within 2 km buffers centred around capture locations in south-central Sweden, during 2017-2020. K = the number of parameters, ΔAICc = the AICc difference with the top-ranked model, w = Akaike weight within the set and LL = log-likelihood of the model.

	K	AICc	ΔAICc	w	LL
Full	8	24.47	0	0.86	-2.85
Environmental Pb	7	28.16	3.69	0.14	-6.02
RSF hunt	7	44.04	19.57	0	-13.96
Lactating	6	45.89	21.42	0	-16.17
Year	5	57.32	32.85	0	-23.12
Null	2	59.36	34.89	0	-27.58

The following effect sizes and confidence intervals (95% CI) are expressed in percent of change, and they were calculated by back-transforming the coefficients (multiplied by the standard deviation for continuous variables), subtracting 1 and multiplying the results by 100. Our models indicated that blood Pb concentration in female brown bears was positively related to the

environmental Pb concentration around the capture location (Figure 5.2; Table 5.3). For every unit-increase of 16.02 mg/kg in environmental Pb concentrations (1 unit of standard deviation), the blood Pb concentrations in female brown bears increased by 18.5 % (Lower: 10.5%, Upper: 27.1%). Similarly, our model predicted higher blood Pb concentrations in brown bears captured in areas where hunters were more likely to kill moose during the previous fall (Figure 5.2; Table 5.3). Blood Pb concentrations in brown bears increased by 9.1% (Lower: 1.5%, Upper: 17.2%) for every increase of 0.17 (1 unit of standard deviation) in the relative probability of moose kill. Lactating females also had blood Pb concentrations that were 37.7% higher (Lower: 17.8%, Upper: 61.0%) when compared to non-lactating females.

Table 5.3 Parameters of the top-ranked model used to predict blood Pb concentrations [log(Pb µg/L)] in female brown bears ($n = 34$ individuals; $n = 61$ samples) from south-central Sweden, during 2017-2020. S.E. = standard error, Hunter RSF = Relative probability of moose kill. Variables were extracted within 2 km buffers centred on capture locations.

Variables	Estimate	S.E.	95% CI	
			Lower	Upper
Intercept	3.262	0.247	2.768	3.757
Background Pb	0.011	0.002	0.006	0.015
Hunter RSF	0.511	0.210	0.090	0.932
Lactating	0.320	0.078	0.164	0.477
year2018	0.035	0.106	-0.177	0.248
year2019	0.287	0.101	0.085	0.490
year2020	0.050	0.102	-0.154	0.256

Multiple R² = 0.56, Adjusted R² = 0.51

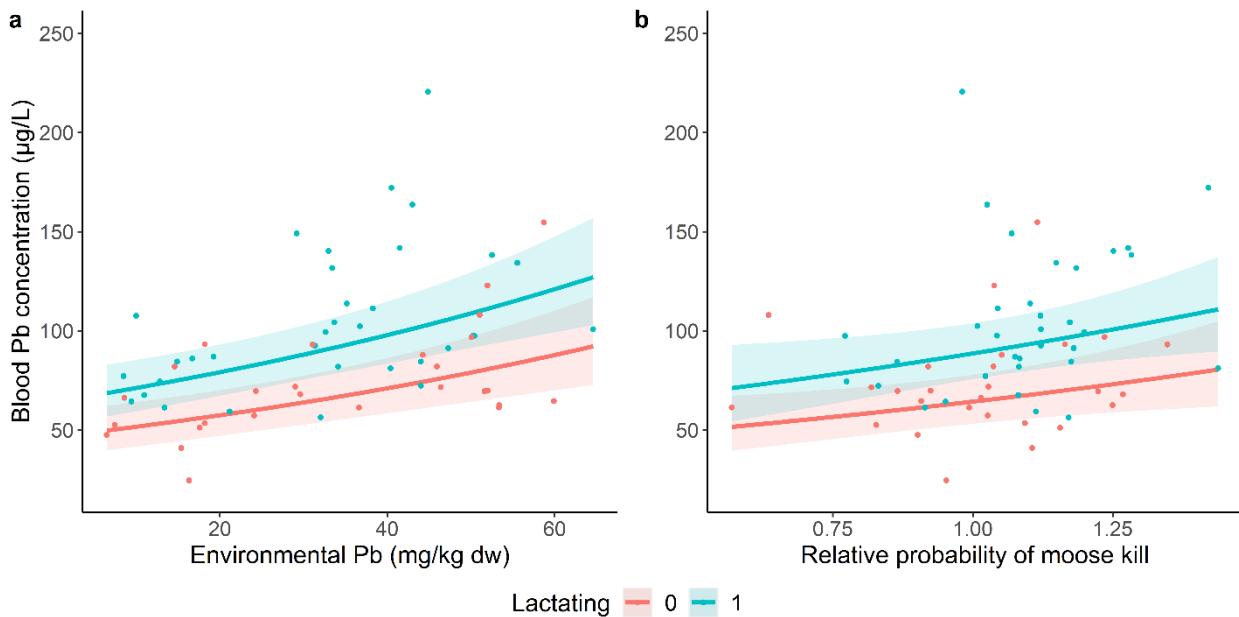


Figure 5.2 Predicted blood Pb concentrations ($\mu\text{g}/\text{L}$) in female brown bears ($n = 34$ individuals; $n = 61$ samples) in relation to a) environmental Pb concentrations (mg/kg) and b) the relative probability of moose kill during the previous hunting season ($t - 1$) around the capture locations (2 km buffer) in south-central Sweden during 2017-2020.

Lines show predictions and shaded polygons represent 95% confidence intervals of the models, whereas the points represent raw data. Blue points/lines indicate that the female was lactating (lactating = 1), whereas red points/lines indicates that they were not (lactating = 0).

5.6 Discussion

Our results support the hypothesis that the environmental Pb levels and moose kills jointly influenced blood Pb concentrations in Scandinavian brown bears. Our model explained 56% of the variation in blood Pb concentrations in female brown bears, while the environmental Pb

concentrations and probability of moose kill explained 20% and 9% of the variations in blood Pb concentrations, respectively. We found strong support for our prediction that higher environmental Pb levels and availability of moose kill by hunters are related to higher blood Pb concentrations in brown bears.

Our results indicate that blood Pb concentrations in brown bears reflect the concentration of Pb that circulates in the environment within their home range. Bears could be exposed to Pb by accidental ingestion of soil when, for example, digging their den or foraging on ants and plants (Gall et al., 2015). Berries are the main food source of bears during hyperphagia in Sweden (Stenset et al., 2016), which may explain why environmental Pb concentrations were a greater contributor to blood Pb levels in bears. We also acknowledge that the environmental Pb concentrations estimated from plant roots may not be entirely representative of Pb concentrations in food items consumed by bears. Different parts of plants may incorporate Pb from different sources. Roots mainly incorporate Pb from the surrounding soil, whereas leaves and stems also incorporate Pb from atmospheric sources (Klaminder et al., 2005); berries may also be coated with dust from atmospheric depositions (Stachiw et al., 2019). Additionally, the rationale behind the use of the plant root data was not to establish a direct link with the bears' diet, but rather to estimate and compare the amount of Pb that circulates in the different regions of our study areas.

Our conservative approach with buffers of various radii centred on capture locations was sufficiently accurate to correlate blood Pb levels with the concentrations of Pb circulating in the environment around those sites. Models predicting the tissue concentration of contaminants in animals can be refined further by incorporating movement or space use parameters (Sorais et al., 2021, 2020). Adding data from GPS transmitters could have improved the performance of our model. Spatially explicit models also need to account for the physiological state of an individual (i.e., reproductive status) and failure to do so may introduce bias in the models, as evidenced by the blood Pb concentrations that were 38% higher on average in lactating females when compared to non-lactating females. During lactation, there is remobilization of calcium

(and Pb) from bones into the bloodstream and lactating females are exposed to an additional endogenous source of Pb (Fuchs et al., 2021).

Our results also indicate that high probabilities of moose kills are linked to higher blood Pb levels in brown bears. Some concerns have been raised previously regarding the risk of Pb exposure from bullet fragments in mammalian scavengers (Kelly et al., 2021; Legagneux et al., 2014; Rogers et al., 2012), but so far this source of Pb exposure had mostly been reported in avian scavengers (Pain et al., 2019). Pb ammunition is an important source of Pb exposure in avian scavengers and can have consequences at both the individual and population levels (Helander et al., 2021; Pain et al., 2019; Slabe et al., 2022). For instance, Pb from ammunition has been linked to increased risk of mortality (Singh et al., 2021) and altered flight behavior (Ecke et al., 2017) in avian scavengers, and has prevented the recovery of the California condor (*Gymnogyps californianus*) (Finkelstein et al., 2012).

The blood Pb levels reported in Scandinavian brown bears are in general below the 180 µg/L hazardous concentration for 5% of mammals reported by Buekers et al. (2009). However, values below toxicity thresholds should not be labelled as “safe” because sublethal and subclinical effects of Pb can still be harmful. For instance, subclinical effects on movement behavior have been reported in golden eagles at blood Pb levels (25 µg/L) well below toxicity thresholds for birds (Ecke et al., 2017), and it has been reported that eagles with blood Pb levels above 25 µg/L were more likely to die compared to individuals below this threshold (Singh et al., 2021). Although the conclusions of these studies cannot be directly translated to brown bears, they suggest that subclinical effects of increased Pb exposure can occur at levels well below commonly reported guidelines and that some bears may be subjected to those consequences. However, we did not investigate this topic and were not able to confirm whether there were deleterious effects in bears. If subclinical or sublethal effects of Pb occur in brown bears, the consumption of slaughter remains discarded by hunters could be considered an evolutionary trap (Schlaepfer et al., 2002), because there is no reason for an opportunistic omnivore to not consume easily accessible, energy-rich and easily digestible foods when

encountered (DeVault et al., 2003; Pritchard and Robbins, 1990). However, this ‘easy meal’ acquired at low costs may be deleterious in the long term because it may contain high concentrations of Pb (Gremse et al., 2014; Hunt et al., 2006; Menozzi et al., 2019; Stokke et al., 2017).

A previous study on Scandinavian brown bear showed that they generally did not modify their behavior in order to gain access to slaughter remains during the fall and concluded that the scavenging behavior of bears in Sweden is mostly opportunistic (Brown et al. 2023). Despite this seemingly low exposure rate, we found a positive relationship between blood Pb levels, and the probability of moose kill around the capture locations. Studies conducted on bears from other populations in North America have shown that bears actively use areas where they are likely to find slaughter remains (Lafferty et al., 2016; Legagneux et al., 2014; Ruth et al., 2003), suggesting that bears from other populations may be at greater risk of Pb exposure than Scandinavian brown bears, especially in areas where the peak of the hunting season is earlier during their active period. The risk of increased Pb exposure should thus be evaluated in bears and other mammalian scavengers from other populations with an appropriate design.

The risk of Pb exposure in relation with the timing of the hunting season has been extensively studied in avian scavengers (Ecke et al., 2017; Fisher et al., 2006; Legagneux et al., 2014; Pain, 2009), while other studies have also looked at the risk of Pb exposure across a gradient of harvest density (Kelly and Johnson, 2011; Singh et al., 2021). The distribution of kill sites or harvest density is typically calculated at the scale of management areas by counting the number of animals that were harvested with a firearm within a specific area (Helander et al., 2021; Kelly and Johnson, 2011); however, this approach is based on the assumption that the distribution of hunter kills is uniform within the area. This assumption is inaccurate in most cases. Hunter kills are neither randomly nor uniformly distributed across the landscape, but are rather concentrated around specific features that provide accessibility, concealment, and/or visibility, depending on the hunting style (Gaynor et al., 2022; Norum et al., 2015). Ignoring the fine-scale distribution of kill sites might not matter for avian scavengers because they can efficiently travel between

patches with high harvest densities and easily access slaughter remains (DeVault et al., 2003). However, mammals do not travel as efficiently as most avian scavengers and those movement constraints restrict their ability to access slaughter remains (DeVault et al., 2003), which underlines the importance of reliable estimates of the fine-scale distribution of hunter kill sites. Using an RSF-based approach on ungulate kill sites provided by hunters may be useful for predicting the fine-scale distribution of hunter kills and, by extension the increased risk of Pb exposure, within an area.

The advantage of using an RSF-based approach to predict the fine-scale distribution of harvest locations is that it only requires a subsample of the total harvest. It essentially allows to circumvent the problem of obtaining all the harvest locations within an area. A potential disadvantage is that it still requires a lot of harvest locations, and by extension, it also requires the cooperation of many hunters, which may choose to not disclose or collect information on harvest locations for research purposes. Wildlife management agencies can however obtain this information relatively easily from voluntary hunters, or by making it mandatory to disclose the harvest locations when harvested animals are registered. RSF are relatively easy to fit with widely available statistical softwares, but their results may be difficult to interpret properly. Fortunately, multiples tools are now available to facilitate the implementation of RSF and the interpretation as well as the validation of their results (Fieberg et al., 2021; Muff et al., 2020; Northrup et al., 2022; Roberts et al., 2017).

Potential limitations of our study include the relatively small sample size, the absence of males from the analyses, and the timing of blood sampling. A sample size of 34 females may be small for many species, but considering that, in 2008, the entire population of bears in Sweden was estimated at ~3,300 individuals (Kindberg et al., 2011), our sample size can be considered acceptable. Due to the absence of samples from adult males, we also could not investigate exposure in this demographic group. Larger males commonly monopolize foraging locations (Ben-David et al., 2004; Zedrosser et al., 2013) and could deter females from using slaughter remains; however, it is unlikely a problem in our study because avoidance of males by females

with dependent offspring is more common during the mating season (June-July) compared to the fall when slaughter remains are available (Steyaert et al., 2013). Another potential limitation of our study is that it may be difficult to relate Pb concentrations from blood samples collected during spring to moose hunting activities that occurred during the previous fall. Other studies have shown that the blood Pb concentrations in scavengers decrease during the winter and spring (Craighead and Bedrosian, 2008; Slabe et al., 2022) and our model may have underestimated the contribution of ammunition as a Pb source due to the timing of blood sampling. Nevertheless, our conclusions are similar to those reported by Arrondo et al. (2020) who also found that soil was an important source of Pb exposure in vultures from Spain. Additionally, it is also possible that bears scavenge on thawed slaughter remains after den emergence and are thus exposed to Pb during the spring, as suggested by Fuchs et al. (2021); however, no information is available on the frequency of this behavior.

An alternative explanation based on Pb kinetics is likely a better explanation for the relationship between spring blood Pb levels and the distribution of moose kills during the previous fall. We do not know if and how hibernation affects Pb kinetics, but blood half-life of elimination may be extended because bears do not urinate nor defecate during this period (Nelson et al., 1983), thereby suggesting no or minimal excretion from the body during the winter. However, we can reasonably expect a blood half-life of elimination of four to five weeks in active bears (Arnemo et al., 2022). Due to this rapid turnover rate, blood Pb concentrations typically reflect short time exposure, but this parameter also depends on the equilibrium between the different compartments of the body in which Pb is stored (Rabinowitz, 1991). For instance, Pb stored in bones, which reflects long time exposure, may be remobilized into the bloodstream during periods of nutritional stress, gestation and lactation (Arnemo et al., 2022). Bears do not eat nor drink during hibernation and Pb may be mobilized from bones in all individuals; this phenomenon was especially obvious in lactating females (Fuchs et al., 2021). Therefore, blood Pb concentrations in bears during the spring are likely the results of a mixture of recent intakes and long-term exposure from blood-organ-bone equilibrium (i.e., mobilisation of Pb from bones).

