CONSÉQUENCES ÉCOLOGIQUES ET ÉVOLUTIVES DE LA CHASSE CHEZ L'OURS BRUN (*URSUS ARCTOS*) SCANDINAVE

par

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À ceux et celles pour qui la curiosité
ne s’est pas effacée avec le temps ...

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La planète Terre fait face à sa sixième extinction massive des espèces. Cette fois, l'Homme (*Homo sapiens*) est considéré comme la cause principale de ce phénomène. Une des menaces les plus importantes qui pèsent sur la survie des populations animales est la surexploitation, telle que la pêche et la chasse. L'exploitation diminue la survie des classes d'âges et de sexes qui sont récoltées, mais elle peut également induire des effets écologiques et évolutifs sur les populations sauvages. Bien que les effets écologiques et évolutifs de la récolte puissent influencer le taux de croissance de la population, ils sont peu documentés et quantifiés dans la littérature scientifique et sont rarement pris en compte lors de la gestion des populations exploitées. Cette thèse a donc comme objectif principal de quantifier les effets écologiques et évolutifs de la chasse chez une population de grand carnivore ; l'ours brun (*Ursus arctos*) scandinave. Cette population est suivie de manière longitudinale depuis 1985 par le *Scandinavian Brown Bear Project*. Ce projet de recherche cumule des informations, entre autres, sur l'âge, le sexe, la reproduction, la survie et le comportement des ours bruns, ce qui en fait une des bases de données des plus complètes au monde chez un grand carnivore.

Dans un premier temps, j'ai évalué les effets écologiques de la chasse. La chasse peut déstabiliser la structure spatiale et sociale d'une population récoltée et ainsi augmenter la probabilité d'observer de l'infanticide sexuellement sélectionné. Par conséquent, la chasse a le potentiel de diminuer la survie juvénile même si cette classe d'âge n'est pas directement visée par la récolte. En combinant des informations sur la survie juvénile et la localisation des mâles récoltés à la chasse, j'ai mis en évidence une diminution de la survie d'une portée d'une femelle lorsqu'un mâle était tué à proximité (Chapitre deux). De plus, j'ai montré que la mortalité d'un mâle à la chasse résulte en une restructuration spatiale qui perdure pendant deux années (Chapitre trois). Les résultats obtenus suggèrent que la chasse a des effets écologiques à long terme qui peuvent influencer la viabilité des populations.

Dans un deuxième temps, j'ai évalué les conséquences évolutives potentielles de la chasse. J'ai débuté en montrant qu'il existe de la variabilité comportementale en sélection d'habitat chez l'ours brun (Chapitre quatre), soit une des conditions de l'évolution par sélection naturelle. Ensuite, j'ai colligé de l'information issue de la littérature scientifique afin de montrer que les comportements des animaux peuvent influencer leur vulnérabilité à la récolte, que ce soit la pêche ou la chasse (Chapitre cinq). Ensuite, j'ai montré que les chasseurs peuvent induire des pressions sélectives sur le comportement des ours, soit la deuxième condition de l'évolution par sélection naturelle (Chapitre six). Bien que je n'aie pas quantifié l'héritabilité comportementale dans cette thèse, les résultats des chapitres quatre, cinq et six suggèrent néanmoins qu'il pourrait y avoir de l'évolution induite par la récolte pour les traits comportementaux héritables.

Finalement, j'ai comparé, pour la même population, les données du suivi longitudinal du *Scandinavian Brown Bear Project* aux données du registre d'abattages de chasse. J'ai mis en lumière que les données de registre d'abattages de chasse peuvent être biaisées par rapport à des données issues d'un suivi longitudinal, et ce, même dans un système d'étude où la chasse est considérée comme peu sélective (Chapitre sept). Cette conclusion est importante pour la gestion, la conservation et l'étude des effets écologiques et évolutifs de la chasse qui utilisent souvent les données dans les registres d'abattages de chasse. En effet, ces données constituent souvent une des seules sources d'informations disponibles pour plusieurs espèces exploitées. Bien que les données de registres d'abattages de chasse soient souvent abondantes, elles devraient être utilisées de manière prudente dans les décisions de gestion et de conservation considérant qu'elles sont souvent biaisées.

Les résultats de cette thèse ont permis de quantifier certains effets écologiques et évolutifs de la récolte et de souligner l'importance de ces effets pour la viabilité à long terme des populations exploitées. Mieux documenter les effets des activités anthropiques est primordial afin de pouvoir décider des actions à poser pour réduire ces effets dans une ère où l'Homme est la principale menace à la biodiversité de la planète.

Mots clés : carnivore, effets indirects de la récolte, infanticide sexuellement sélectionné, personnalité animale, sélection artificielle, survie

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GPS	Système de positionnement global | *Global positioning system*
GSM	Système global pour communication mobile | *Global System for Mobile Communications*
RSFs	Fonction de sélection des ressources | *Resource selection functions*
SSI	Infanticide sexuellement sélectionné | *Sexually selected infanticide*
VHF	Très haute fréquence | *Very high frequency*

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CHAPITRE 1

INTRODUCTION GÉNÉRALE

L'Homme (*Homo sapiens*) est une espèce ayant une grande capacité à modifier l'environnement biotique et abiotique dans lequel il vit. L'empreinte laissée par les activités anthropiques peut être observée dans tous les biomes de la planète (Halpern *et al.*, 2008; Kroodsma *et al.*, 2018; Sanderson *et al.*, 2002). Il est d'ailleurs généralement accepté qu'une nouvelle époque géologique ait débuté, l'Anthropocène (Corlett, 2015; Steffen *et al.*, 2011). En effet, la lithosphère et la biosphère sont grandement influencées par les activités anthropiques et nous sommes présentement au cœur de la sixième extinction massive des espèces qui, contrairement aux cinq épisodes précédents, est principalement causée par l'Homme (Ceballos *et al.*, 2015; Corlett, 2015; Steffen *et al.*, 2011). Une des menaces les plus importantes pour la biodiversité planétaire est son exploitation par l'Homme (Maxwell *et al.*, 2016; Pelletier et Coltman, 2018). Même avec des technologies plus primitives, l'exploitation par les humains a joué un rôle important dans l'extinction massive des grands mammifères observée en Amérique de Nord et en Australie lors de la fin du Pléistocène (Barnosky, 2004; Sandom *et al.*, 2014). De nos jours, l'Homme exploite également les espèces fauniques, et ce, à un taux très élevé menaçant la survie des populations (Darimont *et al.*, 2015; Maxwell *et al.*, 2016; Pauly *et al.*, 1998). En plus de réduire l'abondance des individus, l'exploitation peut avoir de nombreuses et importantes conséquences sur l'écologie et l'évolution des espèces. Conséquemment, il est important de bien comprendre et de quantifier tous les impacts de la récolte humaine sur les populations sauvages, incluant les impacts écologiques et évolutifs. Ceci nous permettra d'identifier les actions à poser pour réduire ces impacts et nous assurer de la viabilité à long terme et de la survie des populations exploitées.

Effets écologiques de la récolte

La récolte d'animaux sauvages peut avoir de nombreux effets écologiques (Fenberg et Roy, 2008). En effet, la récolte peut influencer, entre autres, le comportement des individus non récoltés. Par exemple, chez l'éléphant d'Afrique (*Loxodonta africana*), les mâles entre 25 et 30 ans de cette espèce entrent dans un état d'activité sexuelle et d'agressivité élevées nommé « musth » (Poole, 1987). Les éléphants peuvent exprimer ce comportement dès l'âge de 18 ans, mais la présence de mâles dominants retarde l'expression du « musth » chez les mâles plus jeunes. Cependant, la structure d'âge des mâles est plus jeune et la hiérarchie sociale est moins forte dans les populations chassées et on y retrouve généralement des éléphants qui expriment leur comportement de « musth » à un plus jeune âge. Un des effets secondaires d'exprimer ce comportement plus tôt est l'apparition de comportement deviant. En effet, il a été montré que de jeunes éléphants en « musth » peuvent attaquer des rhinocéros blancs (*Ceratotherium simum*), entraînant parfois la mort des rhinocéros (Slotow *et al.*, 2000). Les changements dans la structure d'âge des populations causés par la récolte peuvent donc modifier le comportement de jeunes mâles éléphants. Un autre effet écologique de la récolte est la modification de la structure des communautés. Par exemple, en Californie, la langouste (*Panulirus interruptus*) se nourrit d'oursins pourpres (*Strongylocentrotus purpuratus*), ce qui limite les populations d'oursins. Dans les communautés où la langouste est récoltée, cette pression de prédation est relâchée et les populations d'oursins croissent et consomment l'ensemble des algues disponibles (Lafferty, 2004). Ainsi, dans les communautés où les langoustes sont récoltées, les oursins ne sont plus limités par la prédation, mais par la disponibilité de nourriture et occasionnellement par des épisodes de maladies (Lafferty, 2004). De plus, la récolte d'une seule espèce peut induire des modifications dans l'ensemble d'une communauté animale et être difficilement réversibles, et ce, même une fois la récolte arrêtée (Fenberg et Roy, 2008; Lafferty, 2004; Ordiz *et al.*, 2013).

La récolte peut également avoir un effet écologique en influençant la démographie des populations exploitées. En effet, la récolte augmente la mortalité de certaines classes d'âges et de sexes. De plus, la sélectivité de la récolte peut influencer la démographie puisque l'élasticité de chacune des classes d'âges et de sexes diffère (Benton et Grant, 1999). Des effets démographiques indirects peuvent également être observés. La récolte peut perturber la structure d'âge ou le sexe-ratio de la population et ainsi influencer indirectement le taux de croissance de la population (Milner *et al.*, 2007). Par exemple, lorsque le sexe-ratio est déséquilibré et qu'il y a davantage de femelles ou lorsque la structure d'âge des mâles est jeune, la mise bas est retardée chez le renne (*Rangifer tarandus*) et l'orignal (*Alces alces*) et la masse des jeunes est plus petite, ce qui réduit leur survie (Holand *et al.*, 2003; Saether *et al.*, 2003). Des effets démographiques indirects peuvent également survenir lorsque l'Homme récolte un individu important pour la structure sociale d'une population tels qu'un mâle dominant ou une femelle matriarche (McComb *et al.*, 2001; Milner *et al.*, 2007; Williams et Lusseau, 2006).

La récolte de mâles dominants chez plusieurs espèces de carnivores peut déstabiliser la structure sociale et exacerber les conflits sexuels (Hrdy, 1979; Milner *et al.*, 2007). Par exemple, cinq observations ont été rapportées chez le lion (*Panthera leo*) où, suite à la récolte d'un mâle dominant, un mâle immigrant a pris le contrôle de la troupe de femelles et commis de l'infanticide sexuellement sélectionné (Loveridge *et al.*, 2007). Une étude plus récente, chez la même espèce, montre que lorsque la récolte de mâles dominants est plus élevée, la survie juvénile diminue, même si cette classe d'âge n'est pas récoltée (Loveridge *et al.*, 2016). Chez des espèces moins territoriales, certaines évidences laissent croire que la chasse pourrait également augmenter la fréquence de l'infanticide sexuellement sélectionné. Par exemple, la survie juvénile est plus faible dans les populations de cougar (*Puma concolor*) et d'ours brun (*Ursus arctos*) chassées intensivement que dans les populations où la pression de chasse est plus faible ou absente (Swenson *et al.*, 1997, 2001; Wielgus et Bunnell, 2000; Wielgus *et al.*, 2013). De plus, la sélection d'habitat des femelles cougars pendant la période de reproduction diffère davantage de celle des mâles dans les populations fortement chassées que dans les populations faiblement chassées (Keehner *et al.*, 2015). Ce comportement laisse croire que dans les populations fortement chassées les femelles tentent davantage de réduire le risque de subir de l'infanticide sexuellement sélectionné. Les évidences de l'exacerbation de l'infanticide sexuellement sélectionné causé par la chasse s'accumulent, mais sont souvent le résultat d’études qui comparent des observations issues de deux populations distinctes. Il serait fort intéressant de mener des études à une échelle spatiale plus fine et de vérifier au sein d’une même population si l’endroit et le nombre de mâles récoltés à la chasse se traduisent par une augmentation de la fréquence d’infanticide sexuellement sélectionné.

Chez les espèces non territoriales comme le cougar et l’ours brun, le mécanisme reliant la chasse et l’augmentation de l’infanticide sexuellement sélectionné demeure inconnu. Deux hypothèses sont présentes dans la littérature. L’une d’elles, nommée l’hypothèse du mâle immigrant, prédit qu’un mâle tué à la chasse serait remplacé par des mâles immigrants, plus enclins à tuer des oursons qui lui sont fort probablement non apparentés (McLellan, 2005). En effet, une des conditions pour que l’infanticide sexuellement sélectionné soit adaptative est que le mâle ne doit pas tuer sa propre progéniture (Hrdy, 1979). Cette hypothèse est souvent utilisée pour expliquer la présence d’infanticide chez des espèces non territoriales (Swenson *et al.*, 1997; Wielgus *et al.*, 2013), mais elle est rarement supportée par des observations en milieu naturel (McLellan, 2005). La seconde hypothèse est nommée la reconnaissance des partenaires (McLellan, 2015). Cette hypothèse suggère que tous les mâles peuvent commettre de l’infanticide sexuellement sélectionné, incluant les mâles résidents. La décision d’un mâle de commettre ou non de l’infanticide serait basée sur la reconnaissance des partenaires sexuels des années précédentes et la chasse augmenterait la recherche de partenaires pendant la période de reproduction et la possibilité qu’un nouveau mâle résident puisse être présent à proximité d’une femelle. Cette hypothèse a également rarement été testée, quoiqu’elle semble plus probable chez les espèces ayant de grands domaines vitaux qui se chevauchent et un système d’accouplement caractérisé par la promiscuité et la polygynie comme chez le cougar et l’ours brun. L’étude de l’infanticide sexuellement sélectionné et de l’effet de la chasse sur ce comportement est importante pour bien comprendre les effets écologiques de la récolte et l’influence de ces effets sur la viabilité des populations.

Effets évolutifs de la récolte

De nos jours, l'Homme est considéré comme une des pressions sélectives dominantes qui définissent les traits des espèces (Palumbi, 2001). En effet, l'Homme cause des changements phénotypiques plus rapides que la plupart des effets environnementaux (Hendry *et al.*, 2008), particulièrement lorsqu'il exploite des populations animales (Darimont *et al.*, 2009). Le développement technologique a permis à l'Homme d'augmenter son efficacité et de récolter de grandes proportions des populations sauvages (Darimont *et al.*, 2015; Pauly *et al.*, 1998). Ainsi, l'Homme induit des pressions sélectives sur les traits d'histoire de vie des populations récoltées par le simple fait d'augmenter la mortalité. Cette sélection peut ensuite être traduite en évolution pour les traits d'histoire de vie qui sont héritables. Plusieurs études en milieu naturel montrent effectivement que les pêcheries commerciales induisent de l'évolution vers une augmentation de la fécondité ainsi qu'une maturation à un plus jeune âge et une plus petite taille (Allendorf et Hard, 2009; Jørgensen *et al.*, 2007; Sharpe et Hendry, 2009). De plus, des études en milieu expérimental ont montré que des changements évolutifs peuvent survenir en quatre ou cinq générations seulement (Conover et Munch, 2002; Uusi-Heikkilä *et al.*, 2015). Ces études soulignent l'importance d'étudier les effets évolutifs de la récolte afin de mettre en place des mesures de mitigation pour limiter l'impact de la récolte sur les populations sauvages.

La recherche et la récolte d'un phénotype désiré peuvent également induire des pressions sélectives sur la morphologie des populations exploitées. En effet, la récolte est souvent sélective et il existe des types de récolte basés exclusivement sur la morphologie, tant en milieu marin qu'en milieu terrestre, qui sont reconnus pour engendrer de l'évolution sur les traits morphologiques (Allendorf et Hard, 2009; Allendorf *et al.*, 2008; Jørgensen *et al.*, 2007). Par exemple, en milieu marin, les filets maillant peuvent causer une pression sélective sur la taille des poissons (Edeline *et al.*, 2009; Hamon *et al.*, 2000). Une des évidences les plus concluantes de l'évolution morphologique induite par la récolte en milieu terrestre est l'évolution des cornes du mouflon d'Amérique (*Ovis canadensis*) en Alberta. En raison d'une chasse au trophée visant les béliers ayant les plus longues cornes, la chasse a entraîné une pression sélective qui a conduit à une diminution évolutive de la taille des cornes dans cette population (Coltman *et al.*, 2003; Pigeon *et al.*, 2016). Paradoxalement, la récolte sélectionne habituellement contre les phénotypes qui sont désirés. En plus de diminuer la fréquence des phénotypes désirables au sein des populations, la récolte pourrait également hausser la difficulté de récolter des individus, soit par l'apprentissage de ceux-ci à éviter d'être récolté de nouveau (par exemple, lors de la remise à l'eau), soit par évolution comportementale (Askey *et al.*, 2006; Philipp *et al.*, 2009).

La récolte peut également agir comme pression sélective sur le comportement des populations. Une des études phares sur la sélection comportementale induite par la récolte est une expérience en milieu lacustre. Les truites arc-en-ciel (*Oncorhynchus mykiss*) qui étaient plus hardies avaient une probabilité plus élevée d'être capturées dans les filets maillant que les truites plus timides (Biro et Post, 2008). Cette étude a été la première à montrer que la récolte basée sur la taille pouvait sélectionner pour des traits comportementaux. Il existe également quelques exemples qui montrent que la chasse peut induire des pressions sélectives sur le comportement. En effet, les wapitis (*Cervus elaphus*) qui sont récoltés à la chasse ont des taux de déplacement plus élevés et utilisent davantage les habitats sans couvert forestier que les wapitis qui survivent à la récolte (Ciuti *et al.*, 2012). Bien que la sélection comportementale induite par la récolte soit importante pour la conservation et la gestion des populations exploitées, ces effets ont reçu beaucoup moins d'attention dans la littérature que les effets sur les traits morphologiques ou les traits d'histoire de vie (Heino *et al.*, 2015; Uusi-Heikkilä *et al.*, 2008). Ceci est d'autant plus vrai pour la récolte en milieu terrestre, soulignant l'importance de l'étude des effets évolutifs comportementaux induit par la chasse.

La récolte induit des pressions sélectives comportementales qui dépendent de l'interaction entre la méthode de récolte, le comportement des animaux et celui des humains (Arlinghaus *et al.*, 2017; Diaz Pauli et Sih, 2017; Frank *et al.*, 2017). Par exemple, la probabilité qu'un animal sauvage soit capturé pourrait grandement être influencée par l'endroit où les humains décident de récolter et du comportement de sélection d'habitat de l'animal. Par conséquent, dans cette thèse, je mettrai une emphase particulière sur les effets évolutifs de la récolte sur le comportement de sélection d'habitat des animaux. Ce comportement est fondamental en écologie puisqu'il relie les individus aux ressources dont ils ont besoin pour survivre et se reproduire, en plus de nous informer sur la répartition des individus dans le paysage. Afin d'étudier les effets évolutifs de la récolte sur la sélection d'habitat, je m'attarderai à deux des trois conditions de l'évolution par sélection naturelle, soit la sélection et la variabilité (voir la conclusion pour l'héritabilité). L'étude de la variabilité interindividuelle en sélection d'habitat représente un certain décalage avec les études contemporaines en selection d'habitat, puisque ces dernières combinent généralement l'ensemble des patrons individuels de sélection d'habitat afin d'obtenir des inférences à l'échelle de la population. Ainsi, contrairement à la majorité des études en sélection d'habitat, la variabilité individuelle ne sera pas traitée comme un problème statistique (Gillies *et al.*, 2006), mais bien comme une opportunité de vérifier si les chasseurs peuvent induire de l'évolution comportementale. Cependant, pour ce faire, des informations comportementales détaillées doivent être disponibles.

Biais des données issues de la récolte

L'étude des effets écologiques et évolutifs de la récolte est complexe puisque des informations tant sur les individus qui sont récoltés que sur ceux qui survivent doivent être disponibles. Idéalement, les données d'une population qui fait l'objet d'un suivi longitudinal à long terme seraient utilisées puisque les effets écologiques, tout comme les effets évolutifs, peuvent survenir plusieurs années après la récolte. Ces suivis à long terme sont cependant rares, particulièrement pour les populations animales exploitées en milieu terrestre. Dans certaines jurisdictions, par contre, il existe des registres d'abattages de la faune contenant plusieurs informations sur tous les individus qui sont récoltées. Plusieurs études utilisent ces registres d'abattages pour dériver des proxys de l'abondance et de la productivité des populations sauvages (Cattadori *et al.*, 2003; Flanders-Wanner *et al.*, 2004). Certains utilisent même ces registres d'abattages pour étudier l'effet de la récolte sur les tendances phénotypiques des populations exploitées (Büntgen *et al.* 2018; Engan, 2014; Monteith *et al.*, 2013; Nuzzo et Traill, 2014). Il est important de noter cependant que des simulations montrent que les livres de records de chasse ne capturent pas, ou du moins, sous-estiment les tendances phénotypiques observées dans une population puisque les livres de records ne représente qu'une partie tronquée de la distribution des phénotypes dans la population (Festa-Bianchet *et al.*, 2015). Une étude empirique en milieu naturel montre également que les registres d'abattages sous-estiment le déclin de la taille des cornes de mouflons d'Amérique dans un système de chasse au trophée (Pelletier *et al.*, 2012). Par conséquent, l'utilisation des données dans les livres de records de chasse ou des registres d'abattages issus de chasse sélective, comme la chasse au trophée, devrait être faite de manière prudente puisque les résultats obtenus peuvent être biaisés. Ces résultats soulignent également l'importance des études longitudinales à long terme pour bien quantifier les conséquences écologiques et évolutives de la récolte. Il reste à savoir cependant si ces registres d'abattages sont également biaisés dans des systèmes de chasse moins sélectifs que la chasse au trophée. En effet, il serait possible que la majorité des registres d'abattages soient biaisés puisqu'une étude a montré que différentes formes de chasse (e.g. au trophée ou avec des chiens) dans une même population entraînent une sélection pour différentes masses chez *Cervus elaphus* (Martínez *et al.*, 2005). Il est donc important de comparer des données d'un suivi à long terme et les données d'un registre d'abattages de chasse dans un système peu sélectif afin de vérifier si ces dernières sont biaisées.

Objectifs

L'objectif principal de cette thèse est de documenter et quantifier les effets écologiques et évolutifs de la chasse. Pour atteindre cet objectif, j'utiliserai les données d'un programme de recherche à long terme sur une population d'ours brun scandinave. Pour la première section de cette thèse (chapitre deux et trois) portant sur les effets écologiques de la chasse, les objectifs spécifiques sont :

1. Quantifier les effets spatiotemporels de la récolte de mâles sur la survie juvénile
2. Documenter la restructuration spatiale des domaines vitaux suite à la récolte d'un mâle

Dans la seconde partie de cette thèse (chapitre quatre, cinq et six), je documenterai deux des trois prémisses de l'évolution par sélection naturelle, soit la variabilité et la sélection. Pour ces chapitres, les objectifs spécifiques sont :

3. Quantifier les différences individuelles en sélection d'habitat des ours
4. Documenter la sélection comportementale induite par la récolte en milieu marin et terrestre
5. Vérifier si les chasseurs exercent une pression de sélection sur le comportement des ours

Et finalement, dans la dernière partie de cette thèse (chapitre sept), je vérifierai si l'utilisation des données d'un registre d'abattages, dans un système de chasse moins sélectif que la chasse au trophée, peut se solder en des conclusions biaisées. L'objectif spécifique de ce chapitre est de :

6. Quantifier les biais dans un registre d'abattages de la faune

Répondre à ces objectifs demande une quantité importante d'informations détaillées sur la survie, la reproduction et le comportement des individus qui sont récoltés et des individus qui survivent à la récolte, et ce, sur plusieurs années. Ma collaboration avec le *Scandinavian Brown Bear Project* m'a permis d'avoir accès à l'une des bases de données les plus détaillées et imposantes au monde à ce sujet, grâce à quoi j'ai pu répondre à ces objectifs. L'ensemble des résultats obtenus lors de mes études doctorales, y compris ceux non détaillés dans la présente thèse (voir Annexe 1A), permettront de mieux comprendre les effets écologiques et évolutifs de la récolte. Ceci s'avère important afin de pouvoir affiner les plans de gestion et de conservation des espèces sauvages ainsi que pour mieux prédire les effets de la récolte sur les populations exploitées.