5.7 Conclusion

We found a link between the distribution of moose kills by hunters and the blood Pb concentrations in bears; however, the environmental Pb level was a greater contributor to bears' blood Pb concentrations. Our results suggest that regulations on both Pb ammunition and other anthropogenic Pb emissions are needed to reduce Pb exposure in bears. Pb from ammunition is mainly available for a few weeks during the hunting season and potentially the spring through the consumption of soft tissues with embedded metal fragments, although slaughter remains also include hides and bone dumps that may last longer. Despite that relatively short period during which Pb exposure from ammunition likely occurs in bears, it still represents a potential risk for bears and possibly other mammalian scavengers. We also propose that an RSF-based approach with harvest locations provided by hunters should be relatively easy to implement in other systems, thereby improving our capacity to better understand the risk of increased Pb exposure from bullet fragments in scavengers.

5.8 Conflict of interest

The authors declare no conflict of interest.

5.9 Funding

The Norwegian Environment Agency, the Swedish Environmental Protection Agency and the Research Council of Norway are the primary funders of the Scandinavian Brown Bear Research Project. Blood sampling and element analyses were funded by the Inland Norway University of Applied Sciences and the Norwegian Environment Agency [grant number 19047048 to JMA]. FP was supported by NSERC Discovery grant [grant number 2018-05405] and E.W.R. Steacie Memorial Fellowship [grant number 549146-2020].

5.10 CRediT author statement

Ludovick Brown: Conceptualization, Formal analysis, Visualization, Writing – original draft.
Boris Fuchs: Data curation, Investigation, Writing – review & editing. **Jon M. Arnemo:** Conceptualization, Investigation, Resources, Funding acquisition, Writing – review & editing.
Jonas Kindberg: Project administration, Writing – review & editing. **Ilia Rodushkin:** Investigation, Resources, Writing – review & editing. **Andreas Zedrosser:** Conceptualization, Supervision, Writing – review & editing. **Fanie Pelletier:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

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CHAPITRE 6

DISCUSSION ET CONCLUSION

6.1 Retour sur les objectifs

Dans cette thèse, j'ai documenté les conséquences de la chasse aux gros gibiers chez deux grands carnivores, l'ours brun en Suède et l'ours noir au Québec. Je me suis particulièrement intéressé aux effets de la chasse sur le comportement des ours, plus spécifiquement aux effets de la chasse sur la sélection de ressources et sur le mouvement, ainsi qu'à l'exposition au plomb provenant des munitions.

Dans le chapitre 2, j'ai voulu spécifiquement documenter les conséquences de la chasse à l'orignal sur la sélection de ressources chez l'ours brun scandinave. Il était important de documenter la réponse des ours face à la chasse à l'orignal, puisque dans ce contexte, les chasseurs représentent autant une menace qu'une source d'accès à la nourriture. Les résultats de cette étude montrent que durant la période de chasse à l'orignal, les ours bruns adoptent des tactiques d'anti-prédation similaires à celles observées durant la période de chasse à l'ours. Plus spécifiquement, j'ai montré que les ours évitent les sites d'abattages d'orignaux et sélectionnent des habitats moins favorables aux chasseurs durant la journée, ce qui supporte notre prédition que les chasseurs sont perçus comme une menace et que ces derniers instaurent un paysage de la peur chez les ours. À l'inverse, notre prédition selon laquelle les restes d'abattage jetés par les chasseurs ont un effet attractif chez les ours une fois la nuit tombée n'a pas été supportée par nos résultats. En effet, mes résultats ont montré que les ours évitent aussi les sites d'abattage durant la nuit. Ces résultats suggèrent que les ours ne font pas la différence entre les deux types de chasse (ours et orignal) et que les restes d'abattage jetés par les chasseurs n'ont pas d'effet attractif chez les ours en Suède. Ce chapitre suggère aussi que les ours consomment probablement les restes d'abattage de façon opportunistes lorsque rencontrés lors de leurs déplacements. Les résultats du chapitre 2 m'ont permis

d'approfondir la discussion entourant les résultats du chapitre 5 sur le risque d'exposition au plomb provenant des fragments de munitions incrustés dans les restes d'abattage jetés par les chasseurs.

Les résultats du chapitre 2 sont aussi intéressants d'un point de vue écologique. Les analyses de sélection d'habitats réalisées au cours de ce chapitre ont révélé que les activités de chasse pouvaient instaurer un paysage de la peur et avoir un effet important sur le comportement des espèces non ciblées par les chasseurs. Bien que ces changements de comportement n'induisent pas directement une plus grande mortalité, ils peuvent néanmoins s'avérer coûteux. Par exemple, nous savons que les ours bruns en Suède adoptent plus de comportements anti-prédation durant les périodes où le risque de mortalité est élevé, ce qui se traduit par une perte d'efficacité au niveau de l'alimentation et ultimement en coûts potentiels au niveau de la reproduction ou de la survie (Hertel et al. 2016). D'après les résultats présentés dans le chapitre 2, nous pouvons nous attendre à ce que la chasse à l'original entraîne des conséquences similaires à celles induites par la chasse à l'ours. Ces coûts devraient être évalués par les gestionnaires de la faune et considérés durant la planification et la gestion des périodes de chasse.

Dans le chapitre 3, j'ai montré que les perturbations causées par les chasseurs pouvaient avoir un impact sur le taux de mouvement des groupes démographiques bénéficiant d'une protection légale contre la récolte. J'ai montré que les femelles avec des jeunes dépendants se déplacent plus rapidement lorsqu'elles se retrouvent près des routes, où le risque de prédation est élevé, durant les heures légales de chasse et cette observation est particulièrement importante tôt le matin quand le risque de mortalité est le plus élevé pour les ours (Hertel et al. 2016). Cela suggère que la chasse pourrait augmenter les dépenses énergétiques d'un groupe démographique vulnérable durant une période critique du cycle annuel chez les ours et que la protection de ce groupe ne protège pas les individus des coûts potentiels induits par un paysage de peur. Les gestionnaires devraient considérer et évaluer les conséquences de la chasse même chez les groupes démographiques qui ne sont pas convoités durant les activités de chasse.

Dans le chapitre 4, je me suis intéressé au lien entre la chasse aux gros gibiers et le risque à long terme d'exposition au plomb provenant des munitions chez un omnivore opportuniste. Cette étude montre qu'il y a une corrélation positive entre la densité de récolte de gros gibiers par arme à feu et la concentration de plomb dans les dents d'ours noirs au Québec. Cela suggère que les ours, et possiblement d'autres mammifères, peuvent s'exposer au plomb en consommant des carcasses de gros gibiers abandonnées par les chasseurs; cette problématique n'est donc pas limitée aux charognards aviaires. Mes travaux suggèrent donc que les chasseurs de gros gibiers ont le potentiel de créer un piège évolutif pour les mammifères charognards comme c'est le cas chez certains oiseaux dont les populations sont négativement affectées par l'exposition au plomb provenant des munitions (Finkelstein et al. 2012, Slabe et al. 2022, Green et al. 2022). Cependant, nous ne savons pas si la hausse que nous avons observée dans les concentrations de plomb à cause de la chasse est suffisamment grande pour induire des effets délétères chez les ours.

Dans le chapitre 5, j'ai réutilisé le modèle de sélection d'habitats basé sur des sites d'abattage d'orignaux du chapitre 2, afin de déterminer s'il y avait un lien entre la distribution des sites d'abattage et le risque d'exposition au plomb chez l'ours brun en Suède, tout en contrôlant pour les variations dans les niveaux de plomb dans l'environnement à l'intérieur de notre aire d'étude. Mes travaux montrent qu'il y a effectivement un lien entre la distribution des sites d'abattage d'orignaux et le risque d'exposition au plomb chez l'ours brun. Les résultats de ce chapitre sont importants puisqu'ils nous permettent de valider de façon indépendante les conclusions du chapitre 4 chez une deuxième espèce provenant d'un système d'étude différent, tout en employant une méthodologie différente. La conclusion tirée du chapitre 5 est donc la même que celle du chapitre 4. Il y a un lien entre le risque d'exposition au plomb chez les mammifères charognards et la distribution des sites d'abattage. La contribution la plus importante du chapitre 5 pourrait toutefois s'avérer être l'usage d'une fonction de sélection de ressources (RSF) dans le but de prédire la distribution des sites d'abattages d'orignaux à fine échelle. La disponibilité des carcasses est un aspect déterminant dans la fréquence de consommation de carcasses chez les charognards (DeVault et al. 2003). Les charognards aviaires peuvent se déplacer efficacement à travers le territoire afin d'acquérir des ressources. Cette efficacité à voyager à travers le territoire pourrait en partie expliquer pourquoi

certaines études ont rapporté un lien entre la période de chasse et l'exposition au plomb chez les charognards aviaires sans intégrer une composante spatiale à leurs analyses (Pain et al. 1997, Craighead et Bedrosian 2008) ou en le faisant à une faible résolution comme à l'échelle des unités de gestion ou zones de chasse (Kelly et Johnson 2011, Garbett et al. 2018).

6.2 Paysage de la peur ou buffet à volonté ?

Dans le chapitre 2, j'ai montré que les ours en Suède perçoivent les chasseurs d'originaux comme une menace et évitent les sites d'abattage. Il est important de souligner ici que le terme « éviter » n'indique pas que les ours n'utilisent jamais les sites d'abattage, qu'ils ne fréquentent jamais ces sites ou qu'ils ne consomment pas les restes d'abattage jetés par les chasseurs. Les résultats indiquent plutôt qu'après un déplacement d'une heure, il est plus probable qu'un ours se retrouve à un endroit dont la probabilité de sites d'abattage est plus faible par rapport aux autres sites qui étaient accessibles à ce moment. En d'autres mots, les ours semblent se déplacer en minimisant le temps passé dans les endroits où il est plus probable que des chasseurs récoltent des originaux. Les comportements charognards chez les ours en Suède semblent donc être de nature opportuniste plutôt que le résultat d'un comportement de quête alimentaire visant spécifiquement à acquérir cette ressource.

Ces résultats contrastent avec ceux des études ayant examiné les comportements des ours pendant les périodes de chasse aux ongulés en Amérique du Nord (Haroldson et al. 2004, Legagneux et al. 2014, Lafferty et al. 2016). En effet, les résultats de ces études montrent que les ours en Amérique du Nord semblent attirés par les carcasses jetées par les chasseurs et qu'ils sont fréquemment observés aux sites d'abattage, alors que ce n'est pas le cas en Suède. Les résultats des chapitres 2 et 3 suggèrent que les ours perçoivent les chasseurs de gros gibier comme une menace et qu'ils les évitent. La consommation de carcasses est avantageuse d'un point de vue évolutif puisque cela permet l'acquisition d'un repas riche en énergie à faibles coûts et il n'y a aucun avantage de ne pas consommer cette ressource (DeVault et al. 2003). Il est donc tout à fait plausible que la peur des humains affecte l'attractivité des carcasses jetées par les chasseurs. Les ours en Europe vivent en

beaucoup plus grande proximité des humains que leurs homologues nord-américains (Linnell et al. 2001) et doivent être en mesure d'éviter le plus possible les interactions avec les humains afin de persister dans ce paysage sous forte influence anthropique. Ce phénomène a d'ailleurs été observé entre différentes régions en Amérique du Nord où les ours développent des patrons d'activités nocturnes dans les endroits où l'empreinte exercée par l'activité humaine est la plus grande (Lamb et al. 2020).

Il semble donc y avoir une dynamique intéressante entre la peur des humains et l'utilisation de restes d'abattage par les ours. Les ours peuvent identifier les endroits risqués et peuvent manger des baies sans s'exposer à un plus grand risque (Ditmer et al. 2018b, Lodberg-Holm et al. 2019). Ils pourraient donc être en mesure d'accumuler suffisamment de réserves d'énergie sans avoir besoin des restes d'abattage jetés par les chasseurs et nous avons de fortes indications que c'est bel et bien le cas (Hertel et al. 2018). Il est possible que ces résultats varient d'une année à l'autre en fonction de l'abondance des baies. Cependant, Hertel et al. (2019) ont montré que l'abondance de cette ressource n'affectait pas le comportement ni l'utilisation spatiale des ours en Suède, ce qui suggère que la prise de risque ne varierait pas en fonction de l'abondance de baies. Un important déficit calorique chez un individu pourrait toutefois pousser ce dernier à prendre plus de risques afin d'obtenir de la nourriture (Blecha et al. 2018, Oates et al. 2019). Ces cas seraient cependant de l'ordre d'une anecdote plutôt qu'une réelle réponse à l'échelle de la population. Les résultats du chapitre 2 suggèrent donc que la peur induite par les activités humaines semble empêcher les ours bruns de chercher à se joindre au « buffet à volonté » produit par la chasse à l'orignal en Suède.

Nous pourrions aussi nous attendre à des résultats différents si nous tentions de reproduire l'étude présentée dans le chapitre 2 dans certaines régions de l'Amérique du Nord, où les ours sont moins exposés aux perturbations provenant de l'activité humaine, ou encore, chez une autre espèce modèle moins craintive envers les humains. D'autres espèces de mammifères comme le coyote (*Canis latrans*) ou le renard roux (*Vulpes vulpes*) sont potentiellement plus à risque d'exposition au plomb provenant de la chasse que les ours. L'impact du paysage de la peur instauré par les chasseurs pourrait être moins important chez ces espèces qui cohabitent en plus grande proximité avec les

humains (Bateman et Fleming 2012), de sorte que les compromis entre la perception du risque et l'acquisition de ressources seraient moins grands que chez les ours.

Les résultats du chapitre 2 sont pertinents dans un cadre de planification et gestion des périodes de chasse. La façon dont les saisons de chasse sont organisées pourrait engendrer de longues périodes durant lesquelles la faune est exposée aux perturbations découlant des activités de chasse. La planification de plusieurs périodes de chasse consécutives permet aux chasseurs de pratiquer leurs activités pendant une plus grande partie de l'année et également de chasser une plus grande variété de gibiers; cependant, cette façon d'organiser les périodes de chasse pourrait ne pas être optimale d'un point de vue strictement écologique. Comme montré dans le chapitre 2, les ours ne font pas la différence entre les chasseurs d'ours et les chasseurs d'orignaux et ils semblent avoir la même réponse comportementale face aux deux types de chasse. Il est donc raisonnable de s'attendre à ce que les coûts comportementaux associés à la chasse à l'ours, tel que suggéré par Hertel et al. (2016), soient aussi associés à la chasse à l'orignal. Il serait ainsi important de garder ce constat à l'esprit quand vient le temps de gérer et planifier les périodes de chasse. Cela devient particulièrement important dans un endroit comme la Suède où la principale méthode de chasse consiste à utiliser des chiens de poursuite afin de faire bouger le gibier convoité et le diriger vers des positions stratégiques où des chasseurs l'attendent en embuscade. Les perturbations générées par ce type de chasse ne sont pas spécifiques au gibier convoité et pourraient affecter d'autres espèces.

Il m'apparaît aussi important de discuter des résultats en apparence contradictoire des chapitres 2 et 5 (les ours évitent les sites d'abattage, mais le risque d'exposition au plomb chez les ours est tout de même lié à la distribution de ceux-ci). En supposant que les ours consomment les restes d'abattage de façon opportuniste, nous pouvons émettre l'hypothèse que le taux de rencontre entre les ours et les restes d'abattage est plus élevé dans les endroits où la densité de sites d'abattage est la plus élevée. La disponibilité des restes d'abattage à l'échelle du domaine vital pourrait être plus importante que la disponibilité à l'échelle du mouvement. Gardons en tête que la sélection, par les ours, de sites avec de plus faibles probabilités de site d'abattage est relative à celle des autres sites

disponibles à l'échelle du mouvement. La notion d'échelle est donc essentielle afin de bien interpréter les résultats du chapitre 5 dans le contexte défini par ceux du chapitre 2.

Prenons l'exemple fictif de deux ours illustrés dans la Figure 6.1, où les deux individus identiques évitent les endroits avec les densités de récoltes les plus élevées à l'échelle du mouvement. Nous pouvons cependant voir qu'à l'échelle du « domaine vital » (c.-à-d. l'encadré noir), l'individu b) à plus de chance de croiser une carcasse lors de ses déplacements étant donné que la densité de récolte est plus élevée à cette échelle (Figure 6.1). Même si l'individu b) évite les zones avec une densité de récolte plus élevée, il doit tout de même traverser ces zones lors de ses déplacements, ce qui devrait augmenter le taux de rencontres opportunistes entre les ours et les restes d'abattage. Considérant que les ours ne semblent pas chercher les sites d'abattage, le taux de rencontre aléatoire avec la ressource devrait donc être dépendant de la densité de carcasses (Kane et al. 2017).

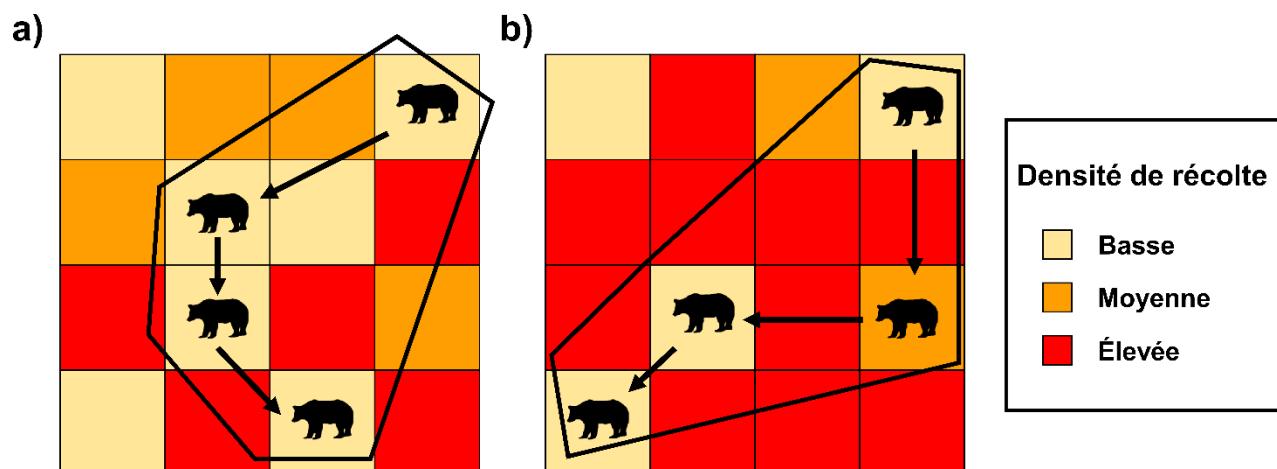


Figure 6.1 Exemple fictif illustrant comment deux ours (a et b) peuvent éviter les endroits avec des densités de récolte élevées à l'échelle du mouvement tout en ayant différentes densités de récolte moyenne à l'échelle du domaine vital.

Les flèches représentent les mouvements, alors que les encadrés noirs représentent les domaines vitaux de deux ours. Cette figure montre qu'il est plus probable que l'ours b) croise une carcasse par hasard lors de ses déplacements par rapport à l'ours a) dont la densité de récolte intra-domaine vital moyenne est plus faible.

Contrairement aux oiseaux, les mouvements des mammifères sont plus restreints et la disponibilité des carcasses (ou sites d'abattage) à fine échelle pourrait être un important déterminant du risque d'exposition au plomb chez ces derniers (Kelly et al. 2021). Obtenir de l'information sur la distribution des sites d'abattages à fine échelle est toutefois une tâche ardue puisque la densité de récolte n'est souvent connue qu'à l'échelle des unités de gestion. Omettre d'intégrer une composante spatiale à fine échelle dans les modèles utilisés pour prédire le risque d'exposition au plomb provenant des munitions chez les mammifères pourrait ne pas avoir la performance escomptée, à en juger par les conclusions d'une des premières études à l'avoir tenté (Rogers et al. 2012). Le problème avec le cadre à fine échelle suggéré ici réside dans la difficulté d'obtenir les coordonnées des sites d'abattage à travers une grande étendue géographique. Ces données n'étant souvent pas collectées par les gestionnaires de la faune nécessitent ainsi la coopération d'un grand nombre de chasseurs.

L'usage d'une RSF pourrait toutefois permettre de contourner la nécessité d'obtenir toutes les coordonnées géographiques des sites d'abattages à l'intérieur d'une région. Ce type d'analyse a principalement été développé pour étudier les jeux de données provenant des colliers émetteurs déployés sur des animaux. L'idée est de déployer des émetteurs (GPS ou autres) sur un sous échantillon d'individus et d'ensuite extrapoler les résultats à l'échelle de la population pour en estimer la distribution. D'un point de vue analytique, il n'existe pas vraiment de différence entre une coordonnée géographique provenant d'un animal équipé d'un émetteur GPS et celle enregistrée manuellement à l'aide d'un GPS; les deux peuvent être analysées avec la même méthode. Il est donc possible d'obtenir la coopération d'un nombre réduit de chasseurs pour ensuite extrapoler les résultats à l'échelle de la population comme le montrent les résultats du chapitre 5. Les RSF sont relativement faciles à modéliser et plusieurs outils sont maintenant disponibles, rendant ainsi l'interprétation des résultats plus accessibles (Signer et al. 2019, Fieberg et al. 2021, Northrup et al. 2022). Je crois que ce cadre peut être aisément répliqué dans d'autres systèmes d'étude et pourrait permettre d'importantes avancées dans l'étude du risque d'exposition au plomb provenant des munitions chez les mammifères.

6.3 Munitions en plomb : les mammifères sont-ils vraiment à risque ?

Les effets toxiques du plomb sont en général bien documentés (Singh et al. 2018, Pain et al. 2019) et mes travaux montrent que les ours ont des niveaux de plomb plus élevés dans leurs tissus dans les endroits où il y a plus de chasse. Chez les humains, il n'y a pas de niveaux d'exposition au plomb considérés sécuritaires (World Health Organization 2022). Il pourrait donc y avoir des effets sous-létaux chez les ours; cependant, nous ne savons pas si c'est réellement le cas. En effet, nous ne savons pas si les hausses que nous avons observées dans les concentrations en plomb chez les ours sont suffisantes pour causer des effets délétères chez ces derniers. Les seuils de toxicité ne sont pas documentés chez les ours, mais nous pouvons tout de même comparer les concentrations de plomb que nous avons mesurées avec les seuils de toxicité chez d'autres espèces, incluant les humains.

Tel que mentionné dans le chapitre 4, il est difficile de contextualiser les concentrations de plomb dans les dents d'ours noirs, puisque peu d'études sont disponibles pour faire des comparaisons. Les concentrations que nous avons mesurées étaient bien en deçà de celles mesurées dans les dents de micromammifères provenant de sites contaminés en Pologne (Appleton et al. 2000). De plus, les dents semblent être surtout utiles dans l'évaluation de l'exposition cumulative et pour faire des comparaisons entre les individus ou les espèces. Nous pouvons affirmer que les concentrations en plomb dans les dents d'ours noirs au Québec sont relativement faibles lorsque comparées aux concentrations rapportées chez les micromammifères par Appleton et al. (2000), mais que certains de nos échantillons étaient comparables aux concentrations mesurées chez des humains qui ont grandi durant l'ère de l'essence plombée aux États-Unis (Robbins et al. 2010). Il semble donc peu probable qu'il y ait d'importants effets délétères associés à un empoisonnement au plomb chez les ours noirs au Québec, mais nous ne pouvons pas exclure de possibles effets sous-létaux. Nous aurions cependant besoin de plus d'information, comme des échantillons de sang, afin de documenter cette affirmation qui reste spéculative pour le moment. Les concentrations en plomb dans des échantillons de sang pourraient être plus facilement comparées avec les seuils de toxicité publiés chez d'autres espèces et faciliteraient grandement la discussion entourant de potentielles conséquences de l'exposition au plomb provenant des munitions chez les ours noirs.

Dans le cas des ours bruns en Suède, nous avons les concentrations de plomb mesurées dans des échantillons de sang. La grande majorité des échantillons de sang prélevés chez des ours bruns en Suède avait une concentration en plomb jugée préoccupante si on se fie au seuil de 50 µg/L utilisé par l’Organisation mondiale de la Santé (Hampton et al. 2018, Fuchs et al. 2021). La concentration moyenne (écart type) rapportée chez l’ours brun était de 96,6 (35,6) µg/L et donc environ quatre fois plus faible que les seuils (~400 à 500 µg/L) habituellement associés à un empoisonnement clinique chez les oiseaux (Finkelstein et al. 2012, Slabe et al. 2022). Il semble donc peu probable qu’il y ait d’importants effets néfastes chez les ours bruns; cependant, comme pour l’ours noir, nous ne pouvons pas exclure de potentiels effets sous-létaux. Des effets sous-létaux sur le taux de mouvement ont été rapportés chez l’aigle royal à des concentrations aussi faibles que 25 ppb (25 µg/L), c’est-à-dire bien en deçà des seuils de toxicité couramment utilisés, et ce seuil a aussi été associé à un risque accru de mortalité (Ecke et al. 2017, Singh et al. 2021). Il est donc plausible qu’il y ait des conséquences sous-létales chez les ours, incluant de potentiels effets sur le comportement (c.-à-d. le taux de mouvement). Vous trouverez à la section 6.4 quelques suggestions afin de vérifier s’il y a bel et bien des conséquences de l’exposition au plomb chez les ours en Suède et au Québec.

Nous avons observé des hausses dans les concentrations de plomb accumulé dans les tissus des ours, mais ces niveaux étaient en général beaucoup plus bas que ceux observés chez certains charognards aviaires (Kelly et al. 2011, Finkelstein et al. 2012, Wiemeyer et al. 2017). Plusieurs facteurs pourraient expliquer ces différences dans le niveau d’exposition au plomb entre les groupes de charognards. Les charognards aviaires sont principalement actifs pendant le jour et cela pourrait leur procurer un certain avantage compétitif par rapport aux mammifères principalement nocturnes (Olea et al. 2022). Dans la majorité des systèmes, les activités de chasse sont principalement restreintes aux heures de la journée (il existe toutefois quelques exceptions). Les charognards aviaires pourraient donc avoir une longueur d’avance de plusieurs heures par rapport aux mammifères en ce qui a trait à la recherche de carcasses ou de restes d’abattage. Ce décalage entre l’activité des mammifères et la chasse couplé à l’efficacité de mouvement chez les charognards aviaires pourrait expliquer pourquoi ces derniers sont généralement les premiers arrivés aux sites d’abattage (Gomo et al. 2017). L’étude de Gomo et al. (2017) montre d’ailleurs que les corvidés consomment la

majorité de la biomasse avec la plus grande teneur en énergie. Cela suggère que la capacité des oiseaux à acquérir les carcasses pourrait largement surpasser celle des mammifères et donc que les charognards aviaires ingèreraient une importante partie du plomb déchargé dans l'environnement par les munitions.

L'impact de la peur induite par les activités humaines est un autre aspect important à considérer afin d'expliquer les différences dans le niveau d'exposition au plomb entre les groupes de charognards. Non seulement les mammifères évitent temporellement les humains (Gaynor et al. 2018), mais ils évitent aussi les endroits les plus perturbés par les activités de chasse (Dobbins et al. 2020). Les résultats du chapitre 2 suggèrent d'ailleurs que les ours bruns en Suède ne font pas exception à cette affirmation. Il existe toutefois des preuves indiquant que ce ne serait pas le cas chez les charognards aviaires et même que certaines espèces pourraient être attirées par les décharges d'armes à feu (White 2005). Il est donc plausible que la peur des humains explique aussi en partie pourquoi les concentrations de plomb dans le sang des ours bruns en Suède sont moins élevées que celles rapportées dans la littérature chez les charognards aviaires.

Le paysage de la peur induit par les chasseurs pourrait donc atténuer les conséquences du piège évolutif qu'ils créent potentiellement en jetant dans l'environnement des carcasses et des viscères contaminées par des fragments de plomb. Ce potentiel effet protecteur pourrait surtout se faire sentir chez les espèces de mammifères comme les ours qui évitent fortement les perturbations humaines (Martin et al. 2010). Certaines études ayant documenté l'activité des communautés de charognards aux sites d'abattages montrent que certaines espèces comme le renard roux et le coyote y sont fréquemment observées (Wikensros et al. 2013, Forsyth et al. 2014, Legagneux et al. 2014, Gomo et al. 2017). Ces espèces pourraient être à risque d'exposition au plomb et elles pourraient être aux prises avec un piège évolutif. Nous avons observé des hausses dans les concentrations de plomb chez deux espèces d'ours provenant de deux systèmes d'études différents. Il est donc probable que des hausses semblables soient présentes chez d'autres espèces de mammifères provenant d'autres systèmes où il y a de la chasse.

6.4 Suites potentielles

Au cours des chapitres 4 et 5, j'ai suggéré l'idée que les chasseurs de gros gibier pourraient conduire les ours, et possiblement d'autres mammifères charognards, vers un piège évolutif en abandonnant des carcasses et viscères contenant des fragments de plomb. Les effets toxiques du plomb sont en général bien documentés (Singh et al. 2018, Pain et al. 2019) et mes travaux montrent que les ours ont des niveaux de plomb plus élevés dans leurs tissus dans les endroits où il y a plus de chasse. Pour le moment, nous ne savons pas si les hausses que nous avons observées dans les concentrations en plomb chez les ours sont suffisantes pour causer des effets délétères chez ces derniers. Il serait donc pertinent de concevoir des études permettant d'investiguer cet important aspect qui n'a pas été directement abordé au cours de ma thèse. Cela nous permettrait de déterminer si les restes d'abattage jetés par les chasseurs peuvent réellement être considérés comme un piège évolutif chez les ours ou possiblement d'autres mammifères.