Méthodes

Espèce étudiée

L'ours brun est un carnivore de la famille des ursidés et occupe une variété d'habitats : de la forêt boréale, en passant par la toundra arctique, jusqu'aux déserts (Pasitschniak-Arts, 1993). L'ours brun est considéré comme une espèce non territoriale, non sociale, ayant une reproduction saisonnière et polygame (Steyaert *et al.*, 2012). Les domaines vitaux des mâles sont plus grands que ceux des femelles et ils se chevauchent tous spatialement (Dahle et Swenson, 2003; Steyaert *et al.*, 2012). Les femelles et les mâles se déplacent sur de grandes superficies pendant la période de reproduction afin de maximiser les rencontres avec des partenaires (Steyaert *et al.*, 2012). Ainsi, dans une saison de reproduction, une femelle copule en moyenne avec trois à cinq mâles différents, ce qui augmente la probabilité d'avoir plusieurs paternités dans une même portée qui compte de 1 à 4 oursons (Bellemain *et al.*, 2006; Craighead *et al.*, 1995). Cette tactique de la femelle pourrait lui permettre de confondre la paternité et, ainsi, réduire le risque de subir de l'infanticide sexuellement sélectionné (Steyaert *et al.*, 2012). Au contraire, les femelles avec des oursons de l'année vont, quant à elles, réduire leur taux de déplacement et s'isoler spatialement des mâles pendant la période de reproduction en utilisant, par exemple, des habitats plus près des habitations humaines (Steyaert *et al.*, 2013). Ce comportement des femelles, pense-t-on, vise également à réduire la probabilité d'infanticide sexuellement sélectionné. En effet, il a été montré que les femelles qui réussissent à élever leurs oursons à maturité se retrouvent plus près des habitations humaines que les femelles qui perdent leurs oursons pendant la période de reproduction (Steyaert *et al.*, 2016).

L’aire d’étude

L’aire d’étude est située au centre-sud de la Suède (61°N, 15°E) et couvre une superficie de 55 000 kilomètres carrés (Figure 1.1). On retrouve dans l’aire d’étude des tourbières, des lacs et une forêt de conifères productive. La forêt est aménagée de manière intensive et consiste en de petites parcelles de différents âges. La forêt est dominée par le pin sylvestre (*Pinus sylvestris*), le pin tordu (*Pinus contorta*) et l’épinette de Norvège (*Picea abies*) et il y a également la présence d’espèces décidues comme le bouleau (*Betula pubescens* et *B. pendula*) et le peuplier faux-tremble (*Populus tremula*). En sous-étage on retrouve des lichens, des éricacées (*Empetrum* spp., *Vaccinium* spp.) et des graminées. La topographie est caractérisée par des paysages vallonnés oscillant entre 150 et 1000 mètres au-dessus du niveau de la mer. Quelques routes pavées (0,14 kilomètre par kilomètre carré) sont présentes dans l’aire d’étude, mais les routes en gravier (0,7 kilomètre par kilomètre carré) sont plus abondantes en raison des activités forestières (Martin *et al.*, 2010). De petits villages et des maisons isolées (0,3 habitation par kilomètre carré) sont répartis de manière presque uniforme dans l’aire d’étude (Martin *et al.*, 2010). La présence humaine est plus importante durant l’été et l’automne en raison de la cueillette de petits fruits et la période de chasse.

Le projet de recherche sur l’ours brun scandinave

Le *Scandinavian Brown Bear Project* est un projet de recherche à long terme sur l’ours brun en Scandinavie. Depuis 1985, ce projet de recherche cumule de l’information sur l’écologie des ours au centre-sud de la Suède (Figure 1.1). Pour ce faire, un suivi longitudinal a été mis en place et les individus capturés sont suivis, lorsque possible, de leur naissance jusqu’à leur mort. Les captures sont réalisées en avril, quelque temps après que les ours émergent de leur tanière hivernale. Lors de ces captures, le sexe, la masse et plusieurs mesures morphométriques sont notés. Pour les ours dont l’âge est inconnu, une prémolaire vestigiale est récoltée afin de faire un compte des anneaux de cément qui nous indique l’âge de l’ours (Matson, 1993). Les femelles sont quant à elles observées quelques fois pendant la saison

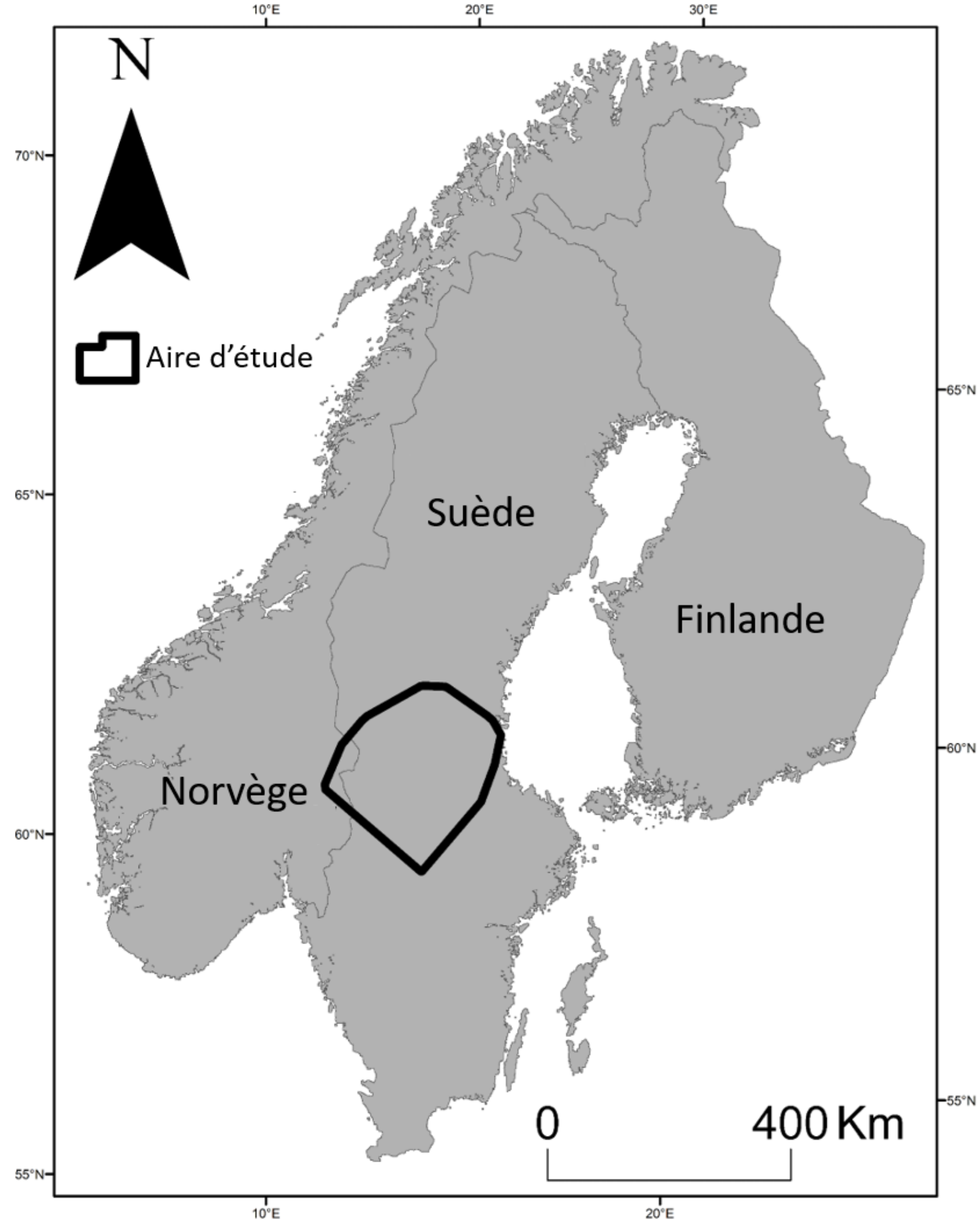

Figure 1.1 **Aire d'étude qui couvre une superficie de 55 000 kilomètres carrés au centre sud de la Suède.**

estivale à l'aide d'observations sur le terrain ou de relevée aériens afin de mettre à jour leur statut reproducteur. De 1985 à 2003, les ours étaient équipés de collier VHF (Telonics, modèle 500). Depuis 2003, la majorité des ours capturés ou recapturés sont équipés de collier GPS-GMS (Vectronic, GPS Plus) et la masse du collier représente moins de 2% de la masse de l'ours. De manière générale, les colliers GPS-GMS ont été programmés pour prendre au moins une localisation toutes les heures, sauf pendant la période de tanière où une localisation par jour a été obtenue. Pour des raisons éthiques, les femelles accompagnées d'oursons de l'année ne sont pas capturées. Depuis le début du projet de recherche, 527 ours ont été capturés et suivis. De ce nombre, 159 ours ont été équipés de collier GPS-GMS et plus de 1,5 million de localisations GPS ont été utilisées dans cette thèse. Toutes les captures et les manipulations d'ours ont été approuvées par les autorités en place (*Swedish Board of Agriculture, Uppsala Ethical Committee on Animal Experiments* et le *Swedish Environmental Protection Agency*). Pour plus de détails sur la capture et la manipulation des ours, veuillez consulter Zedrosser *et al.* (2007) et Fahlman *et al.* (2011).

La chasse à l'ours en Suède

L'ours brun est chassé en Suède et le nombre d'ours récolté a augmenté au cours des trois dernières décennies (Figure 1.2; Swenson *et al.*, 2017). La chasse est une des causes de mortalité les plus importantes chez l'ours brun scandinave, particulièrement pour les ours de deux ans et plus (Bischof *et al.*, 2009; Bischof *et al.*, 2018). La saison de chasse débute habituellement le 21 août et se termine lorsque le quota de récolte, fixé à l'échelle du comté, est atteint (Ordiz *et al.*, 2012). La chasse est permise une heure avant le lever du soleil jusqu'à deux heures avant le coucher du soleil. Les groupes familiaux sont protégés et ne peuvent être récoltés légalement, peu importe l'âge des oursons (Bischof *et al.*, 2008). Ce règlement de chasse favorise la survie des femelles qui promulguent des soins maternels plus longs (Van de Walle *et al.*, 2018). Aucun permis n'est nécessaire pour la chasse à l'ours brun en Suède, mais tous les chasseurs fructueux doivent présenter la carcasse de l'animal à un inspecteur le jour de la récolte. Plusieurs informations sont colligées par l'inspecteur, tel que le sexe et la masse de l'animal, une dent est extraite afin d'estimer l'âge de l'ours et la localisation de la récolte est prise en note (Bischof *et al.*, 2008). Ces informations sont ensuite entrées dans un registre d'abattages.

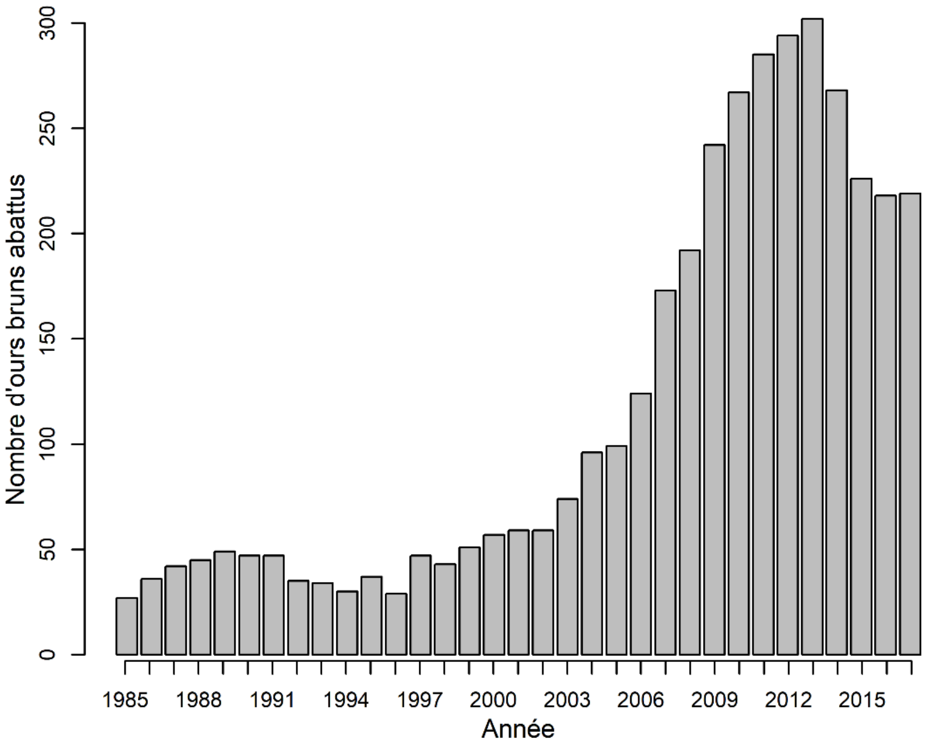

Figure 1.2 Nombre d'ours bruns (*Ursus arctos*) abattus annuellement lors de la chasse automnale en Suède entre 1985 et 2017. Les données ont été extraites de Swenson *et al.* (2017) et du site internet de l'Institut vétérinaire de Suède.

CHAPITRE 2

CHASSE ET INFANTICIDE SEXUELLEMENT SÉLECTIONNÉ

Description de l'article et contribution

La chasse a le potentiel de déstabiliser la structure sociale et d'augmenter l'infanticide sexuellement sélectionné chez certaines populations animales. Il existe, cependant, très peu d'évidences de cet effet écologique de la chasse puisqu'il est nécessaire d'obtenir des données démographiques et comportementales individuelles détaillées, autant sur les individus qui sont récoltés que ceux qui survivent à la récolte. Dans cet article, grâce aux données récoltées par le *Scandinavian Brown Bear Project* sur deux décennies (1991-2011), j'ai pu quantifier l'effet spatial et temporel de la récolte de mâles ours bruns sur la survie juvénile. Les résultats montrent que lorsqu'un mâle était tué à proximité du domaine vital d'une femelle, la survie de ses oursons était plus faible pour les deux années suivantes. De plus, la survie juvénile augmentait lorsque la distance au mâle tué le plus près était de plus de 25 kilomètres. Les résultats suggèrent que la distribution spatiale des mâles tués à la chasse peut influencer la survie juvénile chez l'ours brun scandinave.

Cet article a été issu d'une collaboration entre Jacinthe Gosselin et moi. Jacinthe Gosselin a initié le projet et construit la base de données. Ensuite, nous avons effectué les analyses, écrit le manuscrit et effectué les corrections dans une proportion équivalente. Fanie Pelletier a été impliquée et servie de mentor à toutes les étapes du processus. Les autres coauteurs ont contribué aux multiples révisions du manuscrit en plus d'être consultés à quelques reprises pendant les analyses statistiques.

Hunting promotes sexual conflict in brown bear

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Abstract

1. The removal of individuals through hunting can destabilize social structure, potentially affecting population dynamics. Although previous studies have shown that hunting can indirectly reduce juvenile survival through increased sexually selected infanticide, very little is known about the spatiotemporal effects of male hunting on juvenile survival.

2. Using detailed individual monitoring of a hunted population of brown bears (*Ursus arctos*) in Sweden (1991-2011), we assessed the spatiotemporal effect of male removal on cub survival.

3. We modeled cub survival before, during, and after the mating season. We used three proxies to evaluate spatial and temporal variation in male turnover; distance and timing of the closest male killed and number of males that died around a female's home range center.

4. Male removal decreased cub survival only during the mating season, as expected in seasonal breeders with sexually selected infanticide. Cub survival increased with distance to the closest male killed within the previous 1.5 years and it was lower when the closest male killed was removed 1.5 instead of 0.5 year earlier. We did not detect an effect of the number of males killed.

5. Our results support the hypothesis that social restructuring due to hunting can reduce recruitment and suggest that the distribution of the male deaths might be more important than the overall number of males that die. As the removal of individuals through hunting is

typically not homogeneously distributed across the landscape, spatial heterogeneity in hunting pressure may cause source-sink dynamics, with lower recruitment in areas of high human-induced mortality.

Keywords: cub survival, hunting, male reproductive strategy, Scandinavia, sexually selected infanticide, social restructuration, *Ursus arctos*.

Introduction

Human exploitation affects wild vertebrates globally (Milner, Nilsen & Andreassen 2007; Allendorf & Hard 2009) and is considered one of the greatest evolutionary pressures on wildlife (Darimont *et al.* 2009). Large vertebrates are typically harvested for sport hunting, subsistence, or population management (Festa-Bianchet 2003). Human-induced mortality in these species generally increases mortality rates in age and sex classes that typically show high natural survival rates (Ginsberg & Milner-Gulland 1994; Langvatn & Loison 1999; Bonenfant *et al.* 2009). Although several studies have documented the direct demographic consequences of hunting on wild populations, fewer have explored its potential indirect effects (Milner, Nilsen & Andreassen 2007). Indirect effects of hunting often occur through the removal of individuals of specific sex or age classes, mostly through size-selective hunting, and can destabilize social structures (reviewed in Milner, Nilsen & Andreassen 2007), with negative consequences, such as loss of social knowledge (McComb *et al.* 2001), changes in operational sex ratio (Milner-Gulland *et al.* 2003), and sexually selected infanticide (SSI) (Swenson *et al.* 1997; Loveridge *et al.* 2007). Understanding the extent of the ecological consequences of hunting is critical when developing sustainable management plans.

Sexually selected infanticide occurs when competition between members of one sex for the reproductive investment of the other sex makes it advantageous for an individual, usually a male, to kill another individual's dependent offspring in order to gain reproductive opportunities (Hrdy 1979). SSI is adaptive when it is directed at young unlikely to be direct descendants of the male (Hrdy 1979). It has been suggested that males assess their paternity through mating history and tend not to kill dependent young (hereafter referred to as juveniles) of females they have mated with (Soltis *et al.* 2000). Therefore, males encountering unfamiliar females with juveniles (hereafter referred to as male turnover) will have a higher probability of perpetrating infanticide. Male turnover has been shown to increase SSI (Swenson *et al.* 1997; Agrell, Wolff & Ylönen 1998; Andreassen & Gundersen 2006), potentially exacerbating the effects of hunting on population dynamics by increasing juvenile mortality after an adult male has been killed (Wielgus *et al.* 2013; Gosselin *et al.* 2015).

The impact of hunting and SSI on juvenile survival may be scale-dependent and vary temporally. SSI is only adaptive if the male can increase its reproductive opportunities, typically by shortening the interval until the female's next estrus (Hrdy 1979). Therefore, in seasonal breeders, where females can only be receptive during a short period of the year, SSI is only expected to occur during the mating season and in species where females have the ability to enter estrus again shortly after losing their young (Hrdy 1979; Steyaert, Swenson & Zedrosser 2014). Juvenile survival should vary spatially, as hunting pressure is often not evenly distributed across the landscape (Lebel *et al.* 2012; Steyaert *et al.* 2016). A female whose home range is near the site where a male has been killed should be more likely to suffer SSI than a female further away. Accordingly, increasing the number of males killed near a female’s home range may increase the risk of SSI by opening more space to unfamiliar males. Previous studies have reported that hunting can lead to home range shifts and takeovers in carnivores (Loveridge *et al.* 2007; Maletzke *et al.* 2014). To assess the spatiotemporal effects of male removal on female fitness, however, one needs long-term detailed monitoring of harvested population with detailed information on female reproduction, offspring mortalities at different times of the year, and spatial information on male harvest sites.

Here we evaluated the spatiotemporal effects of hunting adult males on juvenile survival using a long-term study of marked brown bears (*Ursus arctos* L.), a seasonal breeder, in Scandinavia. Brown bears are solitary, nonterritorial animals and most interindividual interactions occur during the mating season (Dahle & Swenson 2003c; Bellemain, Swenson & Taberlet 2006). Home ranges overlap both intersexually and intrasexually; home ranges of males are larger (median of 1,055 km² in our population) and overlap with several female home ranges (median of 217 km² in our population) (McLoughlin, Ferguson & Messier 2000; Dahle & Swenson 2003b). On a local scale, males adjust their home range size according to population density (Dahle & Swenson 2003b). Home ranges of males only overlap partially, and it is likely than when a male die, the neighbouring adult males will move, adjust, or expend their home range in the following years to take advantage of the newly available space (Loveridge *et al*. 2007; Maletzke *et al*. 2014). Due to these home range adjustments, surrounding males may encounter unfamiliar females in the new area they are using. Immigrant males may also take over the newly available home range, however immigrant males are likely to be young dispersing males, who are less likely to successfully commit infanticide than established older and larger males, as females actively defend their young (Hessing & Aumiller 1994; Støen *et al.* 2006). In this population, most young (95%) are weaned as yearlings and are therefore only dependent during their first year of life (Dahle & Swenson 2003a). A large proportion of litters suffer from partial (17.7%) or total (26.2%) mortality (Gonzalez *et al.* 2012). Approximately 80% of the mortality of cubs of the year (hereafter referred to as cubs) occurs during the mating season (mid-May to mid-July, see Figure S2.1), and all causes of death that could be assessed during this period were due to male infanticide (Steyaert 2012; Gosselin *et al.* 2015). Harvest of adult males has been shown to reduce cub survival (Swenson *et al.* 1997; Swenson *et al.* 2001; Zedrosser *et al.* 2009), but we do not know whether the number of bears killed, or their location, affects SSI. We predicted (P1) that increased male turnover would decrease cub survival only during the mating season, (P2) a positive relationship between cub survival and the distance to the closest killed male, and (P3) a negative relationship between cub survival and the number of males killed near a female's home range. We also tested whether the timing of the kill (0.5 or 1.5 years earlier) affected cub survival.

Materials and methods

The study area was located in southcentral Sweden (61°N, 15°E). Approximately 80% of females and 50% of males of the study population were fitted with VHF radio-transmitters (Telonics®, model IMP/40/L HC) or GPS-GMS transmitters (GPS Plus, Vectronic Aerospace GmbH®). For further information on capture and handling of bears, see Arnemo, Evans & Fahlman (2011) and Zedrosser *et al.* (2007b). To ascertain timing of cub loss, females with cubs were observed from the ground or from a helicopter at least three times; at den emergence before the breeding season (early May), after the breeding season (mid-July), and in autumn before denning (late September, early October). Using these censuses, we assessed cub survival before (den emergence to mid-May), during (mid-May to mid-July), and after the mating season (mid-July to November). The mating season was defined from observation of adult pairs in our study area (Dahle & Swenson 2003a; Steyaert 2012; see Figure S2.1).

Male turnover

There is a fall bear hunting season in Sweden. Successful bear hunters are required by regulation to provide authorities with the location of the kill, sex of the bear, and a tooth for age determination (see Bischof *et al.* 2008 for details). We also have information on damage-control kills and accidental deaths. We used all known records of mortality of adult male bears (≥3 years old, age of sexual maturity; Zedrosser *et al.* 2007a) to ascertain male turnover, as the impact of a male's death on social structure should be the same regardless of the cause of death. We are confident that we have records of almost all adult male deaths in our study area, because it is legally required to report any bear killed or found dead, regardless of cause of death (including hunting, management removal, and accidents), to the appropriate authorities. Illegal kills are rare in this area (Swenson *et al.* 2001; Bischof *et al.* 2009) and natural mortality is low (1.9%, based on 104 mortality records of radio-marked adult males). Hunting accounted for 85.4% of the 254 male mortalities in the database used in our analyses. Other human causes of mortality explained almost all of the remaining mortality. Hunting is additive to natural mortalities in our study area (Bischof *et al.* 2009). For each female with cubs, we extracted data on all known adult male deaths that occurred within 80 km from the center of her home range. We chose 80 km, because the maximum documented distance between home range centers of a reproductive pair was 76.8 km (Bellemain *et al.* 2006). Females' home range centers were calculated from the arithmetic center of annual locations (mean of 57 locations/female/year) for the year their litters were born. Females' home ranges are relatively stable from one year to the next, with home range centroids moving by 1.6 km per year on average. We looked at the impact of past male death on the present cub survival, because male turnover does not occur immediately after male removal (Swenson *et al*. 1997). Therefore, we used data on kill sites for all males in the previous 1.5 years, as it has previously been shown that cub survival is lower when at least one male had been killed in the same area 0.5, and especially 1.5, years earlier (Swenson *et al*. 1997). For each female with cubs in a given year, we calculated the distance between her home range center and the locations of every male that died during the previous 1.5 years. We used three proxies to evaluate variation in male turnover; distance and timing (0.5 or 1.5 years earlier) of the closest male killed and number of males that died around a female's home range center.

Control covariates

To account for other factors likely to affect cub survival, we included two environmental factors; an annual food index (Zedrosser, Dahle & Swenson 2006) and a population density index, i.e. an approximation of the number of bears within 1000 km^2 around the home range center of a female (Zedrosser, Dahle & Swenson 2006). Covariates describing maternal characteristics were parity (primiparous or multiparous) and female age, their interaction, and litter size at first observation after den emergence (litters of 1 cub n=29, 2 cubs n=80, 3 cubs n=77, and 4 cubs n=7).