Premièrement, il serait souhaitable de collecter des échantillons de sang chez les ours noirs d'Amérique en période d'hibernation ou de quelques jours à quelques semaines suivant l'émergence de la tanière. Nous aurions donc l'opportunité de directement comparer les concentrations de plomb des ours en Suède et au Québec. Cela nous permettrait aussi de mieux situer les concentrations de plomb mesurées chez les ours noirs par rapport au seuil de toxicité rapportés chez d'autres espèces. Afin de déterminer si les chasseurs de gros gibier créent effectivement un piège évolutif pour les mammifères charognards, je suggère de concentrer les futurs travaux sur les effets sous-létaux et plus spécifiquement, sur de potentiels effets comportementaux causés par l'exposition au plomb chez l'ours brun Scandinave. Ecke et al. (2017) ont montré que le taux de mouvement et l'altitude de vol étaient réduits chez les aigles royaux dont la concentration sanguine en plomb dépassait le seuil de 25 µg/L (ou 25 ppb). Les ours en Suède ont une concentration sanguine moyenne (écart-type) de plomb de 96,6 (35,6) µg/L (Fuchs et al. 2021), ce qui est environ quatre fois supérieur au seuil rapporté par Ecke et al. (2017). Les données de plomb chez les aigles et les ours ne peuvent pas être directement comparées, mais il serait pertinent de vérifier si le plomb affecte le taux de mouvement chez les ours. Les données provenant d'ours bruns équipés d'un collier GPS devraient

permettre de réaliser cette étude qui nous permettrait de déterminer s'il y a réellement des conséquences mesurables de l'exposition au plomb provenant de la chasse chez les ours.

Deuxièmement, une autre suite potentielle pourrait être d'utiliser l'ablation au laser (ex. LA-ICP-MS) afin de déterminer la distribution des éléments dans les dents d'ours ou d'autres espèces de mammifères. Cette méthode analytique consiste à utiliser un laser afin de brûler une zone précise sur un échantillon et peut être utilisée afin de déterminer la concentration d'un élément dans un tissu spécifique de la dent (Kohn et al. 2013). Comme les différents tissus d'une dent se forment à différents moments, cela permettrait d'étudier l'exposition aux contaminants durant certaines périodes de la vie (Barbosa et al. 2005). Une analyse plus approfondie des couches de cément par ablation au laser pourrait s'avérer particulièrement intéressante puisque cela pourrait permettre de reconstruire l'historique d'exposition au plomb (ou d'un autre élément) chez un individu. Ce type d'étude a été réalisée par Clark et al. (2020) qui ont pu montrer que l'accumulation de zinc dans les dents de morse (*Odobenus rosmarus*) était liée à l'atteinte de la maturité sexuelle chez cette espèce.

Finalement, il serait également souhaitable de mesurer les concentrations de plomb dans les tissus d'autres carnivores vivant en plus grande proximité avec les humains, tels que le coyote ou le renard roux. Ces deux espèces ont aussi été observées sur les sites d'abattage d'orignaux au Québec (Legagneux et al. 2014) et le renard roux visite les restes d'abattage d'orignaux en Norvège (Gomo et al. 2017). Elles pourraient donc être à risque d'exposition au plomb et elles pourraient même l'être plus que les ours. Tel que discuté dans la section 6.3, la peur des humains chez les ours pourrait leur conférer une certaine protection face au piège évolutif généré par les chasseurs qui abandonnent des restes d'abattage contenant des fragments de plomb. Cette « protection » serait probablement amoindrie chez des espèces qui évitent moins fortement les humains, du moins spatialement. Il serait donc intéressant de concevoir une étude permettant d'investiguer la relation entre la peur des humains et l'utilisation de restes d'abattage. Par exemple, il serait possible d'utiliser des caméras automatiques pour documenter l'activité des charognards à des sites spécifiques et ensuite évaluer les changements dans leur activité après l'introduction d'une carcasse (ou d'un appât). Cette expérience pourrait être réalisée à travers un gradient de perturbations humaines, ce qui permettrait

de vérifier comment l'attractivité des carcasses varie en fonction de l'environnement où elles se trouvent. Il serait ensuite possible de collecter des échantillons de tissus après la période de chasse et d'en mesurer la teneur en plomb qui pourrait être mise en relation avec l'activité des charognards autour des carcasses. Une étude basée sur le renard roux ou le coyote pourrait aussi s'avérer utile afin d'étudier le risque d'exposition au plomb chez les mammifères charognards dans le sud du Québec, où la densité de récolte de cerf de virginie est élevée, mais où très peu d'ours sont récoltés à la chasse (Figure 4.1). Ceci nous permettrait d'avoir une meilleure vue d'ensemble du risque d'exposition au plomb provenant des munitions chez les mammifères.

6.5 Comment régler la problématique des munitions plomb ?

La meilleure façon de résoudre les problèmes causés par les munitions en plomb est d'en réduire l'usage. L'empoisonnement au plomb chez les charognards est le résultat d'une sous réponse face à un risque potentiellement mortel (Smith et al. 2021). Les charognards ne sont pas en mesure de correctement identifier les risques associés à l'ingestion de fragments de munition incrustés dans les carcasses (Nadjafzadeh et al. 2015) et l'empoisonnement au plomb n'est donc pas le fruit d'une réponse inadéquate face à l'augmentation de la biomasse disponible durant la période chasse. En effet, dans plusieurs écosystèmes, la chasse fournit une grande quantité de nourriture aux charognards durant une période critique avant l'hiver (Wikens et al. 2013, Lafferty et al. 2016). Certaines pratiques comme, par exemple, enterrer les organes internes à la suite de l'éviscération du gibier ou l'interdiction de jeter les restes d'abattage dans l'environnement pourraient réduire le risque d'exposition au plomb chez les charognards (Sato et al. 2016), mais pourraient cependant avoir d'importantes conséquences chez les charognards qui dépendent de cette ressource (Mateo-Tomás et Olea 2010, Mateo-Tomás et al. 2015). En revanche, interdire les munitions en plomb pour tout type de chasse permettrait de réduire le risque d'exposition au plomb chez la faune en général (Stevenson et al. 2005, Kelly et al. 2011), tout en gardant disponible la biomasse provenant des restes d'abattage, ce qui permettrait aux charognards de continuer à bénéficier de cette ressource importante.

Les restrictions concernant l'usage des munitions en plomb sont efficaces pour réduire le risque d'exposition au plomb chez la faune, sans affecter le succès des chasseurs, et cela peut être illustré en évaluant l'impact des restrictions concernant l'usage de munitions en plomb dans le cadre de la chasse à la sauvagine et l'exemple de la Californie. Au Canada, il est interdit d'utiliser de la grenaille de plomb pour chasser les oiseaux migrateurs depuis le 1^{er} septembre 1999, mais quelques restrictions régionales avaient préalablement été implantées au cours des années 90 (Stevenson et al. 2005). À la suite de la mise en place de ces interdictions, les concentrations en plomb dans les os de plusieurs espèces de canard ont diminué d'environ deux tiers tant chez les canards barboteurs (de 11 µg/g à 4 µg/g) que chez les canards plongeurs (de 28 µg/g à 10 µg/g) (Stevenson et al. 2005). Dans un autre exemple, il a aussi été montré que sans restriction sur l'usage de munitions en plomb en Californie (États-Unis), le rétablissement de la population de condors de la Californie aurait été impossible (Finkelstein et al. 2012). D'autres espèces telles que l'urubu à tête rouge (*Carthartes aura*) et l'aigle royal en Californie ont aussi montré d'importantes réductions (2,5 et 3 fois) de leur plombémie en seulement une année à la suite de l'interdiction de chasser avec des munitions en plomb (Kelly et al. 2011). L'efficacité de ces mesures montre donc qu'il est pertinent de restreindre ou d'interdire l'usage de munitions en plomb pour la chasse, surtout en considérant que les munitions en plomb n'offrent pas de réels avantages dans un contexte de chasse et qu'il est possible de les remplacer par des alternatives dites « non-toxiques ».

Les munitions en plomb utilisées pour chasser la grande faune ne sont pas essentielles et peuvent facilement être remplacées par des munitions en cuivre qui sont tout aussi efficaces. L'efficacité des munitions alternatives est un grand point d'inquiétude chez les chasseurs (Thomas et al. 2016); cependant, dans le cas de la chasse aux oiseaux migrateurs, il n'y a pas de différence entre le taux de récolte et le taux de blessures non mortelles chez les tourterelles tristes (*Zenaida macroura*) (Pierce et al. 2015) et il y a même une diminution de la fréquence de blessures non-mortelles chez la sauvagine à la suite de l'interdiction d'utiliser des cartouches contenant du plomb (Ellis et Miller 2022). Plusieurs études ont montré des résultats semblables dans un contexte de chasse au gros gibier. McCann et al. (2016) ont utilisé des munitions en cuivre pour abattre des wapitis dans le parc national Theodore Roosevelt aux États-Unis et concluent que ces munitions étaient suffisamment

précises et efficaces, tant dans un contexte de gestion faunique que dans un contexte de chasse. Il a aussi été montré, dans le cadre d'expériences balistiques, que les munitions en cuivre offrent une performance similaire à celles des munitions en plomb en ce qui concerne les dommages aux tissus et le transfert d'énergie (Trinogga et al. 2013, Gremse et al. 2014).

D'autres études ont aussi tenté de documenter quantitativement l'efficacité des munitions en cuivre en utilisant des paramètres comme la distance de fuite par un animal après avoir été atteint par un projectile (Kanstrup et al. 2016, Martin et al. 2017). Kanstrup et al. (2016) ont montré que les chevreuils (*Capreolus capreolus*) et cerfs élaphes (*Cervus elaphus*) abattus avec des munitions en cuivre parcouraient en moyenne moins de 40 m après avoir été atteints, reflétant une mort rapide. Une étude récente de Hampton et al. (2022) montre que dans un contexte de chasse au cerf sambar (*C. unicolor*), les munitions en plomb et en cuivre produisent des distances de fuite similaires, mais que les distances de fuite étaient légèrement plus grandes chez les individus abattus à l'aide d'un projectile en cuivre (35 m versus 22 m). Une différence de 13 m en moyenne est toutefois négligeable d'un point de vue biologique (Hampton et al. 2022). Cette étude montre aussi que l'augmentation de la distance de fuite en fonction de la masse corporelle des individus abattus est semblable avec les deux types de munitions (Hampton et al. 2022). Ce qui suggère que les munitions en cuivre et en plomb gardent une efficacité similaire à travers toute une gamme de masses corporelles. L'efficacité des munitions en cuivre n'est donc pas un réel problème.

Les munitions en cuivre aussi sont disponibles pour les calibres les plus populaires et ce, à un prix comparable à celui des munitions de qualité équivalente en plomb (Thomas 2013). Nous parlons ici d'une différence de moins de 1 à 1,5\$ (dollars canadien) par cartouche selon le fabricant et le calibre. Cette somme est dérisoire lorsque l'on considère, qu'à la base, le coût d'achat des munitions et l'entretien des armes à feu ne représente qu'une infime partie (< 7%) des dépenses annuelles d'un chasseur (MDDEFP 2013). De plus, la disponibilité ne fera que s'améliorer avec l'augmentation de la demande chez les chasseurs étant donné qu'il sera plus rentable pour les manufacturiers de produire des munitions en cuivre (Thomas et al. 2019). Les inquiétudes quant à l'efficacité, au prix et à la disponibilité des munitions en cuivre ne sont donc pas supportées par l'état actuel de nos

connaissances. Bien que la base de ces inquiétudes soit légitime, ces dernières ne représentent pas de réels obstacles à l'implantation de règlements ou d'interdictions concernant l'utilisation de munition en plomb.

Le ralentissement de la transition n'est donc pas dû à un manque de connaissances ni à des problèmes de disponibilité ou de performance, mais plutôt à une opposition d'ordre politico-social (Arnemo et al. 2016). Dans ce contexte, il est impératif de présenter les faits et dévoiler les méthodes que les opposants utilisent afin de propager de la désinformation (Schmid et Betsch 2019). J'aimerais donc profiter de la présente tribune qui m'est offerte afin d'aborder (et corriger) quelques arguments parfois douteux utilisés par certains individus ou organisations afin de ralentir la transition vers des munitions « non-toxiques ». Prenons, par exemple, un article publié sur le site web de MEATEATER (Heffelfinger 2022). Dans cet article, l'auteur avance essentiellement qu'il n'y a pas d'arguments scientifiques supportant l'interdiction des munitions en plomb, que les effets chez les charognards sont rares et négligeables; et qu'il n'y a pas d'effets sur la santé humaine. Évidemment, aucun de ces arguments ne tient réellement la route après une courte revue de la littérature.

Premièrement, l'argument selon lequel les conséquences des munitions en plomb chez les populations de charognards sont généralement négligeables et qu'ils se limitent à quelques cas anecdotiques est erroné. Cet argument est problématique pour deux raisons : 1) il y a bel et bien des conséquences détectables au niveau des populations sauvages (Finkelstein et al. 2012, Slabe et al. 2022, Green et al. 2022) et 2) il est ardu de bien documenter les épisodes de mortalité chez les populations sauvages. À moins d'épisodes de mortalité de masse, les animaux mourants ou les carcasses sont rapidement consommés par les prédateurs et les charognards, ce qui limite notre capacité à détecter et quantifier les épisodes de mortalité (Sindermann 1987). Malgré cette difficulté majeure, plusieurs oiseaux de proie sont retrouvés morts ou mourants à cause d'un empoisonnement au plomb (Radio-Canada 2019, Helander et al. 2021). Seulement une faible proportion de la mortalité est rapportée et la cause de mortalité est confirmée dans une proportion encore plus faible des cas chez les populations sauvages (Vyas 1999). Les quelques cas anecdotiques d'intoxications

ne sont donc que la pointe de l'iceberg et la mortalité réelle est fort probablement beaucoup plus importante que celle qui est présentement connue (Figure 6.2).

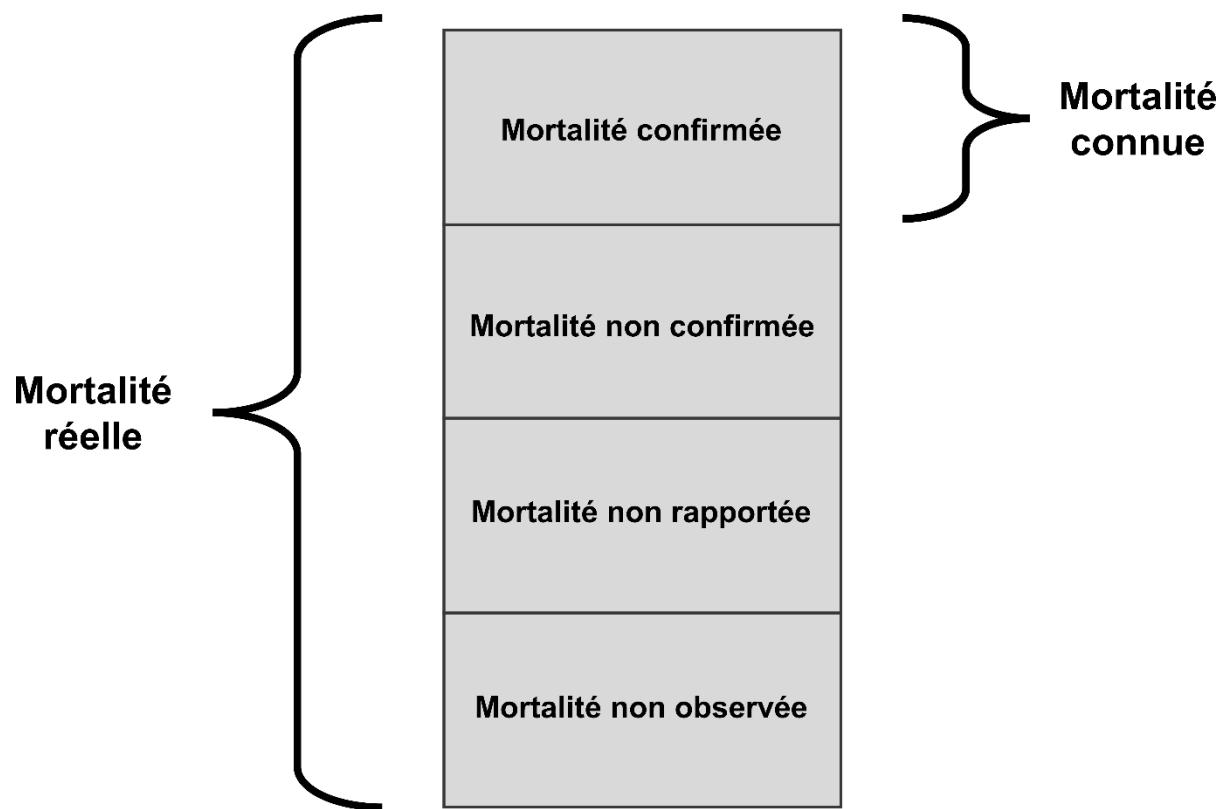


Figure 6.2 Représentation schématique des épisodes de mortalité chez les populations sauvages par rapport l'information disponible.