Statistical analyses

As all covariates were common to a litter, and because survival of cubs within a litter is likely not independent, we modeled cub survival within a litter. We defined cub survival within a litter as the ratio of the number of surviving cubs in relation to the number of cubs in a litter known to be alive at the beginning of each time step: before (after den emergence), during, and after the mating season. Analyses were performed on data from 193 litters of 68 females for a total of 448 cubs. We first evaluated if cub survival (dependent covariate) differed before, during, and after the mating season, using a generalized linear mixed model with binomial error distribution and Year and Female ID as random intercepts. All subsequent analyses were conducted separately by period.

We did not know *a priori* if the relationship between the distance to the closest male killed and cub survival was continuous or discontinuous, as there might be a threshold effect. Therefore, we performed a preliminary piecewise regression (Crawley 2007). For each period, we compared the complete model (including environmental factors, maternal characteristics, and male turnover) with distance to the closest male killed as a continuous or as a discontinuous covariate, with different break points ranging from 10 to 60 km by increments of 5 km (Table S2.1). For each period, distance to the closest male was selected as continuous or discontinuous, based on the Akaike information criterion corrected for small sample sizes (AICc).

We modeled cub survival using generalized linear mixed models. We evaluated eight candidate models for each period (Table 2.1). All candidate models were tested with Year and Female ID as random intercepts and fixed effects were based on combinations of the three groups of covariates; environmental factors, maternal characteristics, and male turnover. As all tested models were nested, we selected the model with the fewest parameters within ΔAICc < 2 of the top model (Arnold 2010). For periods where distance to the closest killed male was retained, we further assessed the effect of the number of males killed and the timing of the closest kill (0.5 or 1.5 years before) on cub survival. All analyses were performed with R 3.1.1 (R Core Team 2014).

Results

Between 1991 and 2011, mean cub survival within a litter was 0.945 [95% CIs = 0.913 : 0.977, *n*=193] before and 0.949 [0.911:0.988, *n*=125] after the mating season. It was significantly lower during the mating season (0.632 [0.563:0.702], *n*=185; z-value > 6.94, p-value < 0.001). Of the 185 litters monitored during the mating season, 57% (106) entire litters survived, 32% (60) entire litters died, and 10% (19) experienced partial cub loss. Preliminary analyses showed that distance to the closest male killed had a better fit with breaking points at 55 km and 25 km before and during the mating season, respectively, and when it was considered as a continuous covariate after the mating season (Figure S2.2).

Before the mating season, the most parsimonious model of cub survival only included maternal characteristics (Table 2.2). However, all the confidence intervals of the covariates overlapped with 0 (Table 2.3). During the mating season, the most parsimonious model included maternal characteristics and male turnover (Table 2.2). Litter size, parity, and their interaction influenced cub survival during the mating season (Table 2.3). Cubs of older primiparous females had a higher survival than cubs of younger primiparous females, whereas age of the mother had no effect on cub survival for multiparous females (Table 2.3). Litter size also affected cub survival, with cubs born in litters of 2 or 3 surviving better than cubs born in litters of 1 (Table 2.3). Regarding male turnover, there was no relationship between distance to the closest killed male and cub survival for distances < 25 km (Table 2.3, Figure 2.1), but we found a positive relationship when distances were ≥ 25 km (Table 2.3, Figure 2.1). Overall, cub survival was lower when the closest killed male was within 25 km than when the closest male was killed farther away (Figure 2.1). We further tested whether the timing and/or the number of males killed < 25 km or ≥ 25 km explained variation in cub survival. We found no detectable effect of the number of males killed in either analysis (Table S2.2 and S2.3). However, the timing of the closest kill affected cub survival. When the closest male killed was within 25 km of the female, cub survival was 16.6% lower (β= -0.966 [-1.879 : -0.052]) when the male was killed 1.5 years earlier compared to when the male had been killed 0.5 year earlier (Table S2.2). After the mating season, the null model was the most parsimonious (Table 2.2).

Table 2.1 Candidate models tested to explain litter survival before (*n* = 193), during (*n* = 185), and after (*n* = 125) the mating season in brown bears in Sweden during 1991-2011. The variables Year and Female ID were included as random intercepts in all models.

Model	Covariates
1	None
2	Food index[a] + Population density[a]
3	Age of female + Primiparity of female[b] + Litter size + Age of female × Primiparity of female[b]
4	Distance of the closest killed male (km)[c]
5	Model 2 + Model 3
6	Model 2 + Model 4
7	Model 3 + Model 4
8	Model 2 + Model 3 + Model 4

[a]Scaled covariate where mean=0 and variance=1; [b]Primiparous or multiparous; [c]Distance was modeled with a breaking point at 55 km and 25 km before and during the mating season, respectively, and was modeled without inflexion point after the mating season (see Figure S2.2).

Discussion

Documenting the indirect effects of hunting yields valuable information that helps to ensure sustainable exploitation of wild populations. Long-term datasets on marked harvested populations required for documenting such effects are, however, rare (Milner, Nilsen &

Andreassen 2007; Clutton-Brock & Sheldon 2010). In this study, exceptionally detailed information on kill sites and monitoring of female reproductive success allowed us to evaluate the potential indirect spatiotemporal effects of male removal on cub survival. Our analyses revealed three key findings. First, the effect of male removal on cub survival was only apparent during the mating season, in accordance with P1. Second, females with home ranges located closer to sites where at least one male was killed during the previous 1.5 years suffered increased risk of cub loss, in accordance with P2. Third, females with several killed males close to theirhome range did not suffer an increased risk of cub loss compared to females with only one killed male (contrary to P3), suggesting that even a low rate of harvest can promote SSI.

Cub survival showed a clear temporal pattern, with the lowest survival during the mating season. A study in Alaska also reported higher cub mortality during this period, potentially related to SSI (Gardner, Pamperin & Benson 2014). In contrast, this temporal pattern has not been seen in other North American populations where SSI is thought to be low or absent (Wielgus & Bunnell 1994). In addition to documenting this temporal pattern, we also found that the distance to the closest killed male was a good predictor of cub survival only during the mating season. This temporal effect was expected from the SSI hypothesis, because female brown bears are seasonal breeders and can enter estrus shortly after losing their young, but almost exclusively during the mating season (Bellemain, Swenson & Taberlet 2006; Steyaert *et al.* 2012; Steyaert, Swenson & Zedrosser 2014). Therefore, SSI would only be beneficial for males during the mating season. The fact that we did not find an indirect effect of hunting on cub survival outside the mating season supports the claim that infanticide is a male reproductive strategy (Swenson *et al*. 1997, Swenson *et al*. 2001, Zedrosser *et al*. 2009). If nonparental infanticide were a result of exploitation or competition (for example: LeBoeuf & Briggs 1977; Townsend *et al.* 2007), it should occur throughout the year, with probably more cases early in the year, when cubs are younger and more vulnerable (Hrdy 1979). As such, the observed pattern of cub survival differed from that expected in populations of brown bears where there is no or a low rate of SSI and cub survival is high during the mating season (McLellan 2005).

Table 2.2 **Model selection diagnostics for the candidate models to explain litter survival before (*n* = 193), during (*n* = 185), and after (*n* = 125) the mating season in brown bears in Sweden during 1991-2011. Models are listed with their LogLikelihood (LL), number of parameters (K), difference in AICc to the most parsimonious model (ΔAICc), and their weight (ω_i). For model description see Table 2.1.**

Model	**Before**				**During**				**After**			
	LL	K	ΔAICc	ω_i	LL	K	ΔAICc	ω_i	LL	K	ΔAICc	ω_i
1	-53.27	3	5.12	0.030	-226.12	3	28.35	0.000	-43.95	3	0.00	0.571
2	-49.66	5	2.25	0.134	-225.79	5	31.90	0.000	-43.56	5	3.41	0.254
3	-44.28	9	0.00	0.384	-216.61	9	22.20	0.000	-40.98	9	6.92	0.018
4	-51.02	5	4.81	0.035	-214.26	5	8.83	0.009	-43.71	4	1.60	0.257
5	-42.61	11	1.13	0.218	-216.30	11	26.05	0.000	-40.58	11	25.59	0.003
6	-47.58	7	2.21	0.127	-212.81	7	25.22	0.004	-43.49	6	5.41	0.038
7	-44.29	11	4.50	0.040	-203.27	11	0.00	0.739	-40.67	10	8.53	0.008
8	-42.23	13	4.95	0.032	-202.08	13	2.18	0.248	-40.45	12	12.61	0.001

Table 2.3 Coefficients (*β*) and 95% confidence intervals of the covariates in the best supported model to explain brown bear cub survival in Sweden before (*n* = 193) and during (*n* = 185) the mating season, respectively. After the mating season, the null model was the most parsimonious. Numbers in bold represent covariates for which 95% confidence intervals do not overlap 0.

Covariates	*β*	95 % Confidence intervals	
		Lower limit	Upper Limit
Before the mating season (n = 193)			
Intercept	8.588	2.006	15.171
Age	0.183	-0.170	0.536
Primiparity: primiparous	-10.575	-53.251	32.100
Litter size = 2	1.889	-1.409	5.188
Litter size = 3	2.666	-0.732	6.065
Litter size = 4	0.440	-4.047	4.928
Age × Primiparity primiparous	1.352	-7.355	10.058
During the mating season (n = 185)			
Intercept	-0.240	-1.979	1.499
Age	-0.087	-0.194	0.021
Primiparity: primiparous	**-8.076**	**-13.487**	**-2.666**
Litter size = 2	**2.039**	**0.699**	**3.379**
Litter size = 3	**1.855**	**0.542**	**3.167**
Litter size = 4	1.399	-0.306	3.103
Distance to the closest killed male (< 25 km)	-0.017	-0.080	0.047
Distance to the closest killed male (≥ 25 km)	**0.132**	**0.069**	**0.196**
Age × Primiparity: primiparous	**1.282**	**0.246**	**2.317**

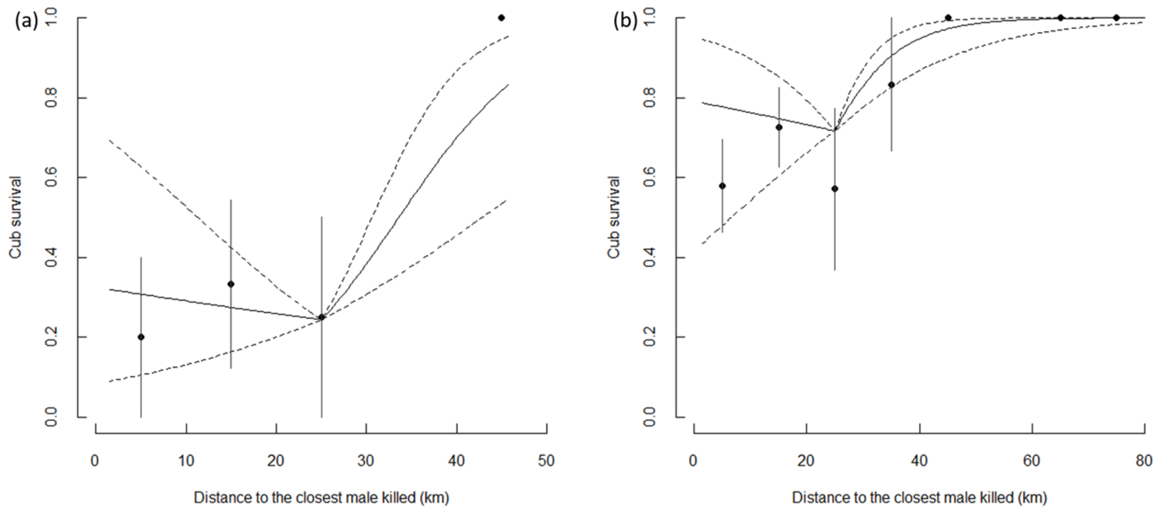

Figure 2.1 **Effects of distance to the closest killed adult male brown bear during the previous 1.5 years on cub survival (*n* = 185) during the mating season in Sweden during 1991-2011. The predictions are for litter size of 1 cub (panel a) and 2 cubs (panel b; predictions for litter size = 3 or 4 were intermediate). The full and dashed lines represent the predictions of the selected model and its 95% confidence intervals. Dots and vertical lines represent mean cub survival and its 95% confidence interval from raw data segmented every 10 km. Cub survival was calculated by averaging the proportion of cubs surviving per litter, independently of litter size.**

Hunting causes home range shift and takeover in carnivores (Loveridge *et al*. 2007; Maletzke *et al*. 2014). Here, we found that the relationship between distance to the closest killed male and cub survival was noncontinuous, with a threshold at 25 km; survival of litters located within a 25-km radius of a male killed during the previous 1.5 years was low and stable, but increased gradually at distances greater than 25 km. This suggests that male home range shifts influence female fitness differently according to the spatial scale. It may appear surprising that the distance to the closest male killed had no effect on cub survival within 25 km from the home range center of a mother and her litter. However, median male home range size in our study area is 1,055 km² (corresponding to a 18.3km radius; Dahle and Swenson 2003b), and males roam over great distances to find females during the mating season, travelling up to 20 km daily (Clevenger, Purroy & Pelton 1990; Dahle & Swenson 2003c). Therefore, any male turnover that occurs within 25 km from a female is likely to increase risk of infanticide. Our results showed that the death of males at a distance ≥25 km was less likely to create turnover affecting a given mother. The closest male killed was within 25 km for 71% of the litters (Figure S2.3). A previous study of Scandinavian brown bears has shown that, for litters where paternity could be assigned genetically, fathers were located within 25 km of the female home range center about 76% of the time and within 40 km 95% of the time (Bellemain *et al.* 2006). This is consistent with the pattern of SSI-caused cub mortality observed in this study.

We expected that an increase in the number of adult males killed near a female would increase turnover rate and thus reduce cub survival. Surprisingly, however, we found no strong support for this prediction (Table S2.2). The models that included the number of males were not selected, but were within ΔAICc < 2 (Table S2.2 model D, β= 0.210, CIs = -0.105 : 0.526). Thus, it is possible that the number of males killed around a female's home range center affects cub survival, but that we were unable to detect this small effect given our dataset. However, based on our results, the distance to the closest male killed and the timing of the kill were the two main proxies of male turnover affecting cub survival. As such, we found a binomial response, with the greatest effect being whether or not at least one male had been killed within a 25-km radius during the previous 1.5 years. This dichotomous relationship between cub survival and male turnover suggests that even low hunting pressure (one male bear killed/1,963km^2) can reduce cub survival. We therefore suggest that, at the landscape scale, the distribution of male kills might be more important for cub survival than the overall number of males killed. This result may appear to contradict a previous study reporting that increasing overall hunting pressure increased the risk of SSI and reduced cub survival in this population (Gosselin *et al*. 2015). However, increasing hunting quotas and the number of killed males will increase the probability of a female being located in area where a male has been removed. Thus, cub survival is expected to be generally lower in periods of high hunting pressure.

We also found that, during the mating season, cub survival was lower when the closest male killed within 25 km was removed 1.5 years earlier compared to 0.5 year earlier. This supported the hypothesis that male turnover is not an immediate response to male removal (Swenson *et al.* 1997). Infanticide seems to be more likely to occur 1.5 years after a male has died, meaning that it takes over a year for surrounding males to adjust their home ranges after the death of an adjacent male. Although not the main focus of our study, we found that the maternal characteristics had an impact on cub survival. Female parity, age, and their interaction influenced cub survival, which might reflect the importance of the mother's experience on the care and protection of cubs (Zedrosser *et al.* 2009). Also, the survival of cubs in litters of 2 or 3 was higher than the survival of cubs in litters of 1 and seemed higher than the survival of cubs in litters of 4. Optimum litter size for cub survival could therefore be intermediate. Competition for resources may lowers cub survival in larger litters (Gonzalez *et al.* 2012) but mothers with larger litters may, however, provide more protection against a potentially infanticidal male, as their investment is larger (Maestripieri & Alleva 1991; Koskela *et al.* 2000). Moreover, the estimate for litter size of 4 should be interpreted with reservation due to low sample size (*n*=7).

Other studies have shown how the removal of one or a few specific individuals (through harvest or poaching) can destabilize social structure and, in some cases, have drastic consequences on harvested populations. For example, hunting has been shown to promote SSI in African lions (*Panthera leo* L.), leopards (*Panthera pardus* L.), and cougars (*Felis concolor* L.) (Packer *et al.* 2009; Wielgus *et al.* 2013). Thus, one might expect similar effects of male harvest distribution on female vulnerability to SSI for those species. Natural mortality can also affect the social structure of a population. If human-caused mortality is additive, as in Scandinavian brown bears (Bischof *et al.* 2009), it will exacerbate this effect. Moreover, in most harvested populations, the human-caused mortality of adults will be greater than their natural mortality (Ginsberg & Milner-Gulland 1994; Langvatn & Loison 1999; Bonenfant *et al.* 2009). Harvest distribution may also affect the social structure of species without SSI. In African elephants (*Loxodonta africana* Blumenbach) and killer whales (*Orcinus orca* L.), it has been argued that the removal of older and more experienced individuals can affect the social network and population persistence, as group members typically rely on social knowledge from those individuals (McComb *et al*. 2001; Williams & Lusseau 2006). Thus, in species with stable social structure, the spatiotemporal distribution of harvest is likely to affect local population dynamics, and even low harvest rate can impact local population dynamics. Therefore, the assumption that reducing harvest intensity should increase population growth rate might not always hold.

Our research adds to a growing number of studies documenting the potential indirect effects of hunting on wild populations. As hunting and human-caused mortalities are usually not distributed homogeneously across the landscape (Grilo, Bissonette & Santos-Reis 2009; Steyaert *et al.* 2016), it is likely to influence the population's local spatial dynamics. Thus, we suggest that spatial heterogeneity in hunting pressure could result in a source-sink dynamic at the scale of the study area, with zones of high human-induced mortality and lower recruitment being sinks and contributing less to population growth (Novaro, Funes & Walker 2005).

Data accessibility

Data will be fully available three years after publication to allow early stage PhD student and postdocs to have priority access to the dataset. In the interim period, we will make the data available upon request to anyone who wishes to collaborate with us or repeat our analysis. Data available from the Dryad Digital Repository: doi:10.5061/dryad.tc2cb.

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CHAPITRE 3

CHASSE ET RESTRUCTURATION SPATIALE

Description de l'article et contribution

Le deuxième chapitre a montré que la chasse peut diminuer la survie juvénile par l'entremise d'une augmentation de l'infanticide sexuellement sélectionné. Une des principales hypothèses qui émerge dans la littérature afin d'expliquer le mécanisme reliant la chasse et l'infanticide sexuellement sélectionné est que le domaine vital laissé vacant par la mort d'un ours est utilisé par les mâles résidents avoisinants. J'ai donc testé cette hypothèse et montré que les mâles adultes avoisinants utilisaient davantage le domaine vital d'un ours tué à la chasse deux ans après sa mort. Ce délai coïncide avec le délai observé de la survie juvénile quantifié au chapitre deux. De plus, la vitesse et l'intensité à laquelle les ours avoisinants utilisent le domaine vital d'un ours tué étaient modulées selon l'âge des ours, la densité de la population et l'intensité de la chasse. Les résultats obtenus montrent que la chasse peut avoir des effets indirects à long terme et soulignent l'importance du comportement animal pour expliquer les délais observés en réponse à la chasse.

Cet article a été un des plus longs et un des plus ardus de mon parcours académique. Bien que simple à première vue, cette hypothèse de travail est complexe à tester. En effet, plusieurs mâles sont récoltés annuellement et il existe beaucoup de chevauchement spatial compliquant les analyses. J'ai tenté à plusieurs reprises et par différentes manières de quantifier le déplacement des domaines vitaux des ours vivants en réponse à la mort d'un ours voisin. J'ai ensuite collaboré avec Shane C. Frank et nous avons trouvé une solution. Nous avons donc déterminé la procédure ensemble, puis j'ai effectué les analyses et écrit la première version du manuscrit. Tous les coauteurs ont participé aux révisions du manuscrit en plus d'être consultés à quelques reprises pendant les analyses statistiques.

Hunting promotes spatial reorganization and sexually selected infanticide

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Abstract

Harvest can affect the ecology and evolution of wild species. The removal of key individuals, such as matriarchs or dominant males, can disrupt social structure and exacerbate the impact of hunting on population growth. We do not know, however, how and when the spatiotemporal reorganization takes place after removal and if such changes can be the mechanism that explain a decrease in population growth. Detailed behavioral information from individually monitored brown bears, in a population where hunting increases sexually selected infanticide, revealed that adult males increased their use of home ranges of hunter-killed neighbors in the second year after their death. Use of a hunter-killed male's home range was influenced by the survivor's as well as the hunter-killed male's age, population density, and hunting intensity. Our results emphasize that hunting can have long-term indirect effects which can affect population viability.

Introduction

Human activities are a major evolutionary force affecting wild populations[1]. There is increasing evidence that human exploitation leads to changes in morphological and life history traits worldwide[1–4]. For example, recent studies have shown that size-selective harvest by commercial fisheries and trophy hunting can induce evolution of heritable traits[5–9]. Harvest-induced evolution might not be desirable as the selection induced by human exploitation can be in the opposite direction of natural selection[10–12].

Hunting can also have indirect effects on wildlife, although such effects are often ignored by managers, even though the removal of key individuals by hunting could change a population's social structure[13]. For example, simulations suggest that the social networks of killer whales (*Orcinus orca*) may be vulnerable to targeted removal of individuals[14]. In African elephants (*Loxodonta africana*) the enhanced discriminatory abilities of the oldest individuals influences the social knowledge and reproductive success of entire groups[15], suggesting that the loss of older individuals could decrease the fitness of all females within the group. In social species, the removal of any individual could affect social dynamics by changing the social structure. However, empirical evidence linking hunting and spatiotemporal reorganization of the social structure is lacking and the data needed to investigate this question are rarely available. Given the large number of species targeted by harvest, understanding the potential effects of removal on subsequent space use, social structure, and the fitness consequences for surviving individuals is critical to achieve sustainable hunting practices.

Here, we used detailed individual behavioral information from a Scandinavian brown bear (*Ursus arctos*) population (monitored from 2008-2015) to evaluate whether surviving adult males (hereafter referred to as survivors) shift their home range use after a neighboring adult male has been killed by hunting. We further investigated the intrinsic and extrinsic factors driving the spatiotemporal reorganization of male spatial structure. In this population, the removal of adult males through hunting increases the risk of sexually selected infanticide (SSI)[16,17], which is a major determinant of population growth[18]. Although important for sustainable wildlife management[19], the mechanism behind the harvest-induced increase of SSI remains unknown [but see Loveridge et al. [20]]. Spatial reorganization due to hunting of males may be the responsible mechanism, by increasing the probability that a female will encounter a new male that is unlikely to be the father of her cubs[13,16].

Methods

The study area was in south-central Sweden (61°N, 15°E) and was composed of bogs, lakes, and intensively managed coniferous forest stands. The dominant tree species were Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), lodgepole pine (*Pinus contorta*), and birch (*Betula spp.*). Elevations ranged between 150 and 725 m asl. Gravel roads (0.7 km/km^2) were more abundant than paved roads (0.14 km/km^2). See Martin et al.[37] for further information about the study area.

We captured brown bears from a helicopter using a remote drug delivery system (Dan-Inject®, Børkop, Denmark). We determined sex at capture and extracted a tooth from unknown individuals for age determination[38]. We equipped bears with GPS collars (GPS Plus; Vectronic Aerospace GmbH, Berlin, Germany) programed to relocate a bear with varying schedules (≤1 hour intervals). See Fahlman et al.[39] for details on capture and handling. All captured bears were part of the Scandinavian Brown Bear Research Project and all experiments, captures and handling were performed in accordance with relevant guidelines and regulations and were approved by the appropriate authority and ethical committee (Naturvårdsverket and Djuretiska nämden i Uppsala, Sweden).

Spatial analysis

We used adult male bears ≥ 4 years in the analysis to exclude natal dispersers[40]. We did not include natal dispersers because all male dispersers moved outside the study area where too few or no other males were GPS-collared. In addition, females actively defend their cubs during infanticide attempts. Therefore, younger dispersing males that have not yet attain full body size are less likely to successfully commit SSI than older, larger and better established males[41]. We screened the relocation data of adult males and removed GPS fixes with dilution of precision values >10 to increase spatial accuracy. To reduce autocorrelation, we used a 6-hour minimum interval between successive positions for a given bear. We excluded bears in years for which an individual had < 75% of days with GPS locations from 1 May to 30 September.