Seulement une faible proportion des cas de mortalité sont rapportés et confirmés (Vyas 1999). Figure inspirée de Vyas (1999).

Deuxièmement, l'argument d'Heffelfinger (2022) selon lequel les munitions en plomb ne posent aucun risque à la santé humaine est tout aussi douteux. Plusieurs études ont montré un lien entre la consommation de viande de gibier et les concentrations de plomb dans le sang chez les humains. Les études en question indiquent que les chasseurs ont généralement des niveaux de plomb plus élevés lorsque comparés aux non-chasseurs et que ces différences s'accentuent avec la fréquence de consommation de viande de gibier (Iqbal et al. 2009, Meltzer et al. 2013, Fustinoni et al. 2017, Buenz

et Parry 2018, Tammone et al. 2021). Il est impératif de souligner que, selon l’Organisation mondiale de la Santé (World Health Organization 2022), il n’existe aucun niveau d’exposition au plomb jugé sécuritaire puisque des effets sur la santé ont été observés pour chaque niveau d’exposition mesuré. Évidemment, nous parlons ici d’effets sur la santé et non pas de mortalité directement liée à une intoxication au plomb. Je dois admettre qu’il me semble peu probable que l’ingestion de plomb provenant des munitions induise directement de la mortalité chez les chasseurs ou leur entourage et il est vrai qu’à ma connaissance cela n’a jamais été rapporté; cependant, de faibles niveaux d’exposition au plomb ont été associés au développement de troubles cardiovasculaires chez les adultes (Navas-Acien et al. 2007) et de troubles neurologiques chez les enfants (Chiodo 2004). L’exposition au plomb additionnelle à laquelle font face les chasseurs (et possiblement leur entourage) n’est donc pas sans risque pour la santé. Même si le risque absolu est faible, il a été montré que lorsque la concentration sanguine passe de 10 µg/L à 60 µg/L le risque de mortalité découlant de troubles cardiovasculaires augmente d’environ 70 % (Lanphear et al. 2018). Il a aussi été montré qu’une concentration de plomb de 48 µg/L était associée à des augmentations de 1 à 2 mmHg (millimètre de mercure) de la tension artérielle et de 30% du risque d’hypertension (Gambelunghe et al. 2016). Au Québec, 1,7% des chasseurs sont exposés à suffisamment de plomb provenant des fragments de munition pour avoir une augmentation de 1 mmHg de leur tension artérielle (Fachehoun et al. 2015). À l’échelle d’une population, disons de 50 000 chasseurs, cela représente tout de même environ 850 individus qui s’exposent inutilement au plomb et les risques y étant associés peuvent facilement être évités en utilisant des munitions en cuivre. Dans tous les cas, le principe de précaution devrait s’appliquer et les munitions en plomb ne devraient pas être utilisées dans un contexte de chasse.

Je crois qu’une piste de solution afin de contrer la désinformation serait d’utiliser les cours d’initiation à la chasse avec armes à feu comme tribune afin de mieux informer les chasseurs sur les risques liés à l’utilisation de munitions en plomb chez la faune et les humains. Ces cours sont obligatoires afin d’exercer le droit de chasser et leur objectif principal est d’enseigner aux futurs chasseurs comment pratiquer la chasse de façon durable, responsable et sécuritaire. Il serait relativement facile et pertinent d’intégrer la problématique des munitions en plomb à ces cours, ce

qui permettrait de transmettre l'information directement aux futurs chasseurs avant qu'ils ne soient exposés à la désinformation. Cette stratégie de communication s'est avérée efficace dans le passé afin de réduire la propagation de la désinformation concernant d'autres enjeux comme les changements climatiques ou la vaccination (Compton et al. 2021). Il a été montré que le fait d'exposer le public aux faits tout en réfutant la désinformation au préalable permet de réduire la portée de celle-ci lorsqu'elle est subséquemment rencontrée (Compton et al. 2021). Évidemment, l'intégration de la problématique des munitions en plomb dans les cours d'initiation à la chasse ne réglerait pas tous les problèmes à elle seule, mais pourrait grâce à une communication directe, réduire la portée de la désinformation circulant sur ce sujet, tout en facilitant l'implantation d'éventuelles restrictions sur l'usage de munitions en plomb pour tous les types de chasse.

6.6 Conclusion

Dans cette thèse, je me suis intéressé aux conséquences de la chasse chez deux omnivores opportunistes, l'ours brun scandinave et l'ours noir d'Amérique. Je me suis particulièrement intéressé aux conséquences de la chasse chez des espèces et groupes démographiques non convoités durant les activités de chasse. Les conséquences de la chasse sont en général assez bien documentées et c'est particulièrement le cas chez le gibier convoité (Ciuti et al. 2012, Bonnot et al. 2013, Norum et al. 2015, Marantz et al. 2016, Thurfjell et al. 2017, Paton et al. 2017, Leclerc et al. 2019), mais seulement quelques rares études ont tenté d'évaluer ces effets chez d'autres espèces ou groupes non-convoités (Grignolio et al. 2011, Brown et al. 2020, Dobbins et al. 2020).

J'ai montré que les chasseurs d'originaux induisaient un paysage de la peur chez les ours et que ces derniers évitent fortement les sites d'abattage même s'ils pourraient y acquérir une importante ressource nutritive (chapitre 2). J'ai aussi montré que les mesures mises en place afin de protéger les groupes démographiques vulnérables contre la récolte durant la période de chasse n'ont pas d'impact sur la perception du risque chez ces groupes et qu'elles pourraient potentiellement conduire à de plus grandes dépenses énergétiques (chapitre 3). Finalement, j'ai montré qu'il y avait un lien entre la distribution des sites d'abattages et le risque d'exposition au plomb tant chez les ours noirs que chez

les ours bruns (chapitres 4 et 5). Les résultats de ces deux derniers chapitres sont importants puisque, jusqu'à maintenant peu d'études, s'étaient intéressées au risque d'exposition au plomb provenant des munitions chez les mammifères et mes travaux indiquent que les mammifères peuvent s'exposer au plomb en consommant les restes d'abattage jetés par les chasseurs. Cette problématique n'est donc pas limitée aux charognards aviaires.

Pour conclure, mes travaux ont permis de mieux comprendre les conséquences de la chasse sur le comportement et le risque d'exposition au plomb chez deux espèces d'ours. Mes travaux permettent d'approfondir nos connaissances des fondements théoriques sur lesquels ils reposent (c.-à-d. paysage de la peur et pièges évolutifs) et pourront, je l'espère, permettre d'améliorer la gestion des effets néfastes de la chasse. Plus particulièrement, j'espère que mes travaux serviront à sensibiliser les gestionnaires de la faune et les chasseurs aux risques liés à l'utilisation de munitions en plomb. Je crois qu'en tant qu'utilisateurs des milieux naturels nous avons le devoir de mieux comprendre et de minimiser les conséquences que nos loisirs peuvent avoir sur la faune et leurs habitats. Cela est vrai pour n'importe quelle activité, incluant celles qui ne posent pas de danger immédiat pour la faune, mais cela devient particulièrement important dans un contexte de chasse, puisque les effets de la récolte s'ajoutent aux perturbations non létales.

ANNEXES

7.1 Annexe chapitre 2

7.1.1. Section S1: Background information

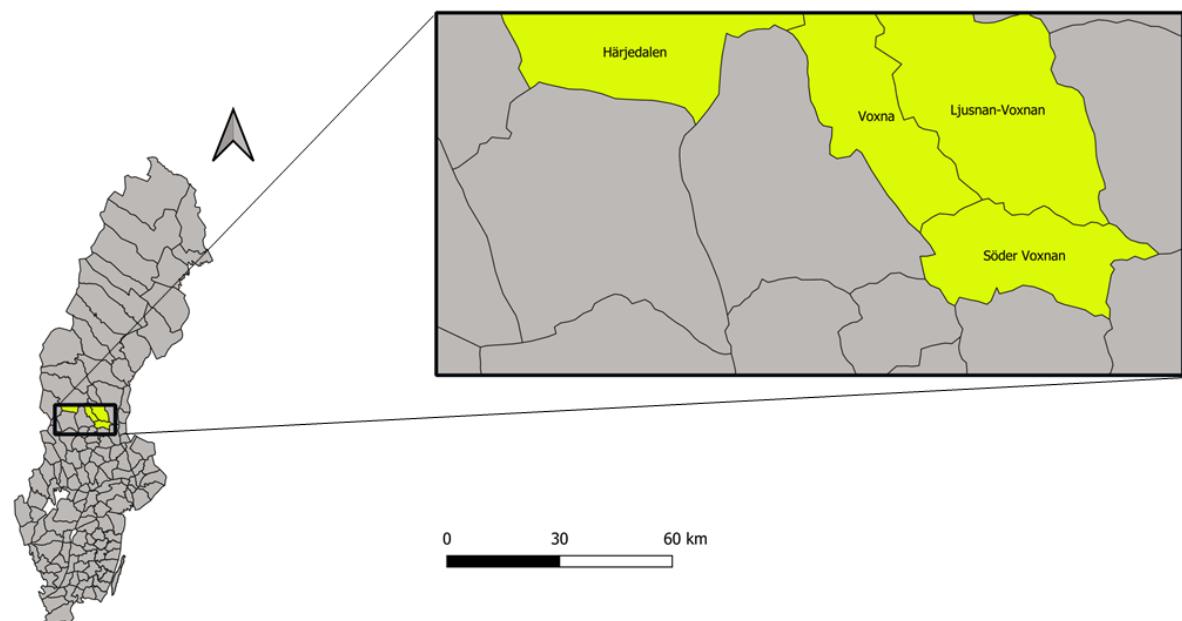


Figure S2.1 Map of the moose management units in Sweden. The rectangle represents the study area where brown bears were marked in south-central Sweden.

The yellow zones (Härjedalen, Voxna, Ljusnan-Voxnan and Söder Voxnan) represent the moose management units from which we extracted moose harvest locations, 2016-2019.

Table S2.1 Variables included in integrated step-selection functions of brown bears ($n = 53$) during the fall in south-central Sweden, 2016-2019.

Variable	Description	Mean \pm SD
Used	Available (0) and used (1) steps	-
Young forest (< 5m)	% forest < 5m tall within 50m-buffer	28.7 ± 34.6
Conifer forest (5-15m)	% coniferous forest (5-15 m tall) within 50m-buffer	11.7 ± 20.3
Mixed forest (5-15m)	% mixed forest (5-15 m tall) within 50m-buffer	2.44 ± 7.85
Deciduous forest (5-15m)	% deciduous forest (5-15 m tall) within 50m-buffer	0.96 ± 4.87
Clearcut	% clearcut within 50 m-buffer	3.94 ± 16.2
Open bog	% treeless bog within 50 m-buffer	4.73 ± 13.9
Distance to road (m)	Distance to the closest road	318 ± 229
Terrain ruggedness	Terrain ruggedness index	11.1 ± 8.33
Step length [log(m)]	Log of distance travelled in 1h	4.25 ± 2.35
Turning angle [cos(rad)]	Cosine of movement direction	0.08 ± 0.71
RSFhunt	Relative probability of moose kill by hunters	1.03 ± 0.36
Hunting	Hunting periods (five level factor)	-

Notes: The mean \pm standard deviation (SD) represent raw landscape features extracted from buffers (radius = 50 m) centered at the end of used and available steps. Step lengths and turning angles are log- and cosine-transformed, respectively. Original Nationella marktäckdata classes were 118 and 128 for young forest, 111 to 113 for coniferous forest, 114 for mixed forest, 115 to 117 for deciduous forest and 2 for open bog.

7.1.2. Section S2: Scaling experiment for resource selection in brown bears

As resource selection is scale-dependent in large carnivores (Pitman et al. 2017), we needed to identify the scale at which variables should be extracted. To choose the appropriate scale, we conducted a scaling experiment, whereby landcover types were extracted within buffers of various

radii [0 m (dummy coded), 50 m, 100 m, 150 m, 250 m, 350 m] centered on the end location of each step. We used the *fit_issf* function from the *amt* package to fit conditional logistic regressions with step ID as strata to each bear-year individually (Signer et al. 2019). We used AICc, as described in the main document, to compare the performance of the following model structure: Used $(0,1) \sim \% \text{ Deciduous (5-15 m)} + \% \text{ Conifer (5-15 m)} + \% \text{ Young forest (< 5 m, >7 years old)} + \% \text{ Bog} + \% \text{ Clearcut (< 7 years old)} + \text{Distance to Road} + \text{Terrain ruggedness} + \log(\text{step length}) + \cos(\text{turning angle})$, with datasets that differed only in the scale (i.e., buffer size) at which landcover types were extracted. We counted the number of bear-years for which each scale explained the most variance and our results suggest that most bears selected resources at the 50 m scale (Figure S2.2). We consequently used this dataset in further analyses. The dummy model returned a warning regarding a potential infinite Beta for the Clearcut class in a single individual; however, that model was not the top-ranked within the set and it did not influence the results of the scaling experiment.

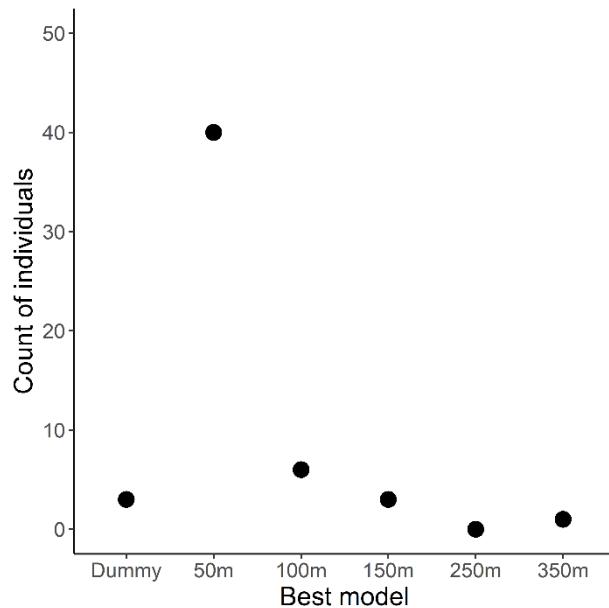


Figure S2.2 The number of individuals ($n = 53$ bear-years, in south-central Sweden, during 2016-2019) for which each scale explained the most variance.