We used an approach adapted from resource selection functions [RSFs[42]] developed by Bischof et al.[43]. For each GPS-collared hunter-killed male we 1) determined its annual 95% kernel home range for the active period (1 May to 30 September or the day before he was killed) of the year in which he was killed and 2) calculated a 40-km radius circular buffer centered on its home range centroid. This radius was used because it represents the distance within which 95% of home range centroids of successful mates occurred[44] and the distance at which the effect of male removal on cub survival seems to disappear[17]. In a given year, we used GPS relocations of the hunter-killed male and all the GPS locations of surviving adult males within the buffer (hereafter called survivors) to 3) calculate a 95% kernel isocline (hereafter called sampling space). For each survivor, we 4) generated as many random as GPS relocations within the sampling space and 5) determined if GPS and random relocations were inside or outside the hunter-killed bear's home range. We repeated steps 3–5 for 3 consecutive years, i.e. the year a hunter-killed male had been killed and the two following years. We updated the sampling space annually by keeping the hunter-killed males' relocations the year he was killed constant for the three years, and used the appropriate relocations of survivors for each year. We only used survivors that were alive and monitored during the three-year period. We repeated these steps for each hunter-killed male. This enabled us to test whether survivors increased their use of a hunter-killed male's home range the years following its death.

For each hunter-killed male we also extracted a population density index derived from county-level scat collections in Sweden. We used the method of Jerina et al.[45] and summed the weighted values of an individual bear's multiple scats across a grid of 10 X 10 km. This was carried out for each county separately, after which the distribution was corrected temporally, using county-level trends of the Large Carnivore Observation Index[46,47], provided by the Swedish Association for Hunting and Wildlife Management. Lastly, we calculated a proxy of hunting intensity based on the number of dead adult males located within the 40-km radius circular buffer centered on a given hunter-killed male's home range centroid over a 3-year period prior to its death [see Gosselin et al.[17] for further details].

Statistical analysis

As a first step, we determined if surviving males shifted their home range use in response to the removal of a hunter-killed male. To do so, we used a generalized linear mixed model (GLMM) with binomial distributed errors. We coded the dependent variable either as GPS (coded 1) or random (coded 0) relocation. As independent variables we used a dummy variable representing whether the relocations were inside (coded 1) or outside (coded 0) the hunter-killed males home range, as well as a variable representing the period of the relocations (3-level factor; the year of the hunter-killed male's death, as well as 1 and 2 years after the hunter-killed male's death). We evaluated 4 candidate models (Table S3.1) and selected the most parsimonious based on the Bayesian information criterion (BIC)[48]. To control for unequal sample sizes across years and individuals (and possible collinearity within survivors – hunter-killed pairs across time), we included Year and the survivor ID nested within the hunter-killed males' ID as random intercepts in all candidate models.

In a second step, we examined how intrinsic (i.e., age of survivor and hunter-killed males) and extrinsic (i.e., population density and hunting intensity) factors influenced the speed and strength at which a survivor would adjust its home range use in response to the removal of a hunter-killed male. We used a GLMM with binomial distributed errors and coded the dependent variable either as GPS (coded 1) or random (coded 0) relocation. We evaluated the effect of six independent variables; inside vs outside the hunter-killed male home range, period, age of the survivor, age of the hunter-killed male, population density, and hunting intensity to build 17 candidate models (Table S3.2). We selected the most parsimonious model based on BIC. To control for unequal sample sizes across years and individuals (and possible collinearity within survivor – hunter-killed pairs across time), we included Year and the survivor ID nested within the hunter-killed males' ID as random intercepts in all candidate models. To facilitate model convergence, we scaled (mean=0, variance=1) all numerical covariates. We assessed the relative importance of variables within the most parsimonious model by dropping each variable and monitoring the ΔBIC. The larger the relative difference in BIC compared to the most parsimonious model, the more important we considered a variable. For all candidate models tested, the variance inflation factor (VIF) value was < 2 [49]. We used R version 3.2.3 for all statistical analyses[50].

We captured and GPS-monitored a total of 15 adult males between 2008 and 2015. The database contained 19,133 GPS and 19,133 random relocations of 11 hunter-killed males and 7 survivors, for a total of 23 survivor – hunter-killed male pairs.

Results

We found that survivors increased their use of the home ranges of hunter-killed males in the second year after their death (Figure 3.1, Table S3.3). This time lag in the response likely is related to the bear's ecology. Bears den from October to April[21,22], shortly after the hunting season in late August—September. The size of the annual home range in our study population is mainly defined by space use during the mating season (May to mid-July), when males exhibit a roam-to-mate behavior[23]. Therefore, we hypothesize that survivors do not readjust their home range until after the first mating season without the hunter-killed neighbor. This could explain the two-year time lag in spatial reorganization. Our results support the contention that the spatiotemporal reorganization of male home ranges is an important mechanism linking hunter harvest to an increase in SSI, described above. It is also consistent with earlier studies in the same population showing lower cub survival following a two-year time lag after a male had been killed[16,17].

We further investigated which intrinsic (ages of hunter-killed and surviving males) and extrinsic factors (population density and hunting intensity) modulated the speed and strength of the survivors' response to hunting removals (Figure 3.2, Table S3.2, Table S3.4). The use of a hunter-killed male's home range by its surviving neighbors was influenced by (in order of decreasing relative importance) survivor's age (ΔBIC = 115), hunting intensity (ΔBIC = 76), population density (ΔBIC = 74), and hunter-killed male's age (ΔBIC = 6). Older survivors used a hunter-killed male's home range less strongly following the hunter-killed male’s death than younger survivors (Fig 2A). This suggests that older males may already have held home ranges with better resources, including food and females. Age-dependent home range quality could also explain why survivors increased their use of an old hunter-killed male’s home range more than that of a younger hunter-killed male (Figure 3.2D).

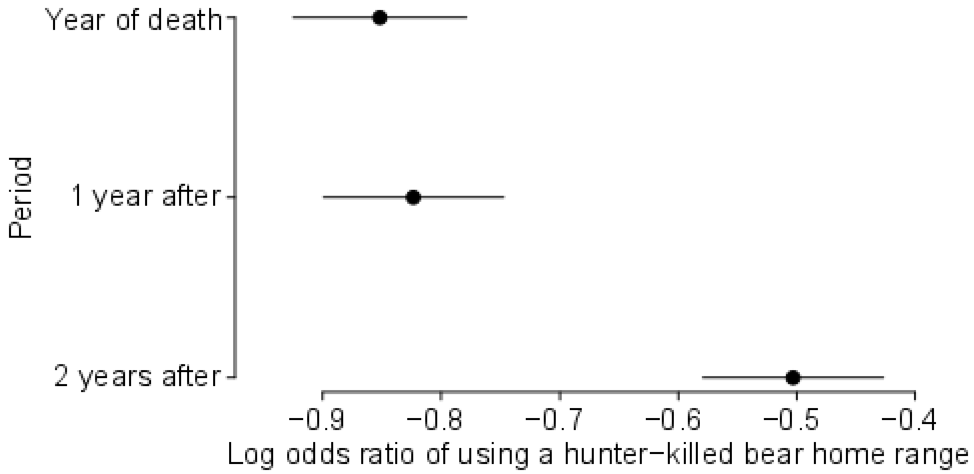

Figure 3.1 Changes in surviving male brown bears use of hunter-killed neighboring males' home ranges over time. Shown are the coefficients and 95% confidence intervals for three consecutive years, i.e. the year the hunter-killed male was shot (baseline) and the following two years.

Survivors more strongly increased their use of a hunter-killed male’s home range in the second year after its death when hunting intensity was greater (Figure 3.2B). As increasing hunting intensity will increase the number of openings for surviving males, this should lead to a higher degree of spatial reorganization. We previously reported that the killing of an adult male within 25 km of a female strongly reduced the survival of her cubs, with a two-year time lag, although an increase in the number of killed males within 25 km had no significant additive effect[17]. Even though the degree of spatial reorganization increased with increased hunting intensity, this might not always translate into a correspondingly lower cub survival, because even though more surviving males may respond to increased hunting removal, only one infanticidal male is sufficient to kill most of females' cubs. The other extrinsic factor affecting shifts in a survivor's home range use was population density (Figure 3.2C). Survivors at higher densities had higher initial overlap with the hunter-killed male and showed a weaker reorganization response than survivors at lower densities (Figure 3.2C). Stronger competition for space between neighbors might explain why we observed higher initial overlap, with a weaker response at higher densities.

Discussion

We identified a key behavioral mechanism linking hunting to an increase in SSI and show how post-hunt spatiotemporal reorganization of males was modulated by both intrinsic and extrinsic factors. By removing males from the population, hunters destabilized the spatial organization of the population for at least two years after a male had been killed. This period of two years might be specific to brown bears, due to their denning period and could be different in other harvested species with SSI, such as lions (*Panthera leo*)[20] or cougars (*Puma concolor*)[24]. Nevertheless, hunting increases shifts in home range use by surviving males and increases the probability of SSI[16,17]. Male bears seem to assess their paternity through their mating history[25], and increasing the magnitude of shifts in home range use would increase the probability that a male could encounter a female with whom he had not previously mated. Such a pattern is expected regardless of the cause of death (e.g., vehicle collision, management kill, natural mortality). However, hunting is often additive to natural mortality, as in our study system[26], which increases the occurrence of SSI compared to unharvested systems.

The spatial distribution of the hunting mortality of bears was not homogenous in our study area[27]. Spatial and social relationships of bears are likely to change more rapidly in areas with higher hunting mortality, thereby potentially decreasing the cohesion of their social network[28,29 but see 30]. Such effects could also influence the female reproductive rate because

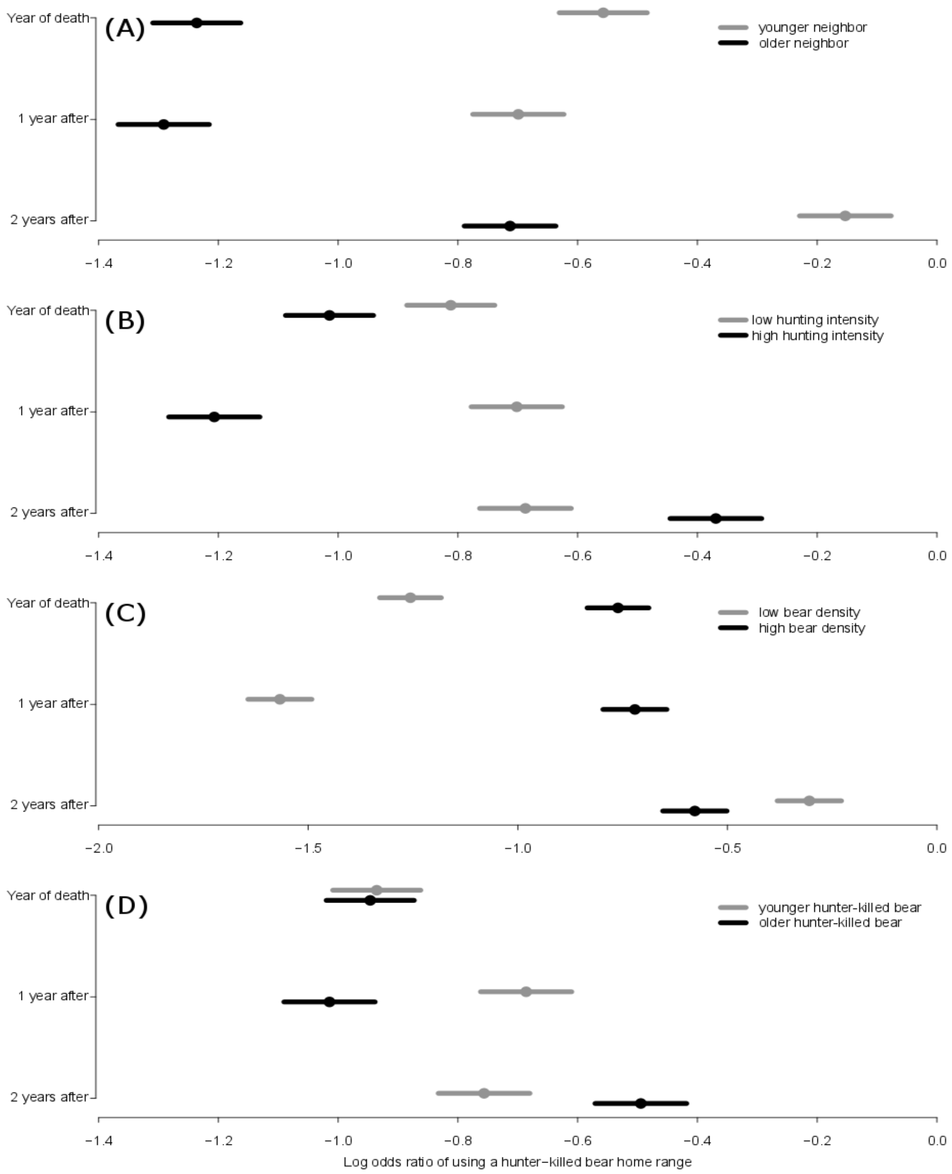

Figure 3.2 **Influence of intrinsic and extrinsic factors on the speed and strength at which a surviving male will use hunter-killed neighboring males' home ranges. Shown are the coefficients and 95% confidence intervals for three consecutive years, i.e. the year the hunter-killed male was shot (baseline) and the following two years, depending on the surviving male's age (A), hunting intensity (B), population density (C), and hunter-killed male's age (D), The low and high values in each panel represent the 25th and 75th percentiles, respectively, in the database.**

female brown bears exhibit kin-related spatial structures[31] and neighbors negatively affect each other's probability of having cubs[32,33]. The direct effect of removals due to hunting, in addition to the indirect effects of increasing cub mortality due to SSI and the potential impacts of decreasing social network cohesion, all increases heterogeneity in survival and reproductive rates. These effects combined could increase demographic variability and ultimately affect effective population size[34,35]. Therefore, we expect spatially structured demographic variability that could potentially result in source-sink dynamics[35,36].

Our study sheds light on the importance of animal behavior to explain time lags in the responses to hunting in the wild. Understanding the indirect consequence of hunting over long time scales is critical for developing sustainable management practices and for the viability of harvested populations.

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Author Contributions

M.L. and S.C.F. carried out statistical analyses, F.P., J.E.S. and A.Z. secured funding. All authors participated in the study design and writing of the manuscript.

Additional information

Supplementary information is linked to the online version of the paper.
Competing financial interests: The authors declare no competing financial interests. Correspondence should be addressed to M.L. (Martin.Leclerc2@USherbrooke.ca).

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CHAPITRE 4

VARIABILITÉ INDIVIDUELLE EN SÉLECTION D'HABITAT

Description de l'article et contribution

La variabilité entre les individus est une des conditions de l'évolution par sélection naturelle. Une méthode fréquemment utilisée pour estimer la variabilité entre les individus est la répétabilité. Des méta-analyses montrent qu'un grand nombre de comportements de plusieurs espèces différentes sont répétables. À ma connaissance, aucun article scientifique n'a jusqu'à présent quantifié la répétabilité du comportement de sélection d'habitat, même si ce dernier est un comportement central en écologie. Dans cet article, grâce à la combinaison de certaines méthodes statistiques, j'ai calculé la répétabilité de la sélection d'habitat des tourbières et des coupes forestières chez l'ours brun. De plus, à l'aide de simulations, j'ai montré que la répétabilité du comportement de sélection d'habitat n'était pas reliée à la significativité statistique du comportement observé à l'échelle populationnelle. Les résultats obtenus dans ce chapitre montrent le potentiel évolutif de la sélection d'habitat.

Cet article est né dans un atelier où nous devions fréquemment rédiger de courts textes sur un sujet d'intérêt. J'ai donc écrit sur la variabilité comportementale ce qui a engendré plusieurs discussions très intéressantes entre Eric Vander Wal et moi. Grâce à ses nombreux conseils et encouragements, nous sommes parvenus à écrire et publier ce manuscrit. J'ai donc construit la base de données, effectué les analyses statistiques, fait les simulations et écrit la première version du manuscrit. Fanie Pelletier et Eric Vander Wal ont commenté tout au long du processus et les autres coauteurs ont participé aux révisions du manuscrit et ont fourni les cartes d'habitats.

Quantifying consistent individual differences in habitat selection

Oecologia 2016, 180, 697-705

Martin Leclerc, Eric Vander Wal, Andreas Zedrosser, Jon E. Swenson, Jonas Kindberg and Fanie Pelletier

Abstract

Habitat selection is a fundamental behaviour that links individuals to the resources required for survival and reproduction. Although natural selection acts on an individual's phenotype, research on habitat selection often pools inter-individual patterns to provide inferences on the population scale. Here, we expanded a traditional approach of quantifying habitat selection at the individual level to explore the potential for consistent individual differences of habitat selection. We used random coefficients in Resource Selection Functions (RSFs) and repeatability estimates to test for variability in habitat selection. We applied our method to a detailed data set of GPS-relocations of brown bears (*Ursus arctos*) taken over a time period of six years, and assessed whether they displayed repeatable individual differences in habitat selection toward two habitat types: bogs and recent timber-harvest cut blocks. In our analyses we controlled for the availability of habitat, i.e., the functional response in habitat selection. Repeatability estimates of habitat selection toward bogs and cut blocks were 0.304 and 0.420, respectively. Therefore, 30.4% and 42.0% of the population-scale habitat selection variability for bogs and cut blocks, respectively, was due to differences among individuals, suggesting that consistent individual variation in habitat selection exists in brown bears. Using simulations, we posit that repeatability values of habitat selection were not related to the value and significance of β estimates in RSFs. Although individual differences in habitat selection could be the results of non-exclusive factors, our results illustrate the evolutionary potential of habitat selection.

Keywords: functional response, personality, repeatability, *Ursus arctos*.

Introduction

Understanding factors that shape animals' habitat selection is a fundamental ecological challenge (Morris 2011), because habitat selection links individuals to the resources required for survival and reproduction. Throughout their lives, individuals are constantly tasked to choose sets of resources (e.g., forage, prey, refuges) distributed within habitats to maximize their fitness (McLoughlin et al. 2010). When individual differences in habitat selection covary with fitness (McLoughlin et al. 2006; Leclerc et al. 2014), this variation, if heritable, represents alternative tactics available to adaptive evolution, which may change in frequency within a population according to density- or frequency-dependent selective pressures (Fortin et al. 2008). So far, however, no approach is available to explore the potential for evolution to act on individual differences in habitat selection behaviour. The first step to tackle this question is to document whether consistent individual variation in habitat selection exists.

Individual differences in behaviour have been studied for several decades (Krebs 1970; Bell et al. 2009). Originally, behaviours were assumed to potentially be completely plastic (Sih et al. 2004). More recently, however, behaviours are viewed as correlated traits that can generate trade-offs (Sih et al. 2004). Behavioural ecologists typically refer to those consistent individual differences as personality traits (Réale et al. 2010; Wolf and Weissing 2012). The study of individual differences in behaviour is of growing interest, because several studies have shown that such differences can have important ecological and evolutionary implications (Réale et al. 2010; Sih et al. 2012; Wolf and Weissing 2012). For example, individual variation in behaviour plays an important role in population dynamics in western bluebirds (*Sialia mexicana*), where aggressiveness and dispersal varies among males (Duckworth 2006; Duckworth and Badyaev 2007). Aggressive males disperse farther and colonize new habitats, whereas less aggressive males disperse less and have higher reproductive success in older established populations (Duckworth 2008). Therefore, for a given population, aggressiveness declines through time as the population becomes older (Duckworth 2008). Consistent individual differences in behaviour also have evolutionary implications, as selective pressures can act upon those differences, because they affect survival and reproduction (see review Smith and Blumstein 2008). For example, in North American red squirrels (*Tamiasciurus hudsonicus*), differences in female aggressiveness were correlated to overwinter offspring survival (Boon et al. 2007). The direction and strength of the relationship between behavioural traits and fitness can also depend on the environment (Nussey et al. 2007; Boon et al. 2007), highlighting the importance of studying consistent individual variation in habitat selection, which has yet to be done.

Morris (2003) defines habitat selection as the process whereby individuals use, or occupy, a nonrandom set of available habitats. Habitat selection is a hierarchical process (Johnson 1980), through which an individual aim to reduce the influence of limiting factors (a factor limiting an individual's fitness) (Rettie and Messier 2000; Leclerc et al. 2012). Consequently, habitat selection patterns may vary according to the spatial scale studied (Morris 1987; Meyer and Thuiller 2006). For example, at large spatial scales, yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) place nests where food abundance is higher, but at a finer spatial scale they place nests where vegetation cover is greater (Orians and Wittenberger 1991). Therefore, careful attention to scale and limiting factors governing habitat selection are essential to accurately estimate biologically relevant behavioural patterns.

Patterns in habitat selection can also result from functional responses to habitat availability. Functional responses in habitat selection are defined as a change in the selection of a habitat type depending on its availability (Mysterud and Ims 1998). The study of functional responses can help our understanding of resource use trade-offs (Mabille et al. 2012), which in turn can influence fitness (Leclerc et al. 2014; Losier et al. 2015). Functional responses in habitat selection are often interpreted at the population level by looking at the habitat selection of individuals in different landscapes (e.g. Mabille et al. 2012). This usually occurs because one individual rarely exists in a variety of landscapes or in all landscapes available to the population during the study period (Figure 4.1). Therefore, functional responses in habitat selection can be seen as a concept analogous to behavioural reaction norm (Figure 4.1) and should be accounted for when evaluating consistent individual differences in habitat selection (Figure S4.1).

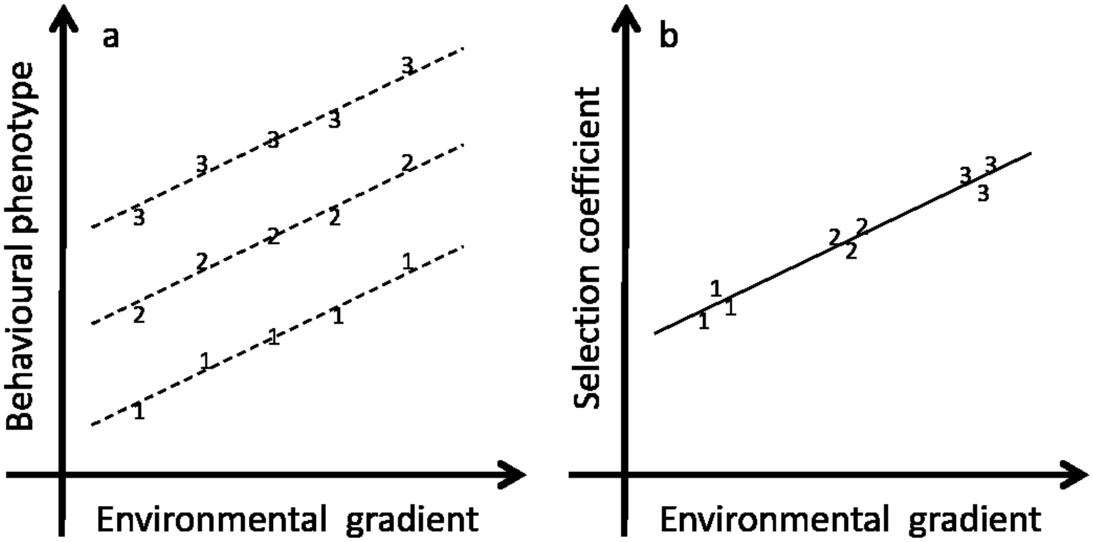

Figure 4.1 **Similarities can be drawn between the behavioural reaction norm (panel a) and the functional response in habitat selection (panel b) concepts. Both evaluate how the behaviour of individuals changes along an environmental gradient. Reaction norms are often evaluated with smaller species in laboratories or in open-field or maze tests. However, functional responses in habitat selection are usually interpreted at the population level, as individuals rarely exist in all landscapes available to the population. Biased estimates of repeatability can be obtained if functional responses in habitat selection are not accounted for (Figure S4.1). Here, we assumed that if one individual would select habitat type "X" (environmental gradient) less strongly than the mean population response, it would do so along the entire environmental gradient. Note that different numbers refer to different individuals.**

This study has three main objectives. First, we extend a method that combines ubiquitous practices from behavioural ecology, namely repeatability analysis and resource selection functions (RSFs), to quantify consistent individual differences in habitat selection. Second, we apply this method to a detailed behavioural data set of GPS-collared brown bears (*Ursus arctos*) and assess whether individual differences in habitat selection are detectable. We focused our analyses on two habitat types, bogs and recent timber-harvest cut blocks (hereafter cut blocks). We used bogs and cut blocks because they are the most abundant anthropogenically undisturbed and disturbed habitat types, respectively, in the study area and because they are avoided and selected for, respectively, at the population scale (Moe et al. 2007; Martin et al. 2010). Finally, using simulations, we explored the relationship between the repeatability in habitat selection across years and the strength at which a habitat type is selected or avoided at the population level. Ultimately, we argue that individual differences in habitat selection should be common in nature, given the evolutionary implications of resource choice strategies (see Fortin et al. 2008 for an example).

Materials and methods

The study area was located in south-central Sweden (61°N, 15°E) and was composed of bogs, lakes, and intensively managed coniferous forest stands of variable ages. The dominant tree species were Norway spruce *Picea abies*, Scots pine *Pinus sylvestris*, and birch *Betula* spp. Elevations ranged between 150 and 1000 m asl. Gravel roads (0.7 km/km^2) were more abundant than paved roads (0.14 km/km^2). See Martin et al. (2010) for further information about the study area.

We captured brown bears from a helicopter (2007-2012) using a remote drug delivery system (Dan-Inject, Børkop, Denmark). We extracted a vestigial first premolar for age determination from each individual not captured as a yearling with its mother (Matson 1993). We equipped bears with GPS collars (GPS Plus; Vectronic Aerospace GmbH Berlin, Germany) programmed to relocate a bear every 30 min. See Fahlman et al. (2011) for details on capture and handling. All bears captured were part of the Scandinavian Brown Bear Research Project and all captures and handling were approved by the appropriate authority and ethical committee (Djuretiska nämden i Uppsala, Sweden).

Spatial analysis

The GPS location fix success rate was >94%. We screened the relocation data and removed GPS fixes with dilution of precision values >5 to increase spatial accuracy. Removed GPS locations were not biased with respect to habitat type (chi-2 test with $P>0.22$) compared to GPS locations retained in our analyses. Preliminary analyses showed consistent results when working with 30 min., 1, 2, or 4 h locations intervals (data not shown). Therefore, we used the complete dataset, i.e. 30 min. location intervals. We used GPS locations from 21 August to 20 September for males and lone females. We choose to use this time period to reduce the influence of seasonality on behaviour: this period is after the onset of the hunting season and during hyperphagia where bears feed heavily on berry. Hereafter, the set of locations of one bear from 21 August to 20 September on a given year will be referred as bear-year.

For every bear-year, we selected the same number of random locations as GPS locations. Random locations were distributed within each bear-year's annual home range (3^{rd} order of selection; sensu Johnson 1980). We defined home ranges as 100% minimum convex polygons (Mohr 1947). To consider the influence of the surrounding environment on habitat selection, we extracted covariates within a circular buffer with a 182-m radius (which corresponds to the mean distance between 2 GPS relocations) centred on each GPS and random location. Covariates were landscape characteristics known or expected to influence the probability of occurrence of bears, based on previous research (Moe et al. 2007; Martin et al. 2010; Steyaert et al. 2013) and were derived from Swedish Corine Land Cover (25 m × 25 m) and a Digital Elevation Model (50 m × 50 m) from National Land Survey of Sweden (licence i2012/901, www.lantmateriet.se). Covariates extracted from each buffer were the % coniferous stands (tree height >5 m and canopy cover of conifers >70%), % cut blocks (tree height <2 m), % water, % bogs (bogs with shrub and tree cover <30%), % mixed–deciduous stands (tree height >5 m and canopy cover of deciduous trees >30%), % young forested stands (tree height 2–5 m), road length, mean elevation, and the coefficient of variation of elevation. We conducted all spatial analyses using ArcGIS 10.0 (ESRI Inc., Redlands, California, USA) and the Geospatial Modelling Environment 0.7.2 (Spatial Ecology LLC).

Statistical analysis

We used RSFs (Manly et al. 2002) to assess habitat selection by conducting logistic regression that compared habitat characteristics at bear GPS locations (coded 1) to those at random locations (coded 0). Habitat type covariates (β coefficients from the logistic regression) can be interpreted as selected or avoided if $\beta > 0$ or $\beta < 0$, respectively, and significantly different from 0. If $\beta = 0$, or is not significantly different from 0, then the habitat type is used in proportion to its availability. More recently, RSFs often include individual as a random effect on the intercept and also include random coefficient (Gillies et al. 2006; Hebblewhite and Merrill 2008). Random intercepts account for differences in sample size among individuals, whereas random coefficients account for differences in selection among individuals (Gillies et al. 2006; Hebblewhite and Merrill 2008). To our knowledge, no study has used random coefficients in RSFs to test if habitat selection constitutes behaviour with consistent individual differences upon which natural selection could act. Prior to statistical analyses, we assessed multicolinearity between covariates using the variance inflation factor (VIF < 5; Graham 2003), and, based on this, removed the % coniferous stands from our analyses which occupied on average >56% of buffer zones. We performed model selection (Burnham and Anderson 2002) and evaluated different candidate models defined *a priori* using the Akaike Information Criterion (AIC).

We first evaluated two different RSF models with differently structured random effects to ascertain whether variance in habitat selection occurred among individuals. In model A, we nested bear-year within BearID and included no random coefficient. This model provided information about habitat selection at the population level and accounted for differences in number of GPS fixes per individual (Gillies et al. 2006). In model B, we also considered differences in selection among individuals by adding % bog as a random coefficient to model A (Gillies et al. 2006). We added % bog to test for individual variation in habitat selection toward an abundant natural habitat type, however, any other habitat covariate of interest could have been used instead (for cut blocks habitat type see Appendix 4A). If supported by

AIC, model B would permit us to extract variances in habitat selection of bogs (random coefficient) within (bear-year) and among (BearID) individuals to calculate repeatability:

$$r = \frac{s_{among}^{2}}{s_{among}^{2} + s_{within}^{2}} \quad [\text{Eq. } 4.1]$$

where r is repeatability, s_{among}^{2} is the variance among individuals (BearID), and s_{within}^{2} is the variance within individuals (bear-year). High repeatability (r=1) will be found if $\mathrm{s}_{\mathrm{among}}^{2}$ is high relative to $\mathrm{s}_{\mathrm{within}}^{2}$, or, in other words, when individuals behave consistently through time (low $\mathrm{s}_{\mathrm{within}}^{2}$) and when individuals behave differently from each other (high $\mathrm{s}_{\mathrm{among}}^{2}$). No repeatability (r=0) will be found when all individuals behave similarly as a homogenous group (low $\mathrm{s}_{\mathrm{among}}^{2}$), but the "group" behaves differently through time (high $\mathrm{s}_{\mathrm{within}}^{2}$).

Using the most parsimonious random structure, we evaluated 4 nested candidate models with different fixed effects. The '*base*' model was composed of the functional response toward bogs only. Functional response was added by including an interaction term between the % bog within the 182-m radius buffer and the % bog within the home range. The '*elevation*' model included the '*base*' model, mean elevation, and the coefficient of variation of elevation. The '*natural*' model included the '*elevation*' model, % water, and % mixed–deciduous stand. The '*full*' model included the '*natural*' model, % cut blocks, % young forested stand, and road length.

Subsequently, we estimated fixed and random coefficients from the most parsimonious model. We extracted variance of bog selection among bears (BearID) and within bears (bear-year) and calculated repeatability according to [Eq. 4.1]. To facilitate model convergence, all numeric covariates were scaled (mean = 0, variance = 1) before inclusion. We conducted all statistical analyses using the lme4 package (Bates et al. 2014) in R 3.0.1 (R Core Team 2013).

Simulations

We performed simulations to ensure that repeatability estimates calculated from the random effects of RSF were not functions of the value of β estimates or their significance. Three scenarios were tested (Appendix 4B). In each scenario, we created a population of 5 individuals living in similar landscapes and monitored for 3 years. In the first scenario, parts of the population always selected habitat type X, whereas others always avoided it with varying intensities among years. In the second scenario, all individuals in the population avoided, used in proportion to availability, and selected habitat type X in the first, second, and third year, respectively, but we did not allow variation among individuals in a given year. In the third scenario, all individuals in the population selected habitat type X with varying intensity between years, but we did not allow variation among bears in a given year. We evaluated repeatability estimates for each scenario (Appendix 4B) using the lme4 package (Bates et al. 2014) in R 3.0.1 (R Core Team 2013).

Results

Between 2007 and 2012, we followed 31 GPS collared bears, 12 males and 19 lone females, aged 2 to 20 years-old. The bears were tracked $\bar{x}$ = 2.81 years (range: 2–5 years) for a total of 87 bear-years, which included a total of 72,744 GPS locations (mean ± sd = 836 ± 197 GPS locations per bear-year). Annual home range availability of bogs differed between bears and bear-year ($\bar{x}$ = 13%, range = 2–27% of annual home ranges).

We evaluated two random structures. Adding a random coefficient for % bog in the RSF increased model support (Table 4.1), suggesting that differences existed in the selection of bogs between BearID and/or bear-year. For the selection of fixed effects, the '*full*' model had the strongest support (Table 4.2). The fixed effect showed that, at the population level, bears selected for cut blocks, young forest, mixed-deciduous stands, and high coefficient of variation of elevation, but avoided high road density, water, and bogs (Table 4.3).

We estimated the repeatability of bog selection by extracting within (bear-year) and among (BearID) bear variances from the '*full*' model. Variance of bog selection within (bear-year) and among (BearID) bears was 0.081 and 0.035, respectively. According to [Eq. 4.1], repeatability of bog selection was 0.304, indicating that 30.4% of the variance in habitat selection of bogs by bears was due to differences among individuals (Figure 4.2). Habitat selection of cut blocks showed similar results (Table S4.1–S4.3). Variation in selection of cut blocks within (bear-year) and among (BearID) bears was 0.034 and 0.025, respectively, resulting in a repeatability of 0.420 (Figure 4.2).

The simulation results suggested that in scenario 1, habitat type X was neither selected nor avoided at the population level, but was highly repeatable at the individual level (>0.8; Table 4.4, Appendix 4B). Habitat type X from scenario 2 was also neither selected nor avoided at the population level, but was not repeatable (<0.001; Table 4.4, Appendix 4B). Finally, in scenario 3, habitat type X was selected at the population level but was not repeatable (<0.001; Table 4.4, Appendix 4B).

Table 4.1 Random structures tested to assess the repeatability of habitat selection of bogs by brown bears in Sweden between 2007 and 2012. Models are listed with their random intercepts, random coefficient, log likelihood (LL), differences in Akaike Information Criterion in relation to the best-supported model (Δ AIC), and Akaike weight (w_i).

MODEL	Random intercept	Random coefficient	LL	Δ AIC	w_i
A	Bear-year nested in BearID	–	-92098	1760	0
B	Bear-year nested in BearID	% bog	-91214	0	1

Table 4.2 **Candidate models tested to assess repeatability of habitat selection of bogs by brown bears in Sweden between 2007 and 2012. Models are listed with their fixed effects covariates, log likelihood (LL), differences in Akaike Information Criterion in relation to the best-supported model (Δ AIC), and Akaike weight (w_i). All models were tested with bear-year nested in BearID as a random intercept and % bog as a random coefficient (model B from Table 4.1).**

MODEL	COVARIATE INCLUDED	LL	Δ AIC	w_i
Base	% bog + % bog in the annual home range + % bog × % bog in the annual home range	-96521	10599	0
Elevation	Base model + mean elevation + coefficient of variation of elevation	-95946	9454	0
Natural[a]	Elevation model + % water + % mixed–deciduous	-93921	5407	0
Full	Natural model + % cut blocks + % young forest + road density	-91214	0	1

[a] The % of coniferous stands was not included to avoid multicollinearity.

Table 4.3 Coefficients (β) and 95% confidence intervals of the fixed effect covariates of the most parsimonious model to assess the repeatability of bog habitat selection by brown bears in Sweden between 2007 and 2012. This model also included bear-year nested in BearID as a random intercept and % bog as a random coefficient (model B from Table 4.1).

Variable	β	95% Confidence Interval	
		Lower	Upper
Intercept	-0.078	-0.132	-0.024
% bog	-0.514	-0.606	-0.422
% bog within annual home range	0.089	0.045	0.133
Mean elevation	-0.110	-0.128	-0.092
Coefficient of variation of elevation	0.080	0.068	0.093
% water	-0.477	-0.496	-0.458
% mixed–deciduous	0.018	0.007	0.029
% young forest	0.168	0.156	0.180
% cut blocks	0.272	0.260	0.284
Roads length	-0.306	-0.317	-0.294
% bogs × % bogs within annual home range	-0.074	-0.158	0.010

Table 4.4 Summary of results from simulations and GPS-collared bears that explored the relationship between the repeatability of habitat selection and the value and significance of β estimates in RSFs. In each scenario, 5 individuals were followed for 3 years and existed in similar landscapes and expressed different habitat selection pattern. For further details on scenarios see Appendix 4B.

	Population level response	RSFs β estimate	Repeatability
Simulations			
Scenario 1	Not selected nor avoided	Non-significant	> 0.8
Scenario 2	Not selected nor avoided	Non-significant	< 0.001
Scenario 3	Selected	Significant	< 0.001
GPS-collared bear data			
% bog	Avoided	Significant	0.304
% cut blocks	Selected	Significant	0.420

Discussion

Although natural selection acts on individual phenotypes, most literature on habitat selection reports population-scale inferences. Here we have extended a traditional method based on RSF to investigate habitat selection at the individual level and showed that individual variation in habitat selection exists in our brown bear study population. By investigating habitat selection at the individual level, we found that individual differences in habitat selection existed, were repeatable, and revealed patterns in selection that were not apparent at the population level.

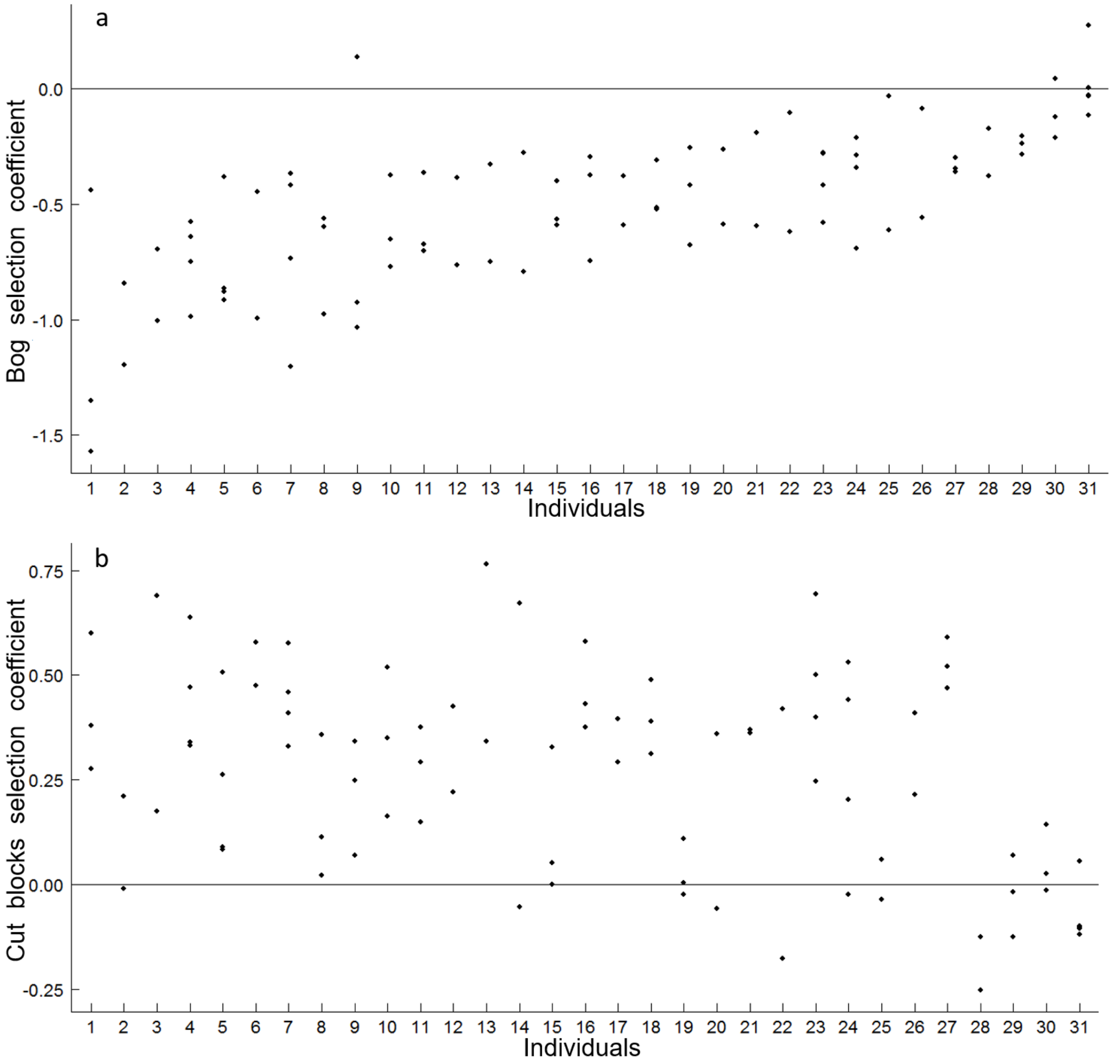

Figure 4.2 **Estimates of coefficients for the selection of bogs (panel a) and cut blocks (panel b) for each bear-year (n = 87) in south-central Sweden from 2007 to 2012. Bear-year is represented by a single dot, whereas stacked dots represent selection coefficients of a given individual (n = 31). Some bears consistently avoided bogs or selected cut blocks more strongly than others. The repeatability estimate of bog and cut blocks selection coefficients was 0.304 and 0.420, respectively, which indicates that individual variation in habitat selection exists and may allow adaptive evolution to occur in this brown bear population.**

Bears avoided bogs at the population level, but with varying intensity. Some bears avoided bogs more strongly than others. A similar pattern was also observed for cut blocks. Cut blocks were selected for at the population level, but consistent individual differences in their selection occurred among bears. Our simulations also suggested that repeatability estimates were not influenced by the pattern of habitat selection at the population level.

In our study we have focused on individual variation in habitat selection toward habitat types that were selected and avoided at the population level. However, we expect that individual variation in habitat selection can also occur regarding habitat types that appear to be used in proportion to their availability at the population level, i.e. in habitat types with a non-significant β estimate in RSFs. For example, we should observe individual variation in habitat selection toward a 'non-significant' habitat type if individuals behave differently from one to another, but the mean population use is equivalent to the mean population availability (Table 4.4; Appendix 4B). Furthermore, if a habitat type is selected or avoided at the population level, i.e., β estimate ≠ 0, this does not imply that selection for or avoidance of this habitat type will be repeatable at the individual level. For example, all individuals in a population could express the same behaviour (low among-individual variation relative to within-individual variation) of avoiding or selecting a habitat type, resulting in a low or zero repeatability (Table 4.4; Appendix 4B). We therefore do not expect a relationship between the value and significance of β estimates in RSFs and their repeatability.

The biological significance of individual differences in habitat selection will be linked to the spatial scale at which a study is conducted. Here, we evaluated habitat selection at the third order of selection (Johnson 1980), where bears should be less influenced by conspecifics and selection should reflect their own trade-offs regarding resource use (see Steyaert et al. 2013 for the mating period). If we had evaluated habitat selection repeatability at the second order of selection, we might have evaluated the consistency of the social structure and intra-specific competition rather than resource use trade-offs (Dahle and Swenson 2003; Støen et al. 2005; Dahle et al. 2006). In addition to choosing the most biologically relevant spatial scale, careful attention must be paid to density-dependent habitat selection (van Beest et al. 2014). Based on Ideal Free Distribution theory, individuals should distribute themselves to reduce resource competition and maximize fitness (Fretwell and Lucas 1970). Favourable habitat types should be used less by individuals when density increases, leading to a generalization in habitat selection (Fortin et al. 2008; van Beest et al. 2014). Therefore, observed habitat selection patterns and repeatability estimates can be functions of varying density over time (lower repeatability) or across the landscape (higher repeatability). We did not control for bear density, as we assumed that it was stable over the study area during the study period (6 years). Furthermore, bears typically show a despotic distribution (Elfström et al. 2014) and density should influence habitat selection of bears at the second, rather than the third, order of selection. Briefly, careful attention must be paid to density-dependent habitat selection and the spatial scale at which we evaluate habitat selection repeatability, which should vary depending on a species' ecology, limiting factors, etc.

Consistent individual variation in behaviour, or animal personality, has been shown to occur across many species for a variety of behaviours (Bell et al. 2009). In a meta-analysis, the average repeatability across all behaviours was 0.37 (Bell et al. 2009), which is similar to the habitat selection repeatability estimates that we obtained. Traditional experiments of personality have consisted mainly of capturing individuals in the wild and quantifying their behaviours in laboratory or open field tests (Bell et al. 2009). Niemelä and Dingemanse (2014) argued that novel environments (e.g., in a laboratory) can elicit behavioural patterns that fail to match behaviours expressed in natural environments. By using remotely sensed data (i.e., GPS collars), we avoid this criticism, having measured behaviour directly in the wild. The advent of technologies, such as GPS telemetry (or camera traps, Passive Integrated Transponder networks, etc.), presents a plethora of opportunities for understanding the repeatability of a diverse range of animal behaviours, e.g., here with habitat selection (see also Ciuti et al. 2012; Kays et al. 2015; Wilmers et al. 2015). Coupling measurements coming from both traditional experiments and personality measures using GPS telemetry will provide new opportunities to assess whether behaviour measured in laboratory or open field tests is associated with behaviour in the wild.

Consistent individual differences in habitat selection may have important ecological and evolutionary implications. As the expression of personality traits can be environment-dependent (Nussey et al. 2007), we suggest that individual variation in habitat selection could have important cascading effects on other behavioural traits (Dubois and Giraldeau 2014). For example, individual variation in habitat selection might canalize individuals into different behavioural patterns. In return, those behavioural patterns might appear as personality traits that could be caused by individual variation in habitat selection. More research linking habitat selection and animal personality is needed to disentangle the causes and consequences of individual variation in habitat selection and its potential cascading effects on other behavioural traits.

Individual differences in habitat selection could be the results of many non-exclusive factors. As bears seek resources that are distributed into habitat types, differences in habitat selection pattern could be the result of different resource needs in relation to sex or age. Therefore, it might not be surprising that we observed high inter-annual variance (bear-year) in habitat selection, as bears are opportunistic omnivores and the distribution of resource availability can differ among years (Bojarska and Selva 2012). Another mechanism that could explain individual differences in habitat selection is natal habitat preference induction, i.e., when experience in a natal habitat increases the level of preference for that habitat later in life (Davis and Stamps 2004; Stamps et al. 2009). Similarly, Nielsen et al. (2013) suggested that habitat selection in brown bears is a behaviour learned from the mother. Finally, as repeatability estimates are considered to be the upper limit of heritability (Falconer and Mackay 1996), our results suggest that patterns of habitat selection may be, at least partly, heritable (Shafer et al. 2014). Thus, we speculate that if these individual differences in habitat selection have a genetic basis and are under selective pressure, we would expect evolutionary change in patterns of habitat selection, which may have important implications for adaptive potential and the maintenance of genetic variation in wild populations.

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CHAPITRE 5

SÉLECTION COMPORTEMENTALE ET RÉCOLTE: UNE REVUE DE LA LITÉRATURE

Description de l'article et contribution

Les activités humaines engendrent d'importantes pressions écologiques et évolutives sur les espèces sauvages. En effet, il a été montré que la récolte par l'Homme peut, entre autres, générer des pressions sélectives et ultimement causer de l'évolution sur la morphologie et les traits d'histoire de vie des populations exploitées. Cependant, il existe beaucoup moins d'information quant à l'effet potentiel de la récolte sur les traits comportementaux, particulièrement en milieu terrestre. Cet article visait à mettre en lumière que la récolte a également le potentiel d'exercer des pressions sélectives sur le comportement, tant en milieu marin qu'en milieu terrestre, en rapportant et discutant des exemples empiriques présents dans la littérature scientifique.

Suite aux suggestions de mon examen prédoctoral en mars 2014, j'ai essayé de trouver des exemples supplémentaires de sélection comportementale induite par la chasse ou par les pêcheries. J'ai été surpris de constater, au cours de ma recherche, qu'il existe peu d'exemples empiriques de ce phénomène dans la littérature. Ensuite est venue l'idée de publier un court manuscrit afin de discuter de cette situation afin, idéalement, de pouvoir stimuler la recherche dans ce domaine. Pour cet article, j'ai fait la revue de littérature et écrit la première version du manuscrit. Andreas Zedrosser et Fanie Pelletier ont participé aux révisions du manuscrit.