The models were named after the buffer sizes (Dummy = 0 m radius) and differed only in the scales from which resources were extracted. Model selection was conducted by AICc.

7.1.3. Section S3: Model selection hunter RSF and bear iSSF

We built seven candidate generalized linear models with a binomial family and a logit link function [*glm* function, *stats* package; (R Core Team 2021)] for the resource selection by moose hunters. The seven models represented competing hypotheses: 1) that the probability of moose kills is random or that it depends on 2) accessibility only (Distance to road, elevation, terrain ruggedness, proportion of human infrastructures), 3) the proportion of open areas (clearcut and open bogs), 4) accessibility and the proportion of open areas, 5) forest composition (Young forest <5m, >7 years old; 5-15m conifer forest; 5-15m mixed forest and 5-15m deciduous forest), 6) forest composition and accessibility and 7) accessibility, the proportion of open areas and forest composition combined (Table S2.2). Model selection was conducted using second order Akaike Information Criterion (AICc) and its derived measures (ΔAICc and Akaike weight) from the *AICmodavg* package (Mazerolle 2020). Models within $\Delta\text{AICc} < 2$ were considered equivalent (Burnham and Anderson 2002).

Table S2.2 Structure of candidate models used to estimate habitat selection coefficients for moose hunters in south-central Sweden, 2016-2019.

Models	Structure
1. Null	Used ~ 1
2. Accessibility	Used ~ Distance to road + Elevation + Elevation ² + Terrain ruggedness + Terrain ruggedness ² + Infrastructure
3. Open	Used ~ Clearcut + Open bog
4. Open + accessibility	Used ~ Distance to road + Elevation + Elevation ² + Terrain ruggedness + Terrain ruggedness ² + Infrastructure + Clearcut + Open bog

Table S2.2 (Continued)

5. Forest composition	Used ~ Young forest + 5-15m conifer forest + 5-15m deciduous forest + 5-15m mixed forest
6. Forest composition + accessibility	Used ~ Distance to road + Elevation + Elevation ² + Terrain ruggedness + Terrain ruggedness ² + Infrastructure + Young forest + 5-15m conifer forest + 5-15m deciduous forest + 5-15m mixed forest
7. Full model	Used ~ Distance to road + Elevation + Elevation ² + Terrain ruggedness + Terrain ruggedness ² + Infrastructure + Clearcut + Open bog + Young forest + 5-15m conifer forest + 5-15m deciduous forest + 5-15m mixed forest

Notes: The model names reflect their underlying hypothesis. All models were fitted using generalized linear models with a binomial family and logit link function. The original Nationella Markätckedata classes were 51 and 52 for the variable infrastructure. See Table S2.1 for the other variables.

We also modelled resource selection at fine temporal scale in brown bears by using iSSF. To determine the best fixed effect structure, we first fitted conditional logistic regressions with step ID as strata by using the *fit_issf* function for each demographic group and for both day and night, separately (Signer et al. 2019). Each set contained three models built with a different set of variables and represented competing hypotheses (Table S2.3). In the Open model, brown bear habitat selection depends only on open habitats and included variables were clearcut, distance to road and open bog. In the second model (Natural model), brown bear habitat selection depends only on forest composition (i.e., young, deciduous, mixed and coniferous forests) and terrain ruggedness. The third model included the variables from both the Natural and Open models. We could not include the relative probability of moose kill in combination with landscape covariates due to lack of independence between this variable and the others. We added the log of step length and the cosine of the turning angle and an interaction between each covariate and the hunting period in all candidate models. The best performing RSF model for moose hunter was the Full model, which had a ΔAICc

of ≥ 11.48 to the next best model (Table S2.4) and was also attributed 100% of the weight within the model set (Table S2.4).

The four best models all included the variables elevation, terrain ruggedness and distance to roads (Table S2.4). For the bear iSSF, the combination of the natural and open models performed best for all demographic groups during both day and night, and this model structure was attributed 100% of the weight in all model sets (Table S2.5).

Table S2.3 Structure of candidate models used to estimate habitat selection coefficients for brown bears ($n = 53$) in south-central Sweden, 2016-2019.

Models	Structure
Open	Used ~ Clearcut/hunting + Open_bog/hunting + Distance to road/hunting + log(Step_length)/hunting + cos(Turning_angle)/hunting
Natural	Used ~ Young_forest/hunting + Coniferous/hunting + Mixed/hunting + Deciduous/hunting + Terrain ruggedness/hunting + log(Step_length)/hunting + cos(Turning_angle)/hunting
Natural + Open	Used ~ Distance to road/hunting + Clearcut/hunting + Open_bog/hunting + Young_forest/hunting + Coniferous/hunting + Mixed/hunting + Deciduous/hunting + Terrain ruggedness/hunting + log(Step_length)/hunting + cos(Turning_angle)/hunting

Notes: All models were fitted using conditional logistic regression with step ID as strata. '/hunting' denotes an interaction between the variables and the hunting periods defined in Figure 2.1 from the main manuscript.

Table S2.4 Model selection by Akaike Information Criterion (AICc) for candidate generalized linear models used to estimate habitat selection coefficients for moose hunters in south-central Sweden, 2016-2019.

Models	K	AICc	ΔAICc	w	LL
7. Full	13	8414.95	0	1	-4194.45
6. Forest composition + Accessibility	11	8426.43	11.48	0	-4202.19
4. Open + Accessibility	9	8430.19	15.24	0	-4206.08
2. Accessibility	7	8450.89	35.94	0	-4218.44
3. Open	3	8662.75	247.8	0	-4328.37
5. Forest composition	5	8692.38	277.43	0	-4341.18
1. Null	1	8696.84	281.89	0	-4347.42

Notes: K = number of parameters, ΔAICc is the difference with the lowest AICc value, w is the model weight and LL is the log-likelihood of the model.

Table S2.5 Model selection by Akaike Information Criterion (AICc) for integrated step-selection models in brown bears during day and night in south-central Sweden, 2016-2019.

	Model	K	AICc	ΔAICc	w	LL
Females with offspring (Day)	Natural+Open	50	79073.22	0	1	-39486.60
	Natural	35	80284.62	1211.40	0	-40107.30
	Open	25	80581.27	1508.05	0	-40265.63
Females with offspring (Night)	Natural+Open	50	46609.50	0	1	-23254.73
	Natural	35	46968.65	359.15	0	-23449.32
	Open	25	47005.23	395.73	0	-23477.61
Solitary females (Day)	Natural+Open	50	74960.88	0	1	-37430.42
	Natural	35	75764.33	803.46	0	-37847.16
	Open	25	76608.09	1647.21	0	-38279.04
Solitary females (Night)	Natural+Open	50	43883.14	0	1	-21891.55
	Natural	35	44209.48	326.34	0	-22069.73
	Open	25	44344.51	461.37	0	-22147.25
Subadult females (Day)	Natural+Open	50	81825.99	0	1	-40862.98
	Natural	35	82480.75	654.76	0	-41205.37
	Open	25	83377.24	1551.25	0	-41663.61
Subadult females (Night)	Natural+Open	50	48904.62	0	1	-24402.29
	Open	25	49072.81	168.19	0	-24511.40
	Natural	35	49179.53	274.92	0	-24554.76

Notes: K = number of parameters, ΔAICc is the difference with the lowest AICc value, w is the model weight and LL is the log-likelihood.

7.1.4. Section S4: Complementary results

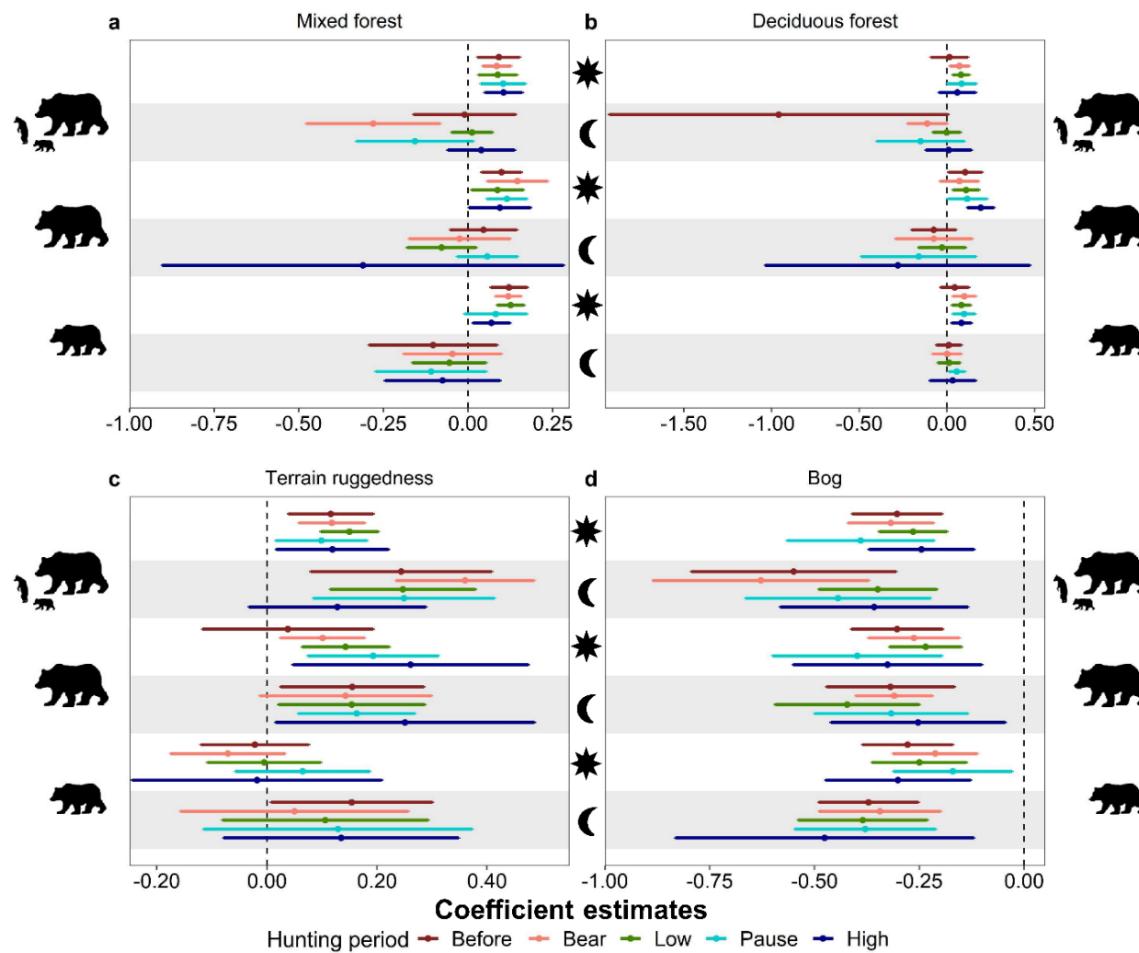


Figure S2.3 Coefficient estimates for a) the selection of mixed forest, b) the selection of deciduous forest, c) the selection of terrain ruggedness and d) the selection of bog with 95% confidence intervals. The coefficients were estimated from integrated step-selection functions for female brown bears with dependent offspring ($n = 18$ bear-years), solitary females ($n = 17$ bear-years) and subadult females ($n = 18$ bear-years) for day and night in south-central Sweden, 2016–2019.

The coefficients were estimated for each hunting period: before hunting (red), bear hunt (pink), low intensity moose hunt (green), pause (cyan) and high intensity moose

hunt (dark blue). Other parameters are presented in Figure 2.3 (main document), Tables S2.6 and Figure S2.4.

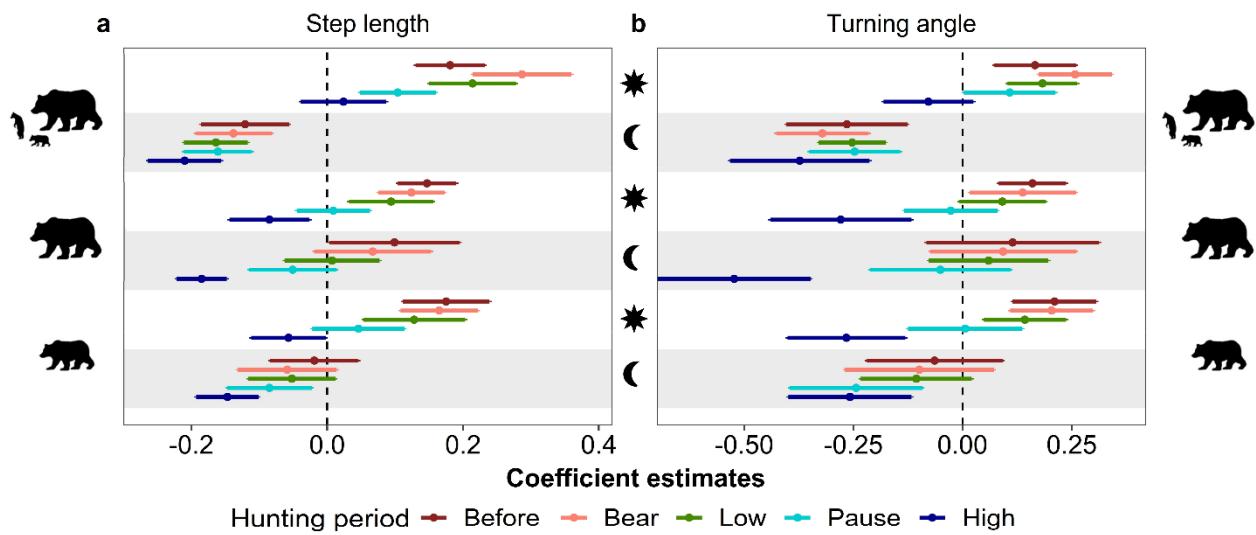


Figure S2.4 Coefficient estimates for a) the log step length and b) the cosine of turning angle with 95% confidence intervals. The coefficients were estimated from integrated step-selection functions for female brown bears with dependent offspring ($n = 18$ bear-years), solitary females ($n = 17$ bear-years) and subadult females ($n = 18$ bear-years) for day and night in south-central Sweden, 2016-2019.

The coefficients were estimated for each hunting period: before hunting (red), bear hunt (pink), low intensity moose hunt (green), pause (cyan) and high intensity moose hunt (dark blue). Other parameters are presented in Figure 2.3 (main document).

Table S2.6 Coefficients of movement parameters with 95% confidence intervals estimated from integrated step-selection functions for female brown bears with dependent offspring ($n = 18$ bear-years), solitary females ($n = 17$ bear-years) and subadult females ($n = 18$ bear-years) for day and night in south-central Sweden, 2016-2019. The coefficients were estimated for each hunting period: before hunting (red), bear hunt (yellow), low intensity moose hunt (green), pause (blue) and high intensity moose hunt (purple). The coefficients presented in this table were estimated from the bear habitat iSSF models.