Harvesting as a potential selective pressure on behavioural traits

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Abstract

1. Human activities are a major evolutionary force affecting wild populations. Selective pressure from harvest has mainly been documented for life-history and morphological traits. The probability for an individual to be harvested, however, may also depend on its behaviour.

2. We report empirical studies that examined whether harvesting can exert selective pressures on behavioural traits.

3. We show that harvest-induced selection on behavioural traits is not specific to a particular harvest method and can occur throughout the animal kingdom.

4. *Synthesis and applications.* Managers need to recognize that artificial selection caused by harvesting is possible. More empirical studies integrating physiological, behavioural, and life-history traits should be carried out to test specific predictions of the potential for harvest-induced selection on heritable traits using models developed in fisheries. To limit selective pressure on behaviour imposed by harvesting, managers could reduce harvest quotas or vary harvest regulations over time and/or space to reduce the strength of selection on a particular phenotype.

Keywords: angling, evolutionary consequences, exploitation, fisheries, gillnet, harvest-induced selection, hunting, passive and active gear, vulnerability

Introduction

Humans are considered as one of the major selective forces shaping traits of species (Palumbi 2001) and may cause faster phenotypic changes than many natural drivers (Hendry, Farrugia & Kinnison 2008; Darimont et al. 2009). Phenotypic changes are particularly drastic when humans act as predators and harvest wild populations (Darimont et al. 2009). Harvesting can induce selective pressures on wild animal populations by increasing mortality and by non-random removal of specific phenotypes. Harvesting has been shown to induce selective pressure in several species (Allendorf et al. 2008) that may ultimately result in evolutionary responses (Jørgensen et al. 2007; Pigeon et al. 2016).

Selective pressure caused by human harvest, hereafter referred to as harvest-induced selection, has mostly been documented for life-history and morphological traits and can be caused by size-selective harvesting. For example, trophy hunting of male bighorn sheep (*Ovis canadensis*) selected for smaller horn size (Coltman et al. 2003; Pigeon et al. 2016), and size-selective fishing affected the evolution of life histories in zebra fish (*Danio rerio*) (Uusi-Heikkilä et al. 2015). In size-selective harvesting, typically a specific phenotype is targeted leading to harvest-induced selection. Harvest-induced selection on behavioural traits, however, can be due to behavioural differences between individuals affecting their probability of being harvested (Uusi-Heikkilä et al. 2008; Heino & Godø 2002). This pattern was observed in behavioural studies showing that the probability of capturing or sampling (for scientific research instead of harvesting) a specific individual in a population could be biased due to consistent individual differences in behaviour, i.e., animal personality (Biro & Dingemanse 2009; Carter et al. 2012; Biro 2013). These individual behavioural differences are often heritable (Postma 2014; Dochtermann, Schwab & Sih 2015). Humans can therefore, consciously or not, modulate the evolution of animal behaviour by removing (harvesting) or reproducing (breeding) specific individuals within a population (Price 1984). Although important for wildlife management and conservation, much less attention has been devoted to harvest-induced selection on behavioural traits compared to life-history or morphological traits (Uusi-Heikkilä et al. 2008; Heino, Díaz Pauli & Dieckmann 2015) and to whether this selection may lead to evolution of behaviours that are different from those favored by natural selection (e.g., Olsen & Moland (2011) for body length in Atlantic cod (*Gadus morhua*)).

Harvesting as a selective pressure on behavioural traits

Most of the theoretical work and predictions for behavioural harvest-induced selection are derived from the fisheries literature. Arlinghaus et al. (2016) suggested that harvest should select for shyer and more vigilant individuals. In fisheries, predictions made on harvest-induced selection often depend on the gear type used, and Alós, Palmer & Arlinghaus (2012) predicted that passive gear should select for individuals with lower activity levels. In sport hunting, a hunter must see an individual of the species of interest before she/he can select a target animal based on a morphological trait or a sex/age class. Therefore, we hypothesize that behavioural traits that increase vulnerability or visibility, such as selection of open areas, more active individuals during hunting hours, or boldness, should have a strong effect on the probability that an individual will present itself as a possible target.

Here we report studies where harvest-induced selection of behavioural traits was clearly investigated. We searched the scientific literature database Scopus® for peer-reviewed papers using different combinations of the following seven keywords: harvesting, hunting, fisheries, behaviour, vulnerability, exploitation, and selective pressure. The literature contains numerous studies on the immediate effects of harvesting on behaviour (i.e., plastic response or "learning") [e.g., Raat (1985), Ordiz et al. (2012)] or studies showing behavioural differences between high and low vulnerability fish strains [e.g. Nannini et al. (2011), Sutter et al. (2012)], or studies showing behavioural differences between fish caught with different methods or lures [e.g. Wilson et al. (2015)], which suggests that harvesting might induce a selective pressure on behaviours. Here, however, we only retained studies that directly examined whether harvesting acted as a selective pressure on behavioural traits. The limited amount of literature examining harvest-induced selection on behaviour likely reflects the difficulties in collecting quantitative information on behavioural traits expressed by harvested and non-harvested individuals necessary to investigate behavioural harvest-induced selection. This is particularly true for fish, because it is rarely possible to make observations on fish that are not captured (Härkönen et al. (2016), but see Olsen et al. (2012)), and longitudinal behavioural time-series data from wild populations hardly exist (Jørgensen & Holt 2013). We categorized the 13 retained studies in two groups: experimental studies in the laboratory or natural conditions, and observational studies in the wild.

Experimental studies

We found seven experimental studies showing that harvest can act as a selective pressure on behavioural traits (Table 5.1; but see Vainikka, Tammela & Hyvärinen (2016)). From the seven studies showing harvest-induced selection of behavioural traits, six were conducted in fishes and one in a crustacean. Individuals showed different vulnerability to angling in largemouth bass (*Micropterus salmoides*) (Philipp et al. 2009) and common carp (*Cyprinus carpio*) (Klefoth, Pieterek & Arlinghaus 2013), and traps removed bolder guppies (*Poecilia reticulata*) and common yabby (*Cherax destructor*) (Biro & Sampson 2015; Diaz Pauli et al. 2015). Trawling removed shyer guppies (Diaz Pauli et al. 2015) and minnows (*Phoxinus phoxinus*) with lower swim speed (Killen, Nati & Suski 2015). These studies suggest that harvesting can act as a selective pressure on a behavioural trait and that passive gear should select against boldness and more explorative individuals, while active gear should select against shyness, and angling selects against more aggressive, bold, and vulnerable individuals (Heino & Godø 2002; Arlinghaus et al. 2016). Harvest-induced selection patterns obtained in laboratory experiments appear to be consistent with those observed in experiments conducted in natural settings (Biro & Post 2008), suggesting that harvesting can act as a selective pressure in the wild.

Observational studies

We found six studies showing harvest-induced selection on different behavioural traits in the wild, ranging from the timing of migration to boldness and defensiveness (Table 5.1). These studies involved fishes, snakes, birds, and mammals in Japan, Norway, United Kingdom, Canada, and the USA. Similarly to experimental studies, observational studies showed that harvest-induced selection was caused by different harvest methods (shotgun, rifle hunting, passive gear, angling), and that behavioural traits under selection may vary in relation to the harvest method used (Table 5.1). In sockeye salmon (*Oncorhynchus nerka*) harvesting selected against individuals that migrated later in the season in a population where exploitation rates vary systematically over the course of the fishing season (Quinn et al. 2007). In this population, migration timing became earlier over the years (Quinn et al. 2007). Such temporal behavioural changes could be caused by environmental factors, but could also be, at least partly, a response to harvest-induced selection if migration timing is heritable (Quinn et al. 2007).

Consequences of behavioural harvest-induced selection

Behavioural traits under harvest-induced selection can only evolve if they are heritable (Postma 2014; Dochtermann, Schwab & Sih 2015). In addition to the changes in migration timing of sockeye salmon discussed above (Quinn et al. 2007), two studies suggested that harvest might have been important in the evolution of a genetic locus related to habitat use of Atlantic cod in Iceland (Árnason, Hernandez & Kristinsson 2009; Jakobsdottir et al. 2011). However, we found no observational studies that could unequivocally show evolution in behaviour caused by harvesting. Absence of evidence for harvest-induced evolution of behavioural traits in the wild, however, does not imply that such evolution is unlikely or uncommon. Instead, it may reflect the difficulties to obtain the necessary longitudinal data on behaviours in harvested populations (Clutton-Brock & Sheldon 2010; Jørgensen & Holt 2013). Even when adequate data are available, it remains challenging to show that harvest is the driver of evolutionary change and to disentangle phenotypic plasticity from genetic change (Merilä & Hendry 2014). Although they have not been documented in the wild,

Table 5.1 Examples of experimental and observational studies showing that harvest can act as a selective pressure on behaviour.

Species	**Harvest method**	**Trait**	**Direction of the selective effect. Harvest selects against individual that are:**	**Reference**
Experimental study in the laboratory or in natural conditions				
Poecilia reticulata	Trap	Bold–Shy	Bolder	Diaz Pauli et al. 2015
	Trawl	Bold–Shy	Shyer	Diaz Pauli et al. 2015
Phoxinus phoxinus	Trawl	Swim speed	Slower	Killen, Nati & Suski 2015
Salmo trutta	Fly-fishing	Exploration	More explorative	Härkönen et al. 2014
Cyprinus carpio	Angling	Vulnerability	More vulnerable	Klefoth et al. 2013
Micropterus salmoides	Angling	Vulnerability	More vulnerable	Philipp et al. 2009
Oncorhynchus mykiss	Gillnet	Bold/Shy–Fast/Slow	Faster-bolder	Biro & Post 2008
Cherax destructor	Trap	Bold–Shy	Bolder	Biro & Sampson 2015
Observational study				
Oncorhynchus nerka	Angling	Migration timing	Migrated later in season	Quinn et al. 2007
Gadus morhua	Passive gear	Habitat use	Use more shallow-water	Olsen et al. 2012
	Passive gear	Vertical migration	Have a strong diel vertical	Olsen et al. 2012

			migration	
	Passive gear	Horizontal movement	Have a predictable movement pattern	Olsen et al. 2012
Gloydius blomhoffii	Not mentioned	Flight distance	Have lower flight distance	Sasaki et al. 2009
	Not mentioned	Defensiveness	More defensive	Sasaki et al. 2009
Phasianus colchicus	Shotgun	Bold–Shy	Bolder	Madden & Whiteside 2014
Cervus elaphus	Rifle hunting	Habitat use	Use habitat with less concealing cover	Lone et al. 2015
	Rifle hunting	Habitat use	Use open areas	Ciuti et al. 2012
	Rifle hunting	Habitat use	Closer to roads and use flatter terrain	Ciuti et al. 2012
	Rifle hunting	Movement rate	Have higher movement rate	Ciuti et al. 2012

evolutionary changes in behavioural traits due to harvest have been shown in experimental studies (Philipp et al. 2009). Laboratory experiments are useful to evaluate the potential for harvest-induced selection and evolutionary response in behavioural traits, but extrapolation of results to natural systems is difficult, as some relationships observed in the laboratory might not persist in the wild (Wilson et al. 2011).

Conclusions

Humans have harvested wild animals for millennia and human evolution is strongly linked with harvesting. However, technological developments have increased our efficiency to harvest, with many consequences (Milner, Nilsen & Andreassen 2007; Fenberg & Roy 2008; Allendorf et al. 2008). Morphological, life-history, and behavioural traits form the phenotype of an individual and thus affect its vulnerability to harvest (Uusi-Heikkilä et al. 2008). There is increasing evidence that behavioural traits are correlated with physiological and life-history traits (Biro & Stamps 2008; Réale et al. 2010). Therefore, even if harvesting specifically targets a behavioural trait, changes in life-history, morphological, and/or physiological traits can be observed. For example, changes in behaviours were observed due to size-selective harvesting in zebra fish (Uusi-Heikkilä et al. 2015), and size-selective harvesting of Atlantic silverside (*Menidia menidia*) resulted in lower larval growth rate, food consumption rate and conversion efficiency, and vertebrae number (Walsh et al. 2006; Duffy et al. 2013). If individuals with certain life-history, morphological and behavioural phenotypes are heavily harvested, selection may quickly lead to the evolution of a population with a lower harvest yield (Conover & Munch 2002), because this population will now mostly be composed of individuals with lower growth rate (Conover & Munch 2002; Biro & Sampson 2015) that are also more difficult to harvest (Philipp et al. 2009). In many cases, selective pressures imposed by harvesting oppose natural selection (Conover 2007; Olsen & Moland 2011). While some traits can genetically recover after harvest-induced selection ceases (Conover, Munch & Arnott 2009), some traits may not (Salinas et al. 2012; Pigeon et al. 2016), which can impair population recovery after harvest has ceased (Laugen et al. 2014).

Recommendations

Even though behaviours are often easier to observe and quantify in terrestrial ecosystems, most of the literature and predictions on behavioural harvest-induced selection comes from fisheries. Despite differences in the harvest methods used in fisheries and hunting, behavioural data from terrestrial harvested populations can be complementary to fisheries data and could offer an opportunity to test predictions developed for fisheries in terrestrial ecosystems. For example, predictions made for passive gear in fisheries could be applied to "still hunting" or "bait hunting", but might not be appropriate for "stalking". Therefore, we suggest a synergistic approach and recommend to increase discussions and collaborations between researchers studying harvest-induced selection in fisheries and terrestrial ecosystems.

Integrating genetic and evolutionary effects of harvesting into management and conservation is central for achieving sustainable harvesting (Conover & Munch 2002; Allendorf et al. 2008). Acknowledging that harvest is selective by nature is the first step toward that goal. Even if harvest is random regarding phenotypes, it increases mortality and therefore selects for faster growing and earlier reproducing individuals ("r" life-history strategy) rather than slow growing and late reproducing individuals ("K" life-history strategy) (Pianka 1970). Ideally, in harvested populations, monitoring programs should be introduced to detect and monitor potential harvest-induced selection and its consequences. Such programs would require longitudinal data on multiple phenotypic traits, including behavioural traits, of harvested and non-harvested individuals in the population. This would allow evaluating the direction and strength of harvest-induced selection in comparison to natural selection. When required, different mitigation measures could be implemented in management plans to reduce the impacts of harvest-induced selection. For example, reducing harvest quotas should reduce the strength of selection or managers could establish harvest regimes that mimic natural selection (Milner, Nilsen & Andreassen 2007).

Such monitoring programs are challenging tasks requiring a considerable amount of time and money. In the meantime, we suggest using a precautionary approach when harvesting natural populations. Harvest quotas should not be based on maximum yield but rather aim at preserving natural variation shaped by natural selection (Fenberg & Roy 2008). We suggest, based on our results, to vary harvest regulations (e.g. based on sex, age, or phenotypes harvested and harvest methods used) spatio-temporally to reduce the strength of selection on a particular phenotype.

Authors' contributions

All authors conceived the idea; ML conducted the literature search and the first draft of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Data accessibility

Data have not been archived because this article does not contain data.

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CHAPITRE 6

SÉLECTION COMPORTEMENTALE INDUITE PAR LA CHASSE

Description de l'article et contribution

Dans le chapitre précédent, j'ai effectué une revue de la littérature et conclu que la récolte peut agir comme une pression sélective sur le comportement. Prédire la direction des pressions sélectives induites par la récolte demeure cependant ardu. Un cadre théorique a été récemment développé en milieu marin, mais aucun cadre théorique n'a été développé pour les milieux terrestres. Dans cet article, j'ai vérifié si les prédictions émises par le cadre théorique développé en milieu marin peuvent être supportées dans un système de chasse en milieu terrestre. En utilisant différents comportements et différentes variables reliées à la survie des ours, j'ai montré, pour l'une des rares fois dans la littérature scientifique, que les chasseurs induisent des pressions sélectives sur le comportement. Cependant, les résultats obtenus ne supportent que partiellement les prédictions émises par le cadre théorique développé en milieu marin, ce qui m'a amené à proposer quelques ajustements à ce cadre théorique. Le développement de collaborations et l'intégration de la littérature entre les chercheurs en milieux marins et terrestres aideront à mieux comprendre et quantifier les effets complexes des pressions sélectives comportementales induites par la récolte.

Pour cet article, j'ai effectué la manipulation des données, les analyses statistiques et j'ai écrit la première version du manuscrit. Tous les coauteurs ont participé aux multiples révisions du manuscrit et ont été consultés lors des analyses statistiques.

Hunters select for behavioral traits in a large carnivore

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Abstract

Human harvest can induce selection on life history and morphology, leading to evolutionary responses. Our understanding of harvest-induced selection on behavioral traits is, however, very limited, particularly in terrestrial ecosystems. In a general framework recently developed in fisheries, two main predictions of behavioral harvest-induced selection have been proposed; active fishing methods such as trawling, should select against shyer individuals, whereas passive fishing methods such as traps, should select against bolder individuals. Here, we assessed whether these predictions hold in a terrestrial ecosystem. We used long-term, exceptionally detailed behavioral and survival data of a heavily harvested brown bear (*Ursus arctos*) population in Sweden, where bears are typically hunted using baying dogs. We assume that bear hunting in Sweden could be analogous to active fishing methods and should select against shyer individuals, i.e., bears that are less active during legal hunting hours, show lower rates of movement, and use habitat farther away from roads. We found that hunting selected against male bears that were less active during legal hunting hours, but we did not find any selection on activity patterns in females. Also, hunting selected against male and female bears that had lower rates of movement and used habitat closer to roads. We provide a convincing empirical example that individual behavior can modulate vulnerability to hunting. By testing behavioral harvest-induced selection in different ecosystems, we could develop more general predictions and gain better insight into the full effects of human harvest on wild populations.

Keywords: Artificial selection, evolution, harvest-induced selection, indirect effects of hunting, Scandinavia

Introduction

The human footprint is apparent in both terrestrial and marine environments on a global scale (Sanderson et al. 2002; Halpern et al. 2008; Kroodsma et al. 2018). Human-induced environmental changes are now considered as main drivers of phenotypic changes in wild populations (Palumbi 2001; Pelletier and Coltman 2018). Phenotypic changes, including both plastic or genetic changes, have been documented in the wild, and meta-analyses suggest that they occur at a faster rate in anthropogenic landscapes, particularly when humans act as predators and harvest wild populations (Hendry et al. 2008; Darimont et al. 2009). Human harvest mortality typically differs from natural mortality, because harvest increases mortality rates for age or sex classes that usually show high survival naturally (Darimont et al. 2015). Human harvest is also often nonrandom and commonly targets specific phenotypes (Fenberg and Roy 2008; Van de Walle et al. 2018), such as in size-selective fisheries or trophy hunting, which can result in harvest-induced selection and evolution (Allendorf and Hard 2009).

Empirical studies have documented evolutionary changes in morphological and life-history traits in responses to size-selective harvest (Uusi-Heikkilä et al. 2015; Pigeon et al. 2016). For example, trophy hunting of male bighorn sheep (Ovis canadensis) selected for smaller horn size (Pigeon et al. 2016). Fisheries have been shown to reduce annual body growth and induce maturation at a lower age and smaller size in several harvested fish populations (Jørgensen et al. 2007; Heino et al. 2015). Biro and Post (2008) showed that size-selective harvesting may also induce selection on behavioral traits. In a whole-lake experiment, fast and bold rainbow trout (Oncorhynchus mykiss) were more likely to be caught in gillnets compared to slow and shy individuals (Biro and Post 2008). This result highlights that harvest-induced selection on behaviors might be widespread given the important use size-selective harvest methods in fisheries. To predict the consequences of harvest-induced selection on behavioral traits in harvested populations can be complex, as they may depend on the interplay between the human behavior, the harvest method applied, and animal behavior (Mysterud 2011; Frank et al. 2017).

Most of the work and predictions on harvest-induced selection of behavioral traits stem from the fisheries literature (Klefoth et al. 2017; Leclerc et al. 2017). Arlinghaus et al. (2017) and Diaz Pauli & Sih (2017) suggested that in aquatic ecosystems, passive fishing methods (e.g. such as baited traps) are more likely to capture bolder than shy individuals, because bolder individuals tend to be more explorative and risk-taking, and should thus have a higher probability of entering such traps in comparison to shier, less explorative, and risk-averse individuals. Therefore, passive fishing methods would select against bolder individuals and select for a widespread timidity syndrome (Arlinghaus et al. 2017). Active fishing methods, such as trawling, should select against shyer and less active individuals, because they are expected be less efficient in escaping approaching fishing gear than more reactive and bolder individuals (Diaz Pauli and Sih 2017). However, empirical tests for such predictions from wild populations are scarce (Leclerc et al. 2017), and to our knowledge, no predictions or theoretical framework exist for the effects of harvesting on behavioral traits in terrestrial systems [but see Arlinghaus et al. (2016)].

The goal of this study was to investigate if and how hunters select against behavioral traits in a heavily harvested terrestrial carnivore population (Bischof et al. 2018). We used detailed behavioral information derived from GPS relocations and activity sensors from individually marked brown bears (Ursus arctos) in a Swedish population, and tested whether predictions from fisheries hold in a terrestrial ecosystem. Brown bear hunting in Sweden takes place in the fall and hunting quotas are set at the county level. As long as the quota has not yet been filled, there is no limit on the number of bears that an individual hunter can harvest (Bischof et al. 2008). During the study period (2003-2016), baiting was not allowed and most hunters used baying dogs to find and track bears (Bischof et al. 2008). We consider brown bear hunting in Sweden as an active hunting method (i.e., no legal use of passive baiting, but active use of dogs), which can be considered analogous to active fishing methods. Therefore, we hypothesize that brown bear hunters harvest predominantly shyer and less active individuals. We predicted that hunters should harvest bears that have lower rates of movement, bears that are less active during legal hunting hours, and bears that use habitats farther away from roads. Alternatively, we can argue that hunting regulations create no incentive for a hunter to pass up an opportunity to shoot a bear (quotas at the county level and no individual limit) and that the probability for a bear to be harvested is mainly driven by its probability of encounter with a hunter. Based on this alternative hypothesis, we expected that hunters should harvest bears that have higher rates of movement, bears that are more active during legal hunting hours, and bears that use habitats closer to roads (Steyaert et al. 2016).

Methods

Study area

The study area was located in south-central Sweden (61°N, 15°E) and comprises of bogs, lakes, and intensively managed coniferous forest stands of variable ages. The dominant tree species were Norway spruce (Picea abies), Scots pine (Pinus sylvestris), and birch (Betula spp.). Elevations ranged between 150 and 1000 m asl. The study area is intersected with a dense network of forest roads. Human population density is among the lowest in the European brown bear range, with humans concentrated in villages in the northern and southern parts of the study area. Small settlements and isolated houses are scattered throughout the area. See Martin et al. (2010) for further information about the study area.

We captured brown bears from a helicopter (2003–2016) using a remote drug delivery system (Dan-Inject, Børkop, Denmark). We extracted a vestigial first premolar for age determination from each individual not captured as a yearling with its mother (Matson 1993). See Fahlman et al. (2011) for further details on capture and handling. We equipped bears with GPS collars (GPS Plus; Vectronic Aerospace, Berlin, Germany) programed to relocate a bear every hour. Collars also included dual-axis motion activity sensors that measured acceleration in two orthogonal directions. Measures of acceleration were averaged every 5 minutes and stored in the collar. All bears captured were part of the Scandinavian Brown Bear Research Project, and all captures and handling were approved by the appropriate authority and ethical committee (Djuretiska nämden i Uppsala, Sweden).

Brown bear hunting in Sweden starts on August 21 and the hunting season lasts until the scheduled season end date (15 October in the study area) or until the harvest quota is reached (whichever comes first). Legal hunting hours (hereafter 'hunting hours') last from one hour before sunrise until two hours before sunset. Family groups, i.e. female accompanied with offspring, are protected and cannot be legally harvested (Swenson et al. 2017). Trophy hunting is rare, but financially motivated guided hunts have increased in Sweden in recent years (Bischof et al. 2008; Swenson et al. 2017).

Data handling

We used information from GPS collars and dual-axis motion activity sensors from individual bears in years when they could be legally harvested (i.e. bears that were not in a family group). We use data from 1 August to 30 September each year to cover the period before and after the start of the hunting season. We screened GPS relocation data and removed GPS fixes with dilution of precision values >10 to increase spatial accuracy. We then used these GPS data to quantify two behavioral traits, i.e. rates of movement and distance to road that may affect vulnerability to hunting. Rates of movement was calculated as the distance travelled by a bear during a 1-hour interval using the "adehabitatLT" package in R 3.4.4 (R Core Team 2018). Proximity to road was calculated with the "rgeos" package and defined as the Euclidian distance between GPS relocations of bears and the closest road using maps of the Swedish National Road Database from the Swedish Transport Administration (© Trafikverket). We averaged the daily Euclidian distances to the closest road for easier model convergence and we calculated road density within each "Bearyear" home range.

The third behavioral trait, activity pattern, was quantified using data from dual-axis motion activity sensors. We calculated for each individual a daily index of activity during hunting hours, corrected for daylight changes, following Hoogenboom et al. (1984):

$$\frac{\frac{SA_h}{D_h} - \frac{SA_{nh}}{D_{nh}}}{\frac{SA_h}{D_h} + \frac{SA_{nh}}{D_{nh}}}$$

where SAh and SAnh are the sum of activity values during hunting hours and nonhunting hours, respectively, and where Dh and Dnh are the duration of hunting hours and nonhunting hours, respectively. This index ranges between -1 and 1, where -1 represents a bear that is only active during nonhunting hours, and 1 represents a bear that is only active during hunting hours.

Statistical analysis

Because we wanted to investigate the direction of harvest-induced selection on behaviors, we used behavioral information from bears that had died from hunting (88.3% of bears that died during the study period; other mortality causes were unknown (8.5%), management (1.2%), vehicle collision (1.2%), and capture (0.8%)). We determined if the behaviors expressed by a bear were correlated with variables describing bear longevity. The first variable was hunting season fate, a dummy variable describing if the bear was harvested or not during the hunting season. The second variable was the number of years alive before being harvested. We ran different candidate models for each sex separately.

To model rates of movement, we used general additive mixed models ("mgcv" package) of the gaussian family, which allow flexible specification of the relationships, instead of being linear or quadratic (Wood 2017). Due to convergence issues and to avoid extensive computational time, we focused on modeling the behavior of individual bears from 0200 to 1200 hrs, which includes the period of the day with the highest hunting mortality risk for brown bears in Sweden (around 0700 hrs, see figure 1 in Hertel et al. (2016)). We tested a set of candidate models constructed hierarchically (Table S6.1), based on the following variables: hour of day, Julian date, age of the bear, hunting season fate, and the number of years alive before being harvested. We log-transformed movement to fulfill assumptions of normality and homogeneity of variance. We also used GAMMS to model activity patterns. As for modeling rates of movement, we tested a set of candidate models constructed hierarchically (Table S6.2) based on the following variables: Julian date, age of the bear, hunting season fate, and the number years alive before being harvested. We modeled the mean daily distance to the closest road with linear mixed models ("nlme" package). We again tested a set of candidate models constructed hierarchically (Table S6.3) based on the following variables: Julian date, road density in the home range, age of the bear, hunting season fate, and the number of years alive before being harvested. The mean daily distance to the closest road was log-transformed to fulfill statistical assumptions. All candidate models tested included "Bearyear" nested in "Bear ID" as random intercepts and an AR1 function controlling for temporal autocorrelation. Bear age and the numbers of years before dying of hunting were not colinear ($r < 0.35$). All candidate models were ranked using AICc (Burnham and Anderson 2002) and all spatial and statistical analyses were performed in R 3.4.4 (R Core Team 2018).

Results

The database included 32,849 rates of movement from 41 males (87 bear-years) and 35,821 rates of movement from 37 females (92 bear-years) during 2003 to 2016. For male, the most parsimonious model (Table S6.1) included a negative effect of age (Figure S6.1a, estimated degree of freedom [edf] = 2.174) and Julian date (Figure S6.1b, edf = 2.542), an interaction between the time of day and hunting season fate (Figure 6.1a), and a positive effect of the number of years before dying of hunting (Figure 6.1b). Predictions suggest that males that died during a hunting season move twice as fast as males that survive a hunting season at 0400 hrs (283 m vs 131 m), while that trend is reversed at 0900 hrs (Figure 6.1a; died=89 m and survive=145m). The male model's marginal R^2 was 23.4%. The most parsimonious model (Table S6.1) for female rates of movement included a negative effect of age (Figure S6.2a, edf = 1.724) and Julian date (Figure S6.2b, edf = 3.357), an interaction between the time of day and the hunting season fate (Figure 6.1c), and a positive effect of the number of years before dying of hunting (Figure 6.1d). The female model's marginal R^2 was 24.2%.

Activity pattern included 3,356 daily values from 38 males (82 bear-years) and 4,145 daily values from 37 females (92 bear-years) during 2003 to 2016. The most parsimonious model (Table S6.2) for male activity pattern included a negative effect of age (Figure S6.3a, edf = 3.507), a positive effect of the number of years before dying of hunting (Figure 6.2, edf = 1) and the effect Julian date (Figure S6.3b, edf = 5.038). The male model's marginal R^2 was 10.5%. For females, the most parsimonious model (Table S6.2) only included age (Figure S6.4a, edf = 3.039) and Julian date (Figure S6.4b, edf = 5.165). The female model's marginal R^2 was 4.1%.

The mean daily distance to a road included 2,566 and 3,711 values from 31 males (69 bear-years) and 35 females (81 bear-years), respectively, during 2003 to 2016. For males, the most parsimonious model (Table S6.3) included a negative effect of road density (Table 6.1), Julian date (Table 6.1), and a positive effect of the number of years before dying of hunting (Figure 6.3a). Age was also included in the most parsimonious model, but its 95% confidence intervals included 0 (Table 6.1). The male model's marginal R^2 was 20.5%. For females, the most parsimonious model (Table S6.3) included a negative effect of road density (Table 6.1) and Julian date (Table 6.1), and a positive effect of the number of years before dying of hunting (Figure 6.3b). Age, hunting season fate, and the interaction between Julian date and the hunting season fate were also included in the most parsimonious model, but their confidence intervals included 0 (Table 6.1). The female model's marginal R^2 was 27.0%.

Discussion

We tested predictions of harvest-induced selection on behavioral traits, based on a framework developed in fisheries, in a heavily hunted large carnivore population. Using detailed individual-based behavioral information from brown bears in Sweden, we showed that males

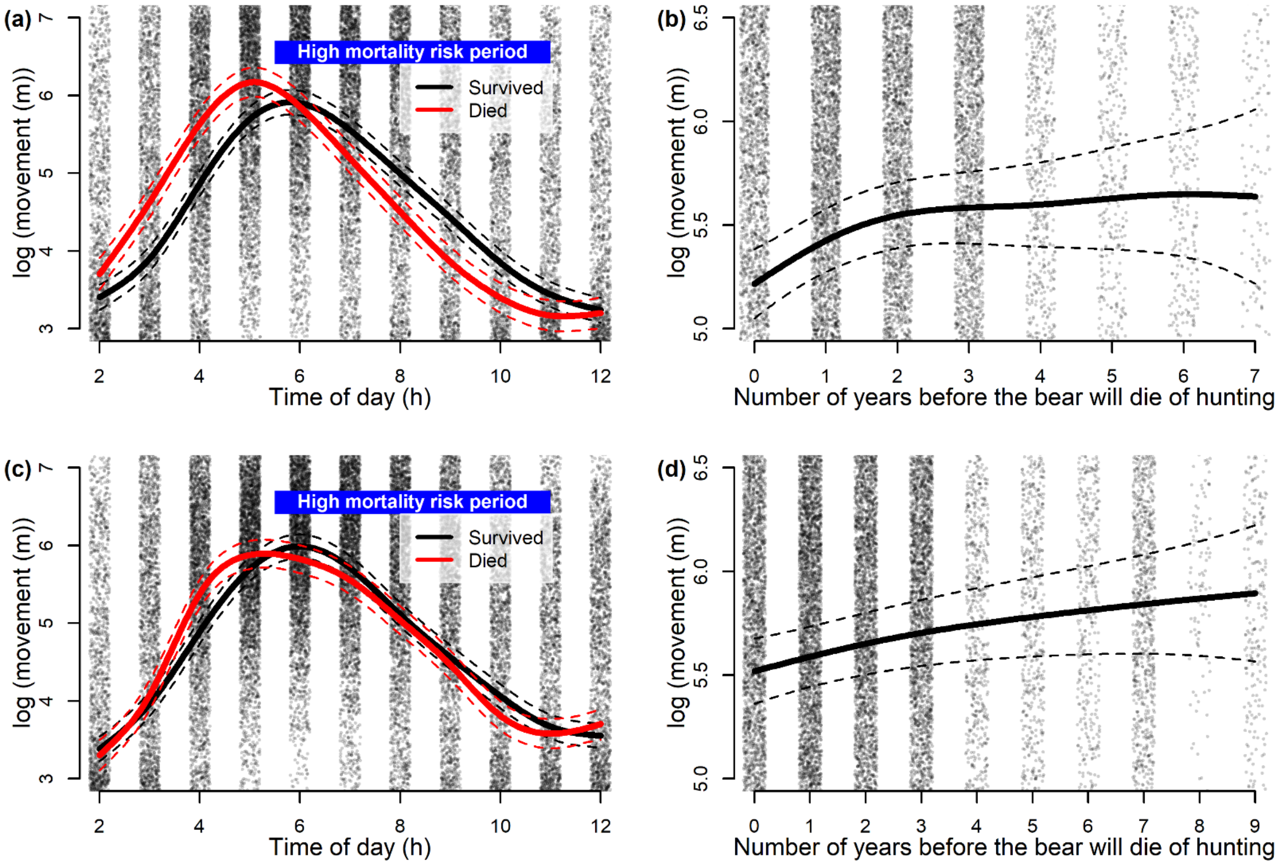

Figure 6.1 **Predicted (full line) variation and 95% CIs (dashed lines) in rates of movement (log-transformed) for the most parsimonious model tested for male and female brown bears in Sweden (2003-2016). Shown are the effect of the time of day (panel a, c) and the number of years a bear will live before dying of hunting (panel b, d) for males (panel a, b) and females (panel c, d).**

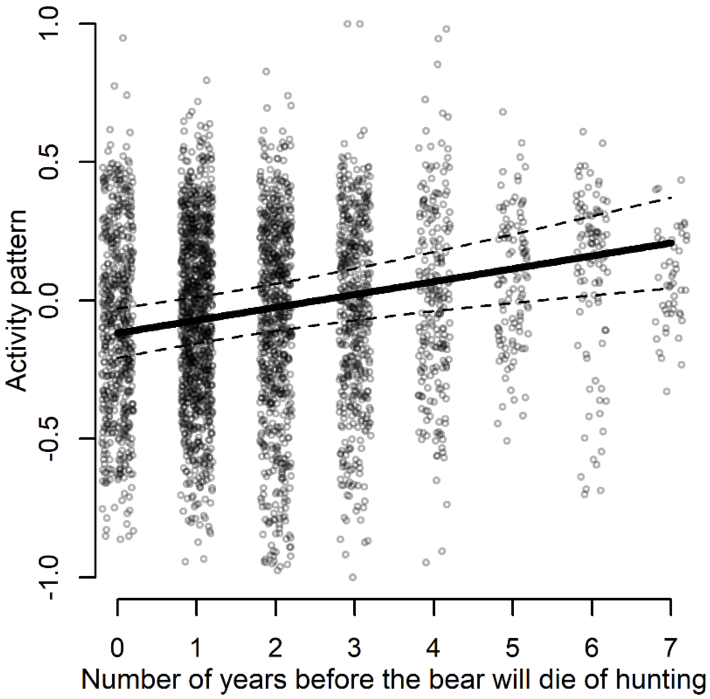

Figure 6.2 Predicted (full line) variation and 95% CIs (dashed lines) in male brown bear activity pattern from the most parsimonious model tested. Shown is the relationship between activity pattern and the number of years remaining before the bear will be harvested. Values of -1 and 1 indicates that all activity occurred during nonhunting and hunting hours, respectively.

that survived longer (more years to live before dying of hunting) had higher rates of movement, were more active during hunting hours, and remained farther away from roads. For females, we found similar effects for rates of movement and distance to roads, however, daily activity patterns were not related to vulnerability to hunting. Also, bears that survived a hunting season showed lower rates of movement before the legal hunting hours and higher rates of movement during the high mortality risk period compared to bears that had been killed during a hunting season. Consequently, we found only partial support for both our main and alternative hypotheses (Table 6.2).

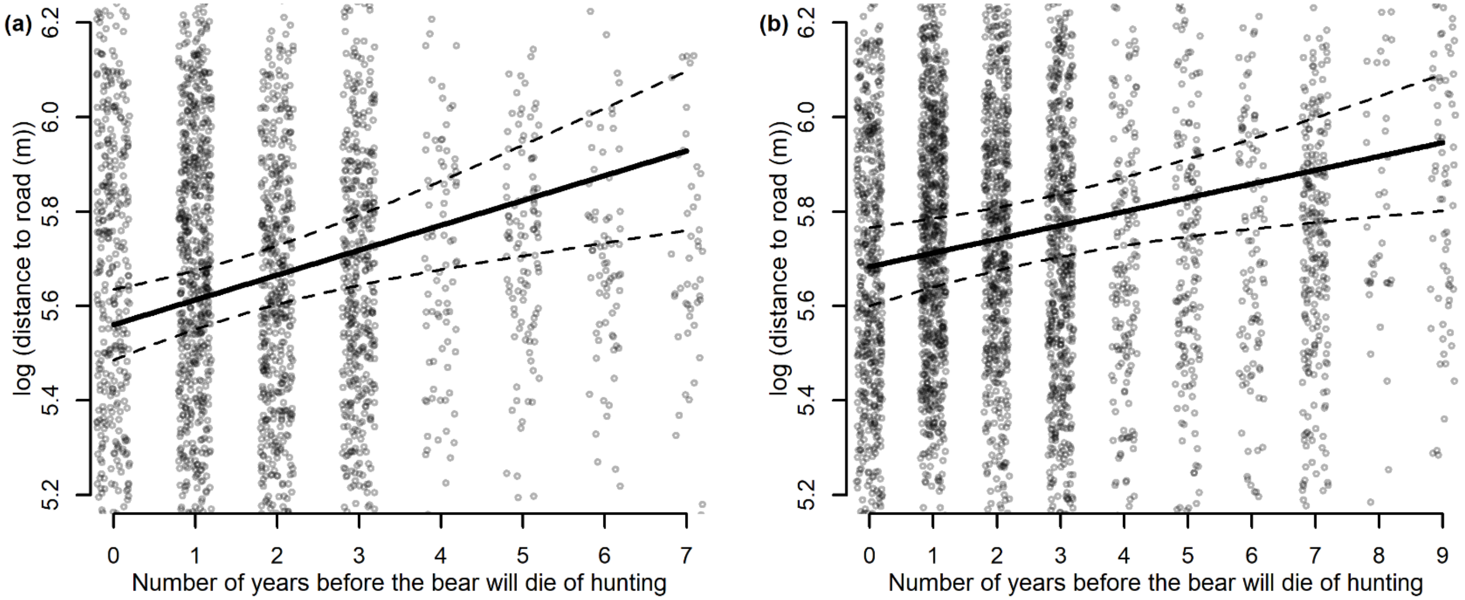

Figure 6.3 **Predicted (full line) variation and 95 % CIs (dashed lines) in the daily mean distance to roads in function of the number of years a bear will live before dying of hunting from the most parsimonious model tested for male (panel a) and female (panel b) brown bears in Sweden (2003-2016).**

Table 6.1 Coefficients (β) and their 95 % confidence intervals (C.I) of the most parsimonious model that explained variation in the daily mean distance to roads of male and female brown bears in Sweden (2003-2016).

	Male (*n* = 31)			Female (*n* = 35)		
Variable	B	Lower C.I.	Upper C.I.	β	Lower C.I.	Upper C.I.
Intercept	**6.265**	**5.871**	**6.658**	**6.118**	**5.812**	**6.424**
Home range road density*	**-0.706**	**-1.089**	**-0.323**	**-0.398**	**-0.669**	**-0.127**
Bear age	0.007	-0.008	0.021	-0.001	-0.014	0.012
Julian date**	**-0.001**	**-0.003**	**-0.000**	**-0.002**	**-0.003**	**-0.001**
Number of years to live	**0.053**	**0.023**	**0.082**	**0.029**	**0.009**	**0.050**
Hunting season fate (died)				-0.080	-0.164	0.005
Julian date × Hunting season fate (died)				-0.002	-0.005	0.002

* km of roads / km^2 ; ** where 0 = August 21, i.e. the start of the hunting season

Table 6.2 **Predictions tested to assess hunters' selection on behavioral traits in a heavily hunted brown bear population in Sweden (2003-2016).**

Hypotheses	Behaviors	Predictions	Predictions supported	
		Hunters harvest bear that:	Male	Female
Bear hunting in Sweden as analogous to active gear in fisheries	Movement	Have lower rates of movement	Partially	Partially
	Activity pattern	Are less active during hunting hours	Yes	No
	Distance to road	Are farther away from roads	No	No
Bear survival driven by the probability of encounter with a hunter	Movement	Have higher rates of movement	Partially	Partially
	Activity pattern	Are more active during hunting hours	No	No
	Distance to road	Are closer to roads	Yes	Yes

Based on studies from fisheries (Arlinghaus et al. 2017; Diaz Pauli and Sih 2017), we had expected that brown bear hunting, as practiced in Sweden during the study period, would be analogous to active fishing methods and thus should harvest shier individuals. We predicted that shier individuals would have lower movement, be less active during hunting hours, and be farther away from roads compared to bolder individuals. Our results, however, suggested mixed support for those predictions (Table 6.2). Our alternative hypothesis, i.e., the probability of a bear to be harvested is mainly driven by the probability to encounter a hunter, was also partially supported (Figure 6.3, Table 6.2). We acknowledge that predicting harvest-induced selection on behavior is complex, as it depends on the interplay between human behavior, the harvest method used, and animal behaviors (Mysterud 2011; Frank et al. 2017). The framework outlined by Arlinghaus et al. (2017) and Diaz Pauli et al. (2017) accounts for the interplay between the harvest method and animal behavior. This framework could allow broader predictions if it also accounted for human behavior (Rivrud et al. 2014; Diekert et al. 2016). Therefore, we propose that every behavior that increases the encounter probability between an animal and a hunter or a fishing gear should be selected against. Once an animal is in the vicinity of a hunter or of fishing gear, bolder and shyer individuals should be harvested more often by passive or active harvest methods, respectively (Arlinghaus et al. 2017; Diaz Pauli and Sih 2017). More studies in both marine and terrestrial ecosystems are needed to test this updated framework and better understand the complex interactions at play in behavioral harvest-induced selection.

It is worth noting that in order to test predictions of harvest-induced selection on behavioral traits with the proposed framework, the behaviors from individuals must be correctly identified as “bold” or “shy”. However, this is not a trivial exercise. For instance, repeatable individual variation in habitat selection of bogs was shown in our population (Leclerc et al. 2016), but it would be tenuous to infer that one bear is bolder than another based on this behavior. To make comparison between studies more feasible and to develop more general predictions, we propose to use the behavior measured or predicted to be under selection, rather than an imprecise secondary term such as “boldness” (David and Dall 2016; Beekman and Jordan 2017).

Using one of the rare, long-term behavioral datasets from a harvested population, we showed that bears that had more years to live were found farther away from roads (Figure 6.3). A previous study in the same population also found a higher mortality risk in habitats closer to roads (Steyaert et al. 2016). Indeed, hunters can use the road network to move through the landscape more easily, thereby increasing the probability to detect a bear, which results in bears being harvested closer to roads. A similar pattern was found in Canada, where hunters preferentially killed brown bear and elk (Cervus elaphus) that were closer to roads (Nielsen et al. 2004; Ciuti et al. 2012). Contrary to our results, however, Ciuti et al. (2012) showed that elk that died from hunting had higher rates of movement than elk that survived. In their study systems, elk with higher rates of movement might have been more easily detected by hunters searching for them using binoculars and spotting scopes (Ciuti et al. 2012). In our study system, however, hunters commonly use dogs, which may explain why we obtained different results. We hypothesized that bears that were more active and had higher rates of movement may initiate the escape from hunting dogs more quickly, which increases bear survival probability, compared to bears that were more inactive and stationary. We also found evidence that hunting may disrupt the activity pattern of bears (Hertel et al. 2016). Indeed, bears become more day-active during hyperphagia, however, this trend stopped and even reversed with the onset of the hunting season (Figure S6.3-S6.4). Similar patterns were observed by Ordiz et al. (2012), who showed that bears are more active during the night after the onset of the hunting season. With advancing age, bears also tended to be more night active and have lower rates of movement (Figure S6.1-S6.4). Such behavioral plasticity within and among hunting seasons might not be adaptive, as bears that survived longer had higher rates of movement and were more day active.

Harvest-induced selection may result in evolution for heritable traits, as documented for life history and morphological traits (Heino et al. 2015; Pigeon et al. 2016). It is unknown if behavioral traits under harvest-induced selection are heritable, however, meta-analyses suggest that behaviors usually have a higher heritability than life history traits (Postma 2014; Dochtermann et al. 2015). Therefore, behavioral harvest-induced evolution could occur in our brown bear population. Even though harvest-induced selection and evolution has been documented and acknowledged by most researchers in marine ecosystems, a debate is still ongoing about hunting-induced selection and evolution in terrestrial ecosystems (Boyce and Krausman 2018; Van de Walle et al. 2018). Here we provide convincing empirical evidence that individual behavior can modulate vulnerability to hunting, based on predictions developed in fisheries. By better integrating the marine and terrestrial literature on harvest-induced selection and by developing collaborations, we should be able to better understand and quantify the full effects of human harvest on wild populations.

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CHAPITRE 7

BIAIS DANS LES DONNÉES DE CHASSE

Description de l'article et contribution

Les décisions de conservation et de gestion des espèces doivent être basées sur des données non biaisées. Il est cependant souvent difficile d'obtenir des données individuelles pour des populations sauvages. Certains chercheurs et gestionnaires utilisent donc les données obtenues lors de l'enregistrement d'animaux récoltés à la chasse. Ces données peuvent par contre représenter un échantillon non aléatoire de la population puisque la chasse elle-même est rarement aléatoire. Ainsi, l'utilisation de ces données pourrait mener à des conclusions biaisées. Dans cet article, j'ai comparé les tendances temporelles (1993-2013) des données du registre d'abattages de chasse à l'ours brun en Suède et les données du *Scandinavian Brown Bear Project* afin de quantifier les biais dans les données du registre d'abattages de chasse. Le déclin de la masse des femelles adultes et des oursons d'un an était sous-estimé par les données de chasse. Bien que les données de chasse puissent être une source d'information abondante pour plusieurs espèces, l'utilisation de ces données doit être faite avec précaution.

Pour cet article, j'ai construit la base de données avec l'aide de Joanie Van de Walle, j'ai effectué les analyses statistiques et écrit la première version du manuscrit. L'idée de cet article a été développée par Fanie Pelletier et tous les coauteurs ont participé aux multiples révisions du manuscrit.

Can hunting data be used to estimate unbiased population parameters? A case study on brown bears.

Biology Letters 12, 20160197

Martin Leclerc, Joanie Van de Walle, Andreas Zedrosser, Jon E. Swenson and Fanie Pelletier

Abstract

Quantifying temporal changes in harvested populations is critical for applied and fundamental research. Unbiased data are required to detect true changes in phenotypic distribution or population size. Because of the difficulty of collecting detailed individual data from wild populations, data from hunting records are often used. Hunting records, however, may not represent a random sample of a population. We aimed to detect and quantify potential bias in hunting records. We compared data from a long-term monitoring project with hunting records of brown bears (*Ursus arctos*) in Sweden and investigated temporal trends (1996–2013) in the ratio of yearlings to adult females, yearling mass, and adult female mass. Data from hunting records underestimated the decline in yearling and adult female mass over time, most likely due to the legal protection of family groups from hunting, but reflected changes in the ratio of yearlings to adult females more reliably. Although hunting data can be reliable to approximate population abundance in some circumstances, hunting data can represent a biased sample of a population and should be used with caution in management and conservation decisions.

Keywords: harvest, hunting regulation, temporal trends, Sweden, *Ursus arctos*.

Introduction

Unbiased sampling is required to detect changes in population size or age and sex structure. For example, information on individually marked animals can be used to estimate population trends. Such data, however, are not always available, due to the high costs and logistic difficulties of monitoring programs. Therefore, large datasets from hunting records are commonly used to obtain biological information (e.g. [1,2]). This practice has been criticized, because data from hunt-killed animals may be biased [3], because hunters almost always select individuals from populations non-randomly, selecting primarily adults, sometimes as large as possible. For example, Martínez et al. [4] showed that different hunting strategies select for different body masses in a red deer (*Cervus elaphus*) population. Pelletier et al. [5] showed that data from trophy-hunted bighorn sheep (*Ovis canadensis*) underestimated temporal declines in horn length. Festa-Bianchet et al. [6] showed with simulations that trophy record books underestimate increasing trends in horn length and do not detect declines in horn length. These biases, however, have mostly been reported for morphological traits targeted through trophy hunting (legal definition or preferences of hunters to shoot an animal based on a morphological trait) and may not exist under less selective hunting regimes [7].