		Step length [log(m)]		Turning angle [cos(rad)]	
		Day	Night	Day	Night
Females with dependent offspring	Before	0.225 ± 0.054	-0.099 ± 0.066	0.181 ± 0.096	-0.275 ± 0.139
	Bear	0.338 ± 0.078	-0.107 ± 0.060	0.263 ± 0.078	-0.326 ± 0.111
	Low	0.279 ± 0.076	-0.144 ± 0.048	0.197 ± 0.082	-0.255 ± 0.078
	Pause	0.167 ± 0.066	-0.131 ± 0.049	0.123 ± 0.113	-0.243 ± 0.108
	High	0.065 ± 0.067	-0.177 ± 0.054	-0.068 ± 0.105	-0.374 ± 0.162
Solitary females	Before	0.199 ± 0.044	0.124 ± 0.097	0.158 ± 0.073	0.117 ± 0.197
	Bear	0.180 ± 0.054	0.094 ± 0.090	0.148 ± 0.125	0.091 ± 0.169
	Low	0.144 ± 0.069	0.047 ± 0.074	0.103 ± 0.099	0.057 ± 0.138
	Pause	0.060 ± 0.056	-0.019 ± 0.066	-0.018 ± 0.106	-0.042 ± 0.160
	High	-0.017 ± 0.048	-0.125 ± 0.039	-0.264 ± 0.161	-0.504 ± 0.166
Subadult females	Before	0.213 ± 0.067	-0.001 ± 0.065	0.216 ± 0.094	-0.061 ± 0.152
	Bear	0.205 ± 0.059	-0.035 ± 0.073	0.211 ± 0.094	-0.099 ± 0.168
	Low	0.191 ± 0.081	-0.029 ± 0.066	0.159 ± 0.098	-0.113 ± 0.132
	Pause	0.094 ± 0.071	-0.059 ± 0.064	0.018 ± 0.134	-0.239 ± 0.154
	High	-0.013 ± 0.061	-0.118 ± 0.045	-0.262 ± 0.137	-0.254 ± 0.138

7.1.5. Section S5: Post-hoc movement iSSF

Following our habitat selection analyses, we decided to investigate the brown bears response to moose hunting. iSSF can also be used to conjointly investigate movement and resource selection (Avgar et al. 2016); however, we could not investigate habitat specific movement in our original

iSSF and included the movement parameters as controls (Signer et al. 2019, Fieberg et al. 2021), which is essential because bears modify their activity patterns during the fall. Investigating movement in an iSSF framework requires extracting resources at the start of each step and adding interactions with movement parameters and habitat variables, whereas resource selection requires the extraction of resources at the end of each step (Signer et al. 2019, Fieberg et al. 2021).

In this article, it was not possible to build a model with both habitat-specific movement and resource selection because we split our analyses according to time of day and it becomes an issue for the steps that overlap the onset of legal hunting hours. Thus, the start and end of these steps were recorded in different time periods and including habitat specific movement and resource selection in the same model could have led to bias estimates. We could also not create separate models for each demographic groups and pooled all individuals due to convergence issues; however, this is not an issue because the movement response to a disturbance is similar in all demographic groups (Ordiz et al. 2013). Therefore, we estimated the movement response to the probability of moose kill at the population levels with separate models for day and night during each of the hunting period with the structure described in Table 1 in the main document.

We fitted tentative Gamma and Von mises distributions for step length and turning angle for moving steps only (moving step = hourly displacement of > 35 m) with all individuals combined with the *fit_distr* function [*amt* package; (Signer et al. 2019)]. We used the coefficients for the log of step length as modifiers of the original Gamma shape, whereas the coefficients for the cos of turning angle were used as modifiers of the original Von mises concentration parameters (Fieberg et al. 2021).

Shape(RSFhunt)

$$= S_0 + \beta(\log \text{step length}) + \beta(\log \text{step length}:RSFhunt) \cdot RSFhunt + \beta(\log \text{step length}:RSFhunt^2) \cdot RSFhunt^2$$

Where S_0 is the original shape parameter, $\beta(\log \text{step length})$, $\beta(\log \text{step length:RSFhun})$ and $\beta(\log \text{step length:RSFhun}^2)$ are the model coefficient for the log of step length and the interactions between the log of step length and the probability of moose kill (RSFhun) and its quadratic term (RSFhun^2).

Kappa(RSFhun)

$$= K_0 + \beta(\cos \text{turning angle}) + \beta(\cos \text{turning angle:RSFhun}) \cdot \text{RSFhun} + \beta(\cos \text{turning angle:RSFhun}^2) \cdot \text{RSFhun}^2$$

Where K_0 is the original concentration parameter (i.e., kappa), $\beta(\cos \text{turning angle})$, $\beta(\cos \text{turning angle:RSFhun})$ and $\beta(\cos \text{turning angle:RSFhun}^2)$ are the model coefficient for the cos turning angle and the interactions between the cos turning angle and the probability of moose kill (RSFhun) and its quadratic term (RSFhun^2).

We calculated the expected speed (m/h) of female brown bears when traveling through low and high probability of moose kill (10% and 90% quantiles) by multiplying the scale and shape of updated gamma distributions for day and night during each hunting period (Table S2.7). The updated Von mises distributions were generated using the *dvmomises* function in the *circular* package (Agostinelli and Lund 2017). We did not need to generate updated Gamma distributions of step length, since we could obtain the mean expected hourly displacement by multiplying the updated shapes with the original scales.

Table S2.7 Mean expected hourly displacement (m/h) with 95% confidence intervals for female brown bears ($n = 53$) when traveling through areas with low and high relative probability of moose kills (RSFhunt) during day and night of each hunting periods in south-central Sweden during 2016-2019.

		Low RSFhunt (10 % quantile)			High RSFhunt (90 % quantile)		
		Expected hourly displacement (m/h)					
		Mean	Lower	Upper	Mean	Lower	Upper
Before	Day	523	513	534	626	585	667
	Night	450	434	467	473	433	513
Bear hunt	Day	545	530	561	614	573	654
	Night	435	417	453	460	422	497
Low intensity moose hunt	Day	528	516	540	580	547	613
	Night	436	423	449	447	419	474
Moose hunt pause	Day	493	483	502	551	510	593
	Night	412	400	424	444	416	572
High intensity moose hunt	Day	462	450	475	501	462	541
	Night	382	374	390	422	392	452

We similarly generated probability densities of turning angles when traveling through low and high probability of moose kill (10% and 90% quantiles) by using the updated Von mises distributions for day and night during each hunting periods (Figure S2.5). Brown bears moved faster and more directionally when traveling through areas with high probabilities of moose kill during day and night in most hunting periods, which supports our interpretation that moose hunters were perceived as a threat.

Brown bears moved faster and more directionally when traveling through areas with high probabilities of moose kill during day and night in most hunting periods, which supports our interpretation that moose hunters were perceived as a threat.

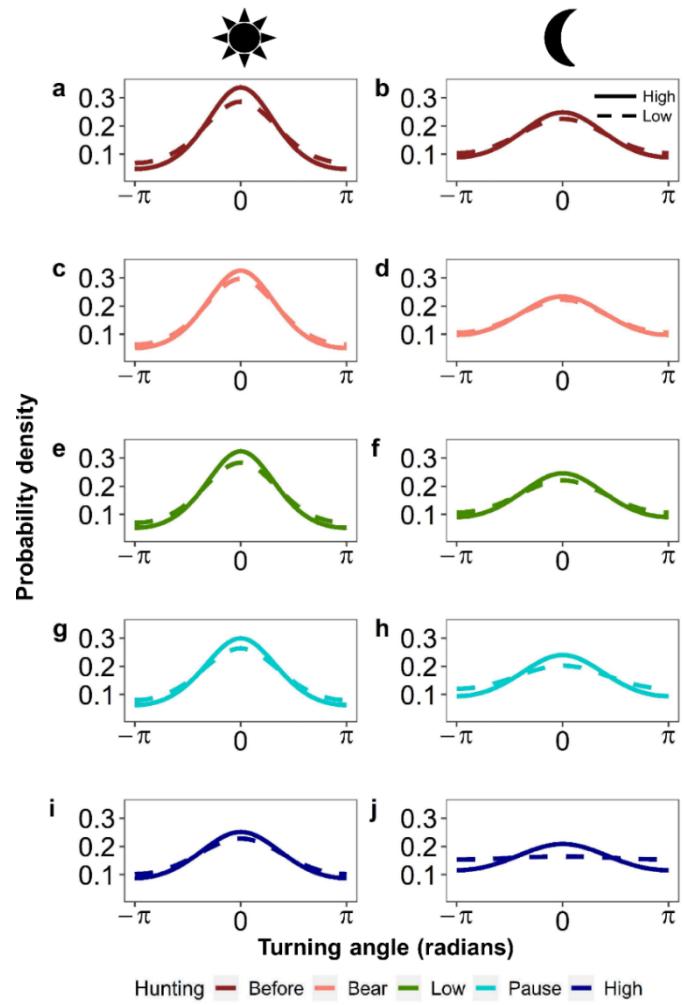


Figure S2.5 Probability densities of turning angles (radians) for female brown bears ($n = 53$) when traveling through areas with low (10% quantile) and high (90% quantile) relative probability of moose kills (RSFhunt) during day and night of each hunting periods in south-central Sweden during 2016-2019.

Before hunting = red, Bear hunt = pink, Low intensity moose hunt = green, Moose hunt pause = cyan and High intensity moose hunt = dark blue.

7.1.6. References

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7.2 Annexe chapitre 3

Table S3.1 Output of linear mixed effect models used to predict the movement rate (log m/h) of females with dependent offspring ($n = 19$ bear-years), lone females ($n = 32$ bear-years), subadult females ($n = 32$ bear-years), and males ($n = 9$ bear-years) in south-central Sweden, before and during the bear hunt between 2016-2019. Statistically significant results ($\alpha < 0.05$) are highlighted in bold. The reference category for hunting variable is “*Before hunting*”.

	Coefficient	Std. Error	t-value	p-value		
Fixed effects		Random effects				
<i>Females with dependent offspring</i>						
Intercept	4.48	0.04	101.59	0.00	Intercept	0.14
Road_C	-0.02	0.03	-0.90	0.37	sin(suntime)	0.18
sin(suntime)	-0.41	0.06	-6.93	0.00	cos(suntime)	0.74
cos(suntime)	-0.64	0.18	-3.65	0.00	sin(2 * suntime)	0.29
sin(2 * suntime)	0.13	0.08	1.68	0.09	cos(2 * suntime)	0.14
cos(2 * suntime)	-1.20	0.05	-23.98	0.00	Residuals	1.41
huntingBear	0.12	0.04	2.68	0.01		
Road_C:sin(suntime)	-0.04	0.03	-1.24	0.22		
Road_C:cos(suntime)	0.01	0.04	0.28	0.78		
Road_C:sin(2 * suntime)	0.03	0.03	0.96	0.34		
Road_C:cos(2 * suntime)	-0.02	0.03	-0.49	0.63		
Road_C:huntingBear	-0.07	0.04	-1.90	0.06		
sin(suntime):huntingBear	0.09	0.06	1.53	0.13		
cos(suntime):huntingBear	-0.06	0.06	-0.99	0.32		
sin(2 * suntime):huntingBear	-0.01	0.06	-0.22	0.82		
cos(2 * suntime):huntingBear	-0.02	0.06	-0.45	0.65		
Road_C:sin(suntime):huntingBear	-0.01	0.05	-0.16	0.88		
Road_C:cos(suntime):huntingBear	-0.16	0.05	-2.96	0.00		
Road_C:sin(2 * suntime):huntingBear	-0.07	0.05	-1.44	0.15		
Road_C:cos(2 * suntime):huntingBear	0.03	0.05	0.68	0.50		

Table S3.1 (Continued)

<i>Lone females</i>						
Intercept	4.60	0.04	113.55	0.00	Intercept	0.17
Road_C	-0.04	0.02	-1.60	0.11	sin(suntime)	0.15
sin(suntime)	-0.41	0.05	-8.96	0.00	cos(suntime)	0.77
cos(suntime)	0.24	0.14	1.71	0.09	sin(2 * suntime)	0.19
sin(2 * suntime)	0.47	0.05	9.92	0.00	cos(2 * suntime)	0.20
cos(2 * suntime)	-1.26	0.05	-26.05	0.00	Residuals	1.47
huntingBear	-0.15	0.04	-3.86	0.00		
Road_C:sin(suntime)	-0.01	0.03	-0.18	0.85		
Road_C:cos(suntime)	-0.04	0.04	-1.22	0.22		
Road_C:sin(2 * suntime)	0.08	0.03	2.70	0.01		
Road_C:cos(2 * suntime)	0.05	0.03	1.63	0.10		
Road_C:huntingBear	-0.01	0.03	-0.34	0.73		
sin(suntime):huntingBear	-0.07	0.05	-1.28	0.20		
cos(suntime):huntingBear	0.00	0.06	0.05	0.96		
sin(2 * suntime):huntingBear	-0.13	0.05	-2.73	0.01		
cos(2 * suntime):huntingBear	-0.06	0.05	-1.29	0.20		
Road_C:sin(suntime):huntingBear	-0.02	0.04	-0.58	0.56		
Road_C:cos(suntime):huntingBear	-0.08	0.05	-1.55	0.12		
Road_C:sin(2 * suntime):huntingBear	-0.04	0.04	-0.96	0.34		
Road_C:cos(2 * suntime):huntingBear	-0.10	0.04	-2.41	0.02		
<i>Subadult females</i>						
Intercept	4.70	0.04	125.81	0.00	Intercept	0.16
Road_C	-0.06	0.02	-2.40	0.02	sin(suntime)	0.21
sin(suntime)	-0.23	0.05	-4.67	0.00	cos(suntime)	0.81
cos(suntime)	-0.70	0.15	-4.73	0.00	sin(2 * suntime)	0.32
sin(2 * suntime)	0.41	0.06	6.35	0.00	cos(2 * suntime)	0.29
cos(2 * suntime)	-1.39	0.06	-23.30	0.00	Residuals	1.41
huntingBear	0.02	0.03	0.58	0.56		
Road_C:sin(suntime)	0.04	0.03	1.44	0.15		
Road_C:cos(suntime)	-0.09	0.04	-2.46	0.01		
Road_C:sin(2 * suntime)	0.03	0.03	0.88	0.38		
Road_C:cos(2 * suntime)	-0.01	0.03	-0.45	0.65		
Road_C:huntingBear	0.04	0.03	1.32	0.19		
sin(suntime):huntingBear	0.02	0.05	0.48	0.63		

Table S3.1 (Continued)

cos(suntime):huntingBear	-0.01	0.05	-0.21	0.83		
sin(2 * suntime):huntingBear	-0.05	0.04	-1.06	0.29		
cos(2 * suntime):huntingBear	0.08	0.04	1.78	0.07		
Road_C:sin(suntime):huntingBear	-0.04	0.04	-0.97	0.33		
Road_C:cos(suntime):huntingBear	0.03	0.05	0.60	0.55		
Road_C:sin(2 * suntime):huntingBear	0.03	0.04	0.80	0.42		
Road_C:cos(2 * suntime):huntingBear	0.01	0.04	0.21	0.83		
<i>Males</i>						
Intercept	4.54	0.16	29.00	0.00	Intercept	0.42
Road_C	-0.07	0.06	-1.17	0.24	Residuals	1.73
sin(suntime)	-0.34	0.09	-3.84	0.00		
cos(suntime)	0.86	0.09	9.06	0.00		
sin(2 * suntime)	0.07	0.08	0.85	0.39		
cos(2 * suntime)	-1.25	0.08	-16.34	0.00		
huntingBear	-0.05	0.12	-0.39	0.69		
Road_C:sin(suntime)	-0.10	0.07	-1.46	0.14		
Road_C:cos(suntime)	-0.07	0.08	-0.88	0.38		
Road_C:sin(2 * suntime)	-0.06	0.07	-0.87	0.38		
Road_C:cos(2 * suntime)	-0.02	0.07	-0.21	0.83		
Road_C:huntingBear	0.00	0.09	-0.03	0.98		
sin(suntime):huntingBear	-0.10	0.14	-0.67	0.50		
cos(suntime):huntingBear	-0.06	0.15	-0.41	0.68		
sin(2 * suntime):huntingBear	0.07	0.12	0.60	0.55		
cos(2 * suntime):huntingBear	0.00	0.12	-0.02	0.99		
Road_C:sin(suntime):huntingBear	-0.09	0.11	-0.85	0.40		
Road_C:cos(suntime):huntingBear	-0.22	0.13	-1.68	0.09		
Road_C:sin(2 * suntime):huntingBear	-0.06	0.11	-0.51	0.61		
Road_C:cos(2 * suntime):huntingBear	-0.08	0.12	-0.71	0.48		

7.2.1. Alternative method with gamm instead of trigonometric functions

We modelled step length in bears with generalized additive mixed models (GAMM) by using the *gamm* function (Wood 2017), which allowed us to include a corCAR1 structure and account for temporal autocorrelation. The models included suntime with a cyclic cubic spline, the distance to the closest road and the hunting period (i.e., *before hunting* versus *bear hunting*). We added interactions between the hunting period and suntime and distance to road variables by using the “by” function.