Assessing the accuracy of hunting record data to estimate population parameters is difficult, as it requires a hunted population that is also the subject of intensive unbiased, longitudinal monitoring research, which is seldom the case [8]. To our knowledge, only two populations fulfill these requirements: bighorn sheep in Canada (trophy hunting) and brown bears (*Ursus arctos*) in Scandinavia. We used data from the individual-based, long-term monitoring by the Scandinavian Brown Bear Research Project (SBBRP), which captured and marked approximately 80% of the females bear in the study area, and data from hunting records in the same area in Sweden. We aimed to compare temporal trends from both datasets to explore and quantify biases in hunting records. We focused our analyses on proxies of recruitment and individual condition commonly used by managers to assess population performance [9]: ratio of yearlings to adult females, yearling mass, and adult female mass. Trophy hunting for bears is rare in Sweden and hunting mortality rates are similar between sex- and age-classes

[10,11]. However, family groups (females with dependent offspring) are legally protected from hunting [11] and might cause a non-random sampling of the killed individuals, as heavier females might reproduce more than lighter females. Therefore, hunting records might be biased, causing differences in temporal trends between the monitored bears and hunting records.

Methods

We used data collected by the SBBRP in south-central Sweden (Dalarna and Gävleborg counties). The main method of the SBBRP is to capture, mark, and weigh mothers and their yearling offspring after den emergence in spring, and to follow these individuals as long as possible, preferably for life (50–80% of females are marked in the study area). Marked adult females are recaptured and weighed every 2–3 years, depending on their reproductive status. Young bears can be hunted after weaning in June–July (either as yearlings (79% of litters) or 2-year-olds [12]). See Appendix 7A for further details on capture and monitoring.

Bears are hunted during autumn in Sweden. The hunting season ends when the quota is reached, but there is no limit on the number of bears that an individual hunter can kill [11]. Hunters are required to report all bear carcasses for a compulsory inspection on the day of kill to record the bear's sex and body mass [11]. A premolar is extracted for age determination [11]. We used data from bears shot in Dalarna and Gävleborg counties from 1996 to 2013 to spatiotemporally match data from monitored bears (see Figure S7.1).

We calculated annual ratios of yearlings to adult females (≥ 4 years old [13]) and used generalized linear models with binomial error distribution to assess differences in the temporal trend between hunting and monitoring datasets. We used linear models to test the temporal trend for yearling mass and included sex as a covariate to account for sexual dimorphism [14]. Yearling mass was log-transformed to fulfill statistical assumptions. We scaled (mean=0, variance=1) the mass of monitored and hunter-killed bears separately to account for the fact that these measures were taken in spring and autumn, respectively. The initial models included 'Year' and the interaction between 'Year' and bear 'Status' (monitored or hunter-killed) to test for different temporal trends between datasets (see Table 7.1 for model descriptions).

To evaluate temporal trends in adult female mass, the analyses of hunter-killed and monitored bears were performed separately, because monitored females were measured repeatedly, unlike hunter-killed females. Adult female mass in both datasets was scaled to facilitate comparison of model slopes. We used linear models to evaluate trends in the mass of hunter-killed adult females and linear mixed models (random intercept: female identity) for monitored females. The initial models (Table 7.1) included 'Year', 'Age', and 'Age^2' to test for non-linear effects of age. All statistical analyses were performed using backward selection to remove non-significant effects [15] with R 3.2.2 [16].

Results

Hunting records included 108 yearlings and 157 adult females, and the monitoring data included 266 yearlings and 82 adult females weighed between 1–6 times, for a total of 205 body masses (Table S7.1). We found a decline in the ratio of yearlings to adult females over time in both the monitoring dataset and the hunting records (Table 7.1A, Figure 7.1A). However, this ratio was significantly lower in the hunting records (Table 7.1A). Body mass of monitored and hunter-killed yearlings decreased significantly over time (Table 7.1B, Figure 7.1B), but the mass of hunter-killed yearlings declined at a significantly slower rate than the mass of monitored yearlings (Table 7.1B). From 1996 to 2013, the mean mass of monitored and hunter-killed yearlings decreased by 43% (12.5 kg) and 17% (10.2 kg), respectively (Figure S7.2). The mass of hunter-killed adult females showed no temporal trend, but declined significantly over time for monitored bears (Table 7.1C and 7.1D, Figure 7.1C). From 1996 to 2013, the mean monitored mass of adult females decreased by 23% (22.6 kg; Figure S7.3).

Table 7.1 Final models obtained by backward selection to compare hunting records and monitoring data of brown bears in Sweden, 1996-2013. Response variables are: ratio of yearlings to adult females (A), scaled log-yearling mass (B), and scaled adult female mass (C and D).

Variable	Coefficient	SE	Statistic	*P*-values
(A) Ratio of yearlings [Mc Fadden R^2=14.8%]			*z*-value	
Intercept	96.069	32.353	2.97	0.003
Year	-0.048	0.016	-2.96	0.003
Status hunter-killed	-0.493	0.163	-3.02	0.003
Variables removed: Year × Status (*P-value* = 0.31)				
(B) Yearling mass [R^2 = 21.4%]			*t*-value	
Intercept	221.5	23.30	9.50	<0.001
Sex male	0.312	0.092	3.40	0.001
Status hunter-killed	-132.6	43.60	-3.04	0.003
Year	-0.111	0.012	-9.51	<0.001
Year × Status hunter-killed	0.066	0.022	3.05	0.002
Variables removed: None				
(C) Hunter-killed adult female mass [R^2 = 11.1%]			*t*-value	
Intercept	-0.749	0.175	-4.29	<0.001
Age	0.091	0.019	4.75	<0.001
Variables removed: Age^2 (*P-value = 0.77*) and Year (*P-value* = 0.21)				
(D) Monitored adult female mass [R^2= 50.0%]			*t*-value	
Intercept	158	23	6.89	<0.001
Age	0.244	0.045	5.38	<0.001
Age^2	-0.006	0.002	-2.89	0.004
Year	-0.079	0.011	-6.95	<0.001
Variables removed: None				

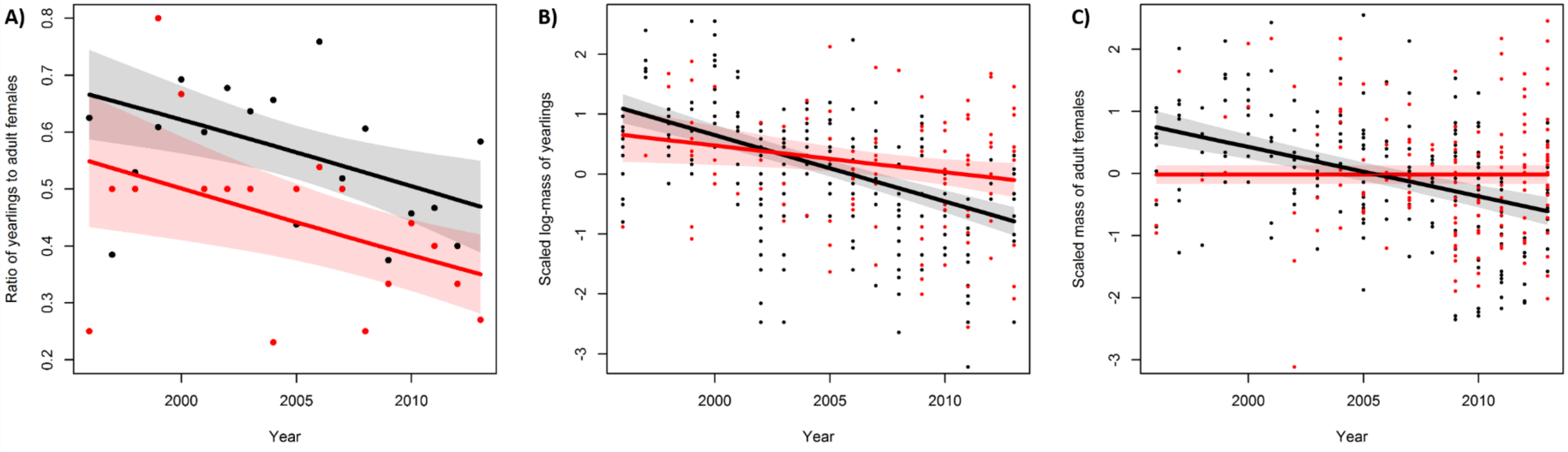

Figure 7.1 Predictions (solid line) and 95% confidence intervals from the final models comparing data from hunting records (red line) with monitored bears (black line) in the ratio of yearlings to adult females (A), scaled log-yearling mass (B; prediction for male), and scaled adult female mass (C; prediction for 8 year old female) in Sweden, 1996-2013. See methods for information on scaling procedure.

Discussion

We showed that hunting data can differ significantly from monitoring data. Although temporal trends in bear hunting records and monitored data were similar in direction in 2/3 of the cases and proved reliable when evaluating a decline in the ratio of yearlings to adult females, they underestimated the decline in yearling and adult female mass observed in the monitoring data.Although datasets were recorded at different times of the year (but see Figure S7.4 and Appendix 7C), differences between the datasets likely reflected bias caused by hunting regulations and ongoing ecological changes. Bear population density has increased during the study period [17]. Density-dependent factors (e.g. food availability [18]) might explain the decline of mass of yearlings and adult females in the monitoring dataset (Figure 7.1). The temporal trends observed in the hunting data, however, did not always match the pattern observed in the monitoring data. In Sweden, all bears can be shot legally, except family groups [11], which may have skewed the hunting data. As yearlings of low mass are more likely to stay with their mother for a second year [12], an under-representation of yearlings of low mass would be expected in the hunting data. Similarly, small adult females might have a lower probability of weaning their offspring as yearlings [12,14]. Therefore, small females might be less available to hunters. Hunting data showed a consistent bias over time in the ratio of yearlings to adult females, which could be explained by an approximately 10% yearling mortality that occurs during summer [10]. In recent years, weaning age has increased, with fewer offspring weaned as yearlings and a higher proportion weaned as 2.5 year olds (SBBRP, unpublished data). This leads to a reduction in the ratio of yearlings in both datasets. However, as both the offspring and mother in a family group are protected from hunting, longer maternal care also implies a lower number of adult females available to hunt, which should prevent further bias in the yearling/female ratio.

Obtaining accurate information on population parameters is critical to establish management plans that ensure sustainable exploitation of wild species. Depending on the hunting system and population parameter studied, the use of hunting records can sometimes be reliable [9,19]. However, our results showed that hunting records should be used cautiously when quantifying fluctuations in individual condition and population recruitment. To ensure that observed trends reflect true population processes, bias should be estimated [20] whenever possible. This could be achieved through a parallel longitudinal monitoring of a subsample of the population. If such monitoring is not possible, simulations based on hunting data could be useful to evaluate if hunting data can detect changes in population trends and parameters (e.g. [6]) and be used in management and conservation decisions.

Data accessibility

The datasets supporting this article have been uploaded as part of the supplementary material.

Competing interests

We have no competing interests.

Ethical statement

All captures and handling were approved by the appropriate authority and ethical committee Swedish Board of Agriculture (#35-846/03, 31-7885/07, 31-11102/12), Uppsala Ethical Committee on Animal Experiments (# C40/3, C47/9, C7/12), and Swedish Environmental Protection Agency (#412-7327-09 Nv)

Authors' contributions

ML, JVdW, and FP developed the idea and all authors participated in the study design. ML carried out statistical analyses. All authors wrote the manuscript and agreed to be held accountable for the content therein and approved the final version of the manuscript. JES and AZ coordinated the SBBRP.

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CHAPITRE 8

DISCUSSION GENERALE ET CONCLUSION

Résumé

Dans cette thèse, j'ai exploré les effets écologiques et évolutifs de la chasse chez l'ours brun scandinave, un carnivore solitaire. Mes analyses ont principalement porté sur les traits comportementaux. Les effets écologiques et évolutifs de la chasse sur les traits comportementaux sont peu documentés dans la littérature scientifique ajoutant une valeur particulière à cette thèse. Ceci est possiblement dû au fait que les traits comportementaux ont souvent un effet moins direct sur le taux de croissance de la population que, par exemple, les traits d'histoire de vie. Néanmoins, les résultats obtenus montrent que la chasse peut induire des effets écologiques comportementaux et réduire la survie des juvéniles même si ces derniers ne sont pas la cible des chasseurs. En effet, dans le deuxième chapitre, j'ai montré que la survie des oursons augmentait avec la distance au mâle tué le plus près (Gosselin *et al.*, 2017). Cette relation était obtenue seulement pendant la période de reproduction, ce qui était attendu selon l'hypothèse de l'infanticide sexuellement sélectionné (Hrdy, 1979; Steyaert *et al.*, 2014). Mes résultats soulignent également l'importance de la distribution spatiale des sites d'abattages de mâles à la chasse, puisque la survie juvénile était réduite dans un rayon d'environ 40 kilomètres autour de ceux-ci (Gosselin *et al.*, 2017). Cette étude est l'une des rares et, selon moi, la plus robuste dans la littérature, qui montrent un lien clair entre la chasse et l'augmentation de la fréquence de l'infanticide sexuellement sélectionné (voir également Loveridge *et al.*, 2016).

Dans le troisième chapitre de cette thèse, j'ai documenté la restructuration spatiotemporelle des domaines vitaux suite à la récolte d'un mâle (Leclerc *et al.*, 2017a). Cette restructuration est considérée comme l'un des mécanismes pouvant expliquer le lien entre la chasse et l'augmentation de l'infanticide sexuellement sélectionné. Mes résultats montrent que les mâles adultes résidents augmentaient leur utilisation du domaine vital d'un ours tué à la chasse, mais seulement deux ans après la mort de ce dernier (Leclerc *et al.*, 2017a; Frank *et al.*, 2018). Ce délai de deux ans coïncide également avec les résultats obtenus sur la survie juvénile dans le deuxième chapitre. En effet, la survie des oursons était influencée par la distance au mâle tué le plus près deux ans auparavant (Gosselin *et al.*, 2017). La restructuration spatiotemporelle des domaines vitaux de mâles variait également en fonction de l'âge des ours, de la densité de la population et de l'intensité de la chasse (Leclerc *et al.*, 2017a). Les résultats obtenus dans les chapitres deux et trois de cette thèse soulignent l'importance d'étudier les effets écologiques comportementaux de la récolte sur plusieurs années. De plus, une étude dans la même population a montré que l'infanticide sexuellement sélectionné peut expliquer jusqu'à 13,6% du taux de croissance de la population (Gosselin *et al.*, 2015). Mises ensemble, ces études montrent qu'il est impératif de quantifier et de prendre en considération les effets écologiques comportementaux induits par la chasse dans les plans de gestion, car ceux-ci peuvent ultimement influencer la viabilité des populations exploitées.

Dans la seconde partie de cette thèse, j'ai vérifié deux des trois prémisses de l'évolution par sélection naturelle, soit la variabilité et la sélection. Dans le quatrième chapitre, j'ai quantifié, à ma connaissance, pour la première fois, la répétabilité du comportement de sélection d'habitat (Leclerc *et al.*, 2016a). La variabilité comportementale est un domaine de l'écologie en pleine croissance depuis le début des années 2000 et plusieurs articles scientifiques ont montré des différences individuelles pour différents comportements (Bell *et al.*, 2009; Réale *et al.*, 2010). Il n'existait cependant aucune étude quantifiant la variabilité comportementale en sélection d'habitat. En effet, l'étude de la sélection d'habitat est souvent effectuée à l'échelle de la population, omettant la variabilité interindividuelle. Cependant, dans une optique où la sélection naturelle ou artificielle agit sur le phénotype d'un individu, il est important de vérifier s'il existe des différences interindividuelles. Dans ce chapitre, j'ai quantifié la variabilité comportementale interannuelle et obtenu une répétabilité de 30,4% et de 42,0% pour la sélection des tourbières et des coupes forestières chez l'ours brun (Leclerc *et al.*, 2016a). Ainsi, je montre qu'il existe de la variabilité en sélection d'habitat des ours sur laquelle des pressions sélectives peuvent agir.

Dans les chapitres cinq et six de cette thèse, j'ai documenté les effets sélectifs de la récolte sur le comportement. Dans la littérature scientifique, je n'ai répertorié que sept études expérimentales et six études en milieu naturel qui montrent que la récolte peut agir comme pression sélective sur le comportement (Leclerc *et al.*, 2017b). Il est intéressant de constater, cependant, que ces études sont effectuées sur plusieurs espèces animales, par différents engins ou techniques de récolte, tant en milieux marins qu'en milieux terrestres. Cela suggère que les pressions sélectives comportementales induites par la récolte pourraient être présentes pour la majorité des formes d'exploitations de la faune, même si, à ce jour, les évidences sont rares. J'ai ensuite montré, dans le sixième chapitre, que la chasse applique une pression sélective sur le comportement des ours bruns en Suède. En effet, certains comportements, tels que la vitesse de déplacement, variaient entre les individus qui étaient récoltés et les individus qui survivaient à une saison de chasse. Ces deux chapitres montrent que la pêche et la chasse peuvent agir comme des pressions sélectives sur le comportement des populations exploitées.

Finalement, dans le septième chapitre, j'ai quantifié les biais retrouvés dans un registre d'abattages de la faune. Les données présentes dans les registres d'abattages de la faune sont souvent utilisées par les gestionnaires. En effet, dans le système de gestion actuel, les ressources financières sont limitées et peu de populations exploitées font l'objet d'un suivi intensif. Ainsi, les données de registres d'abattages représentent souvent une des rares sources d'informations disponibles pour évaluer la condition des individus ou la démographie de la population. Ces données peuvent cependant être biaisées puisque la récolte animale est rarement un processus aléatoire. Dans ce chapitre, j'ai utilisé les données du registre d'abattages de chasse à l'ours brun en Suède que j'ai comparé aux données du *Scandinavian Brown Bear Project*. Ainsi, j'ai montré que les données du registre d'abattages de chasse de 1996 à 2013 sous-évaluaient le déclin de la masse des femelles adultes et des oursons d'un an de 23% et 26%, respectivement (Leclerc *et al.*, 2016b). Les données dans les registres d'abattages semblent donc être inefficaces pour capturer pleinement les tendances observées à l'échelle populationnelle (Festa-Bianchet *et al.*, 2015; Pelletier *et al.*, 2012). Ces données devraient donc être utilisées de manière prudente dans les décisions de gestion et de conservation.

Comment réduire les effets de la récolte?

Dans cette thèse, j'ai documenté les effets écologiques et évolutifs de la récolte chez une population d'ours brun scandinave. Avec ces nouvelles connaissances, il serait intéressant de concrétiser des actions afin de réduire les effets de la récolte. Je propose ici quelques pistes de solutions qui pourraient s'appliquer à la population étudiée dans cette thèse, mais également à plusieurs autres systèmes où la récolte a des effets écologiques et évolutifs.

En réponse aux résultats obtenus au chapitre sept, il s'avèrerait pertinent de mettre en place des programmes de recherche à long terme pour plusieurs populations exploitées. Ces programmes permettraient d'étudier les effets écologiques et évolutifs de la récolte et de comparer la direction et la force de la sélection induite par la récolte à la sélection naturelle (Conover, 2007; Olsen et Moland, 2011). Le déploiement de ces programmes de recherche serait par contre une tâche assez complexe qui demanderait beaucoup de temps et des sommes financières considérables. Bien que ces programmes de recherche soient dispendieux, je crois que l'on doit continuer d'étudier les effets de la récolte afin d'affiner nos connaissances et ultimement mieux informer les gestionnaires de la faune. D'autres mesures de mitigation moins onéreuses pourraient être mises en place plus rapidement. Par exemple, la réduction des quotas alloués devrait permettre de réduire les effets écologiques de la récolte et la force des pressions sélectives induites par la récolte (Kuparinen et Festa-Bianchet, 2017; Kuparinen et Merilä, 2007). La mise en place d'aires protégées où la récolte est interdite permettrait également la réduction des effets de la récolte sur les populations sauvages (Halpern et Warner, 2002). Lorsque la conception des aires protégées est adéquate (Dunlop *et al.*, 2009; Gaines *et al.*, 2010), elles peuvent conserver la biodiversité, agir comme réservoirs de diversité génétique pour les populations exploitées et permettent même d'augmenter le taux de récolte à l'extérieur de leurs limites (Dunlop *et al.*, 2009; Gaines *et al.*, 2010). Les résultats du cinquième chapitre suggèrent également que l'on pourrait faire varier les méthodes de récolte d'une année à l'autre afin de faire varier la direction des pressions sélectives. Les mesures de mitigation possibles sont multiples, mais l'essentiel est que les connaissances acquises sur les effets de la récolte doivent parvenir aux gestionnaires qui pourront alors déterminer ce qui s'applique le mieux à leur système de récolte. En effet, l'intégration des effets écologiques et évolutifs de la récolte dans les plans de gestion et de conservation est centrale afin de réaliser une récolte pérenne (Allendorf *et al.*, 2008; Conover et Munch, 2002).

Quelques pistes de réflexions et travaux futurs

Pendant mes années de doctorat, j'ai eu l'occasion de présenter certains de mes résultats lors de conférences nationales et internationales, tel qu'en 2016, où j'ai présenté les résultats de mon deuxième chapitre à Anchorage, en Alaska. Suite aux questions et aux commentaires obtenus, j'ai constaté certaines tensions au sujet de l'infanticide sexuellement sélectionné. En effet, plusieurs chercheurs débattent de l'existence de l'infanticide sexuellement sélectionné chez l'ours brun et de l'augmentation de la fréquence de ce comportement en présence de chasse. Je crois qu'il est toujours important de questionner et d'apporter un regard critique sur une méthode ou un résultat scientifique. Cette réflexion est le propre de la science et de sa pertinence. Cependant, avec les nombreuses évidences (parfois indirectes) présentes dans la littérature, principalement issue de la population d'ours brun scandinave, il devrait être généralement accepté qu'il existe de l'infanticide sexuellement sélectionné chez l'ours brun et que la chasse peut en augmenter la fréquence (Frank *et al.*, 2017; Gosselin *et al.*, 2017; Steyaert *et al.*, 2012, 2013; Swenson *et al.*, 1997). Ceci étant dit, il est possible que ce comportement ne survienne pas dans certaines populations d'ours brun (McLellan, 2005, 2015). Dans ce cas, il serait fort intéressant de comprendre les facteurs qui modulent la presence ou non de l'infanticide sexuellement sélectionné dans une population, par exemple:

la densité et le sexe-ratio de la population, le dimorphisme sexuel et la durée des soins maternels. Ainsi, il serait possible d'avoir une vision plus holistique de l'infanticide sexuellement sélectionné et des conséquences écologiques de la chasse et permettraient également de décloisonner le débat actuel qui est très dichotomique.

J'ai documenté que la chasse sportive cause une pression sélective sur le comportement des ours en Suède. Cette pression sélective pourrait ultimement causer de l'évolution pour les comportements qui sont héritables. Nous ne savons pas, jusqu'à présent, si les comportements sous sélection des chasseurs sont héritables dans la population d'ours étudiée. Un pedigree de la population a été réalisé en 2016, mais le pouvoir statistique pour détecter de l'héritabilité comportementale est, pour l'instant, limité (Figure 8.1). En effet, des informations comportementales et génétiques sont disponibles uniquement pour 131 individus, dont 23 qui ne sont pas reliés au pedigree. De plus, peu de liens d'apparentement sont observés entre les 108 individus qui sont reliés dans le pedigree (moyenne d'apparentement génétique = 0,029). Bien que je n'ai pas quantifié l'héritabilité des comportements sous sélections dans cette thèse, j'ai quantifié la répétabilité de la sélection d'habitat dans le quatrième chapitre. Sachant que la valeur de la répétabilité d'un trait phénotypique est considérée comme la valeur maximale possible de l'héritabilité de ce trait (Falconer et Mackay, 1996), nos résultats suggèrent donc que le comportement de sélection d'habitat pourrait être en partie héritable. De plus, de récentes méta-analyses dénotent que les traits comportementaux sont héritables et souvent davantage que les traits d'histoire de vie (Dochtermann *et al.*, 2015; Postma, 2014). Par conséquent, il peut être envisageable qu'il y ait de l'évolution comportementale induite par la récolte dans la population d'ours brun étudiée dans cette thèse. Quoique spéculatif, des boucles de rétroaction écoévolutives (Hendry, 2016; Pelletier *et al.*, 2009) pourraient également être plausibles. En effet, une évolution vers des individus ayant un plus haut