We ran separate analyses for each demographic group because the *gamm* function does not accommodate three-way interactions. We also added random slopes for suntime and distance to the closest road by bear-year, thereby accounting for interindividual behavioural differences and added a random intercept for bear-year. We used diagnostic plots to ensure that model assumptions were met. The response variable was log-transformed to achieve normality of the residuals. We set α at 0.05 and all statistical analyses were carried in R version 4.1.0 (R Core Team 2021).

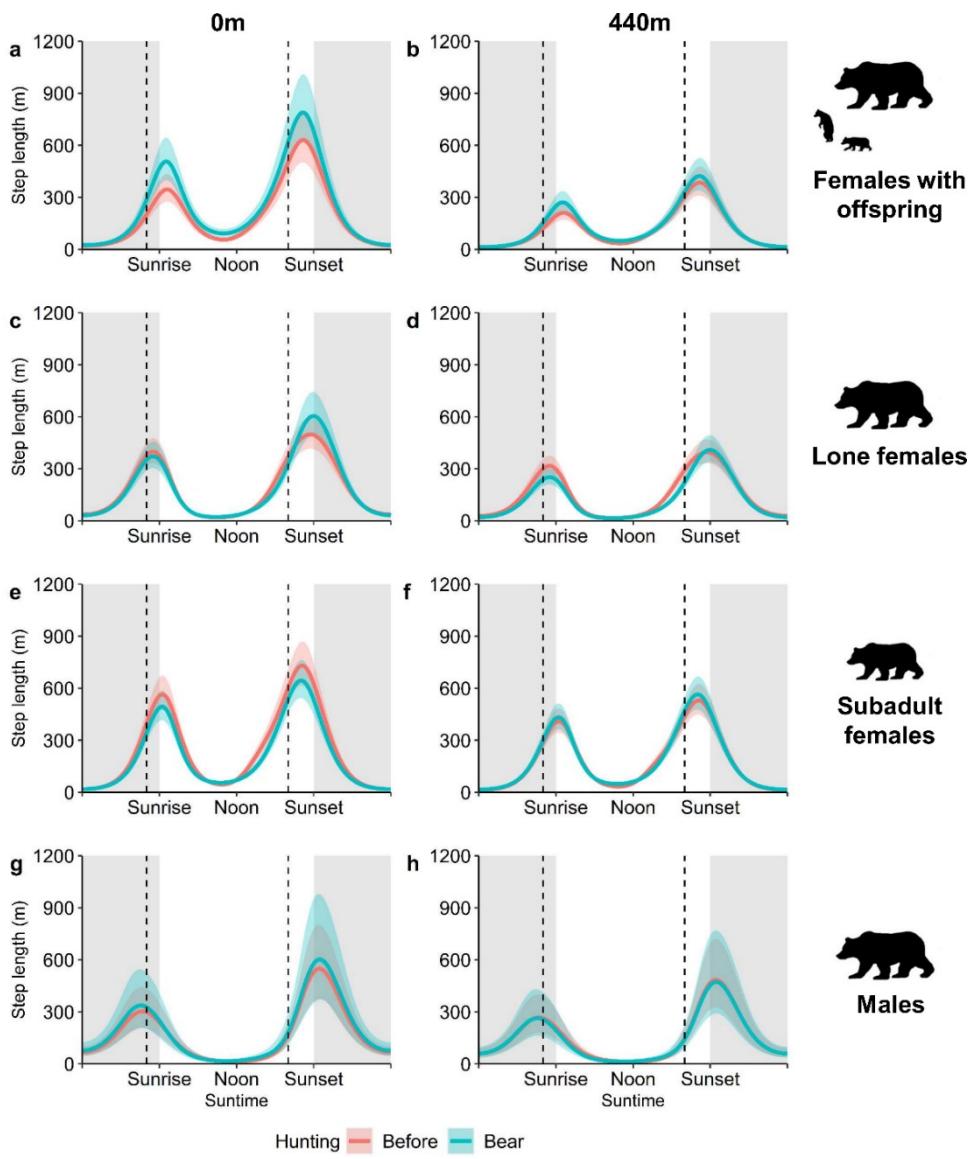


Figure S3.1 Predicted step length (m) with 95% confidence intervals from an alternative approach with generalized additive mixed effect models for brown bears according to time of day during each season (*before hunting* and *bear hunting*) for females with dependent offspring ($n = 19$ bear-years), lone females ($n = 32$ bear-years), subadult females ($n = 32$ bear-years), and males ($n = 9$ bear-years) in south-central Sweden, during 2016-2019.

Step length was predicted at 0 m and 440 m (0 and 75% quantiles) from the closest road and during each season (red = *before hunting*, blue = *bear hunting*). The

vertical dashed lines show the start (left) and end (right) of legal hunting hours. Shaded areas represent nighttime, whereas the white areas represent daytime.

7.2.2. References

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7.3 Annexe chapitre 4

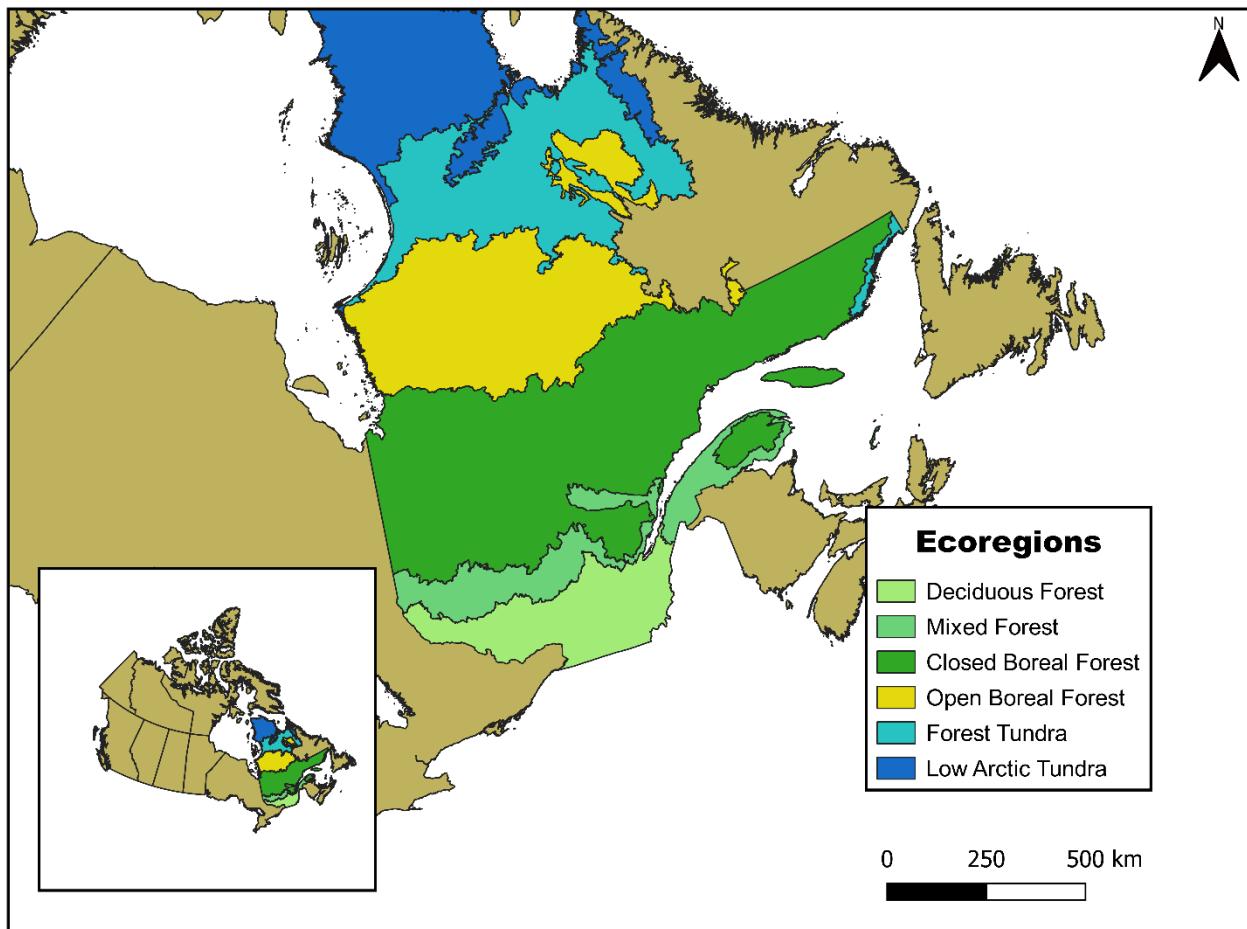


Figure S4.1 Maps of ecoregions within the province of Quebec (Canada).

Table S4.1 Parameters of linear mixed effect models used to predict log-transformed tooth lead (Pb) concentrations ($\mu\text{g/g}$) in hunted female ($n = 80$) American black bears in Quebec, Canada, during 2017-2018. The table shows the parameters of our initial analysis and the same parameters when the potential outlier is excluded from the analysis.

Estimate	95% confidence intervals		Variance	s.d.		
	Lower	Upper				
Original results (80 samples)						
<i>Fixed effects:</i>						
Intercept	-0.318	-0.552	-0.084	Random effects:		
Harvest density (2 km)	0.108	0.028	0.187	Management unit		
Age	0.129	0.098	0.158	Residuals		
Conditional $R^2 = 0.58$, Marginal $R^2 = 0.46$						
"Outlier" removed (79 samples)						
<i>Fixed effects:</i>						
Intercept	-0.304	-0.566	-0.040	Random effects:		
Harvest density (2 km)	0.102	0.005	0.198	Management unit		
Age	0.127	0.094	0.159	Residuals		
Conditional $R^2 = 0.54$, Marginal $R^2 = 0.42$						

Table S4.2 Parameters the linear mixed effect model used to predict log-transformed tooth lead (Pb) concentrations ($\mu\text{g/g}$) in hunted female ($n = 80$) American black bears in Quebec, Canada, during 2017-2018. Harvest densities were calculated within 2 km buffers and were broken down by game species.

	Estimate	95% confidence intervals		Variance	s.d.
		Lower	Upper		
<i>Fixed effects:</i>					
Intercept	-0.285	-0.583	0.027	Management unit	0.042
Deer harvest (2 km)	0.115	0.036	0.195	Residuals	0.158
Moose harvest (2 km)	-0.044	-0.264	0.175		0.397
Bear harvest (2 km)	0.250	-0.384	0.868		
Age	0.128	0.096	0.158		
Conditional R ² = 0.59, Marginal R ² = 0.48					

7.4 Annexes chapitre 5

Table S5.1 Model selection by Akaike information criterion corrected for small sample size (AICc). The model set was used to identify potential sources of Pb exposure in female brown bears (n = 34 individuals; n = 61 samples) with variables extracted within 4 and 6 km buffers centred around capture locations in south-central Sweden, during 2017-2020.

	K	AICc	ΔAICc	w	LL
4 km					
Full	8	27.55	0.00	0.69	-4.39
Background Pb	7	29.20	1.64	0.31	-6.54
RSF hunt	7	44.79	17.23	0.00	-14.34
Lactating	6	45.89	18.33	0.00	-16.17
Year	5	57.32	29.77	0.00	-23.12
Null	2	59.36	31.81	0.00	-27.58
6 km					
Full	8	28.06	0.00	0.74	-4.65
Background Pb	7	30.12	2.06	0.26	-7.00
RSF hunt	7	43.97	15.91	0.00	-13.93
Lactating	6	45.89	17.82	0.00	-16.17
Year	5	57.32	29.26	0.00	-23.12
Null	2	59.36	31.29	0.00	-27.58

Table S5.2 Model selection by Akaike information criterion corrected for small sample size (AICc) used to assess the performance of the top-ranked models with variables extracted at different scales (2, 4 and 6 km). Those models were used to identify potential sources of Pb exposure in female brown bears ($n = 34$ individuals; $n = 61$ samples) in south-central Sweden, during 2017-2020.

	K	AICc	ΔAICc	w	LL
Full 2 km	8	24.47	0.00	0.72	-2.85
Full 4 km	8	27.55	3.08	0.16	-4.39
Full 6 km	8	28.06	3.59	0.12	-4.65

Table S5.3 Parameters of the top-ranked models used to predict blood Pb concentrations [log(Pb µg/L)] in female brown bears ($n = 34$ individuals; $n = 61$ samples) with variables extracted within 4 and 6 km buffers centred on capture locations in south-central Sweden, during 2017-2020. S.E. = standard error, Hunter RSF = Relative probability of moose kill.

Variable	Estimate	S.E.	95% CI	
			Lower	Upper
4km				
Intercept	3.217	0.308	2.599	3.835
Environmental Pb	0.011	0.002	0.006	0.015
Hunter RSF	0.560	0.282	-0.005	1.125
Lactating	0.339	0.079	0.181	0.497
year2018	-0.015	0.110	-0.236	0.205
year2019	0.268	0.103	0.061	0.476
Year2020	0.042	0.105	-0.169	0.253
Multiple R ² = 0.53, Adjusted R ² = 0.48				
6km				
Intercept	3.072	0.358	2.355	3.789
Environmental Pb	0.011	0.002	0.006	0.016
Hunter RSF	0.694	0.333	0.026	1.362
Lactating	0.341	0.079	0.183	0.499
year2018	-0.035	0.111	-0.258	0.187
year2019	0.273	0.104	0.065	0.480
Year2020	0.039	0.105	-0.172	0.251
Multiple R ² = 0.53, Adjusted R ² = 0.48				

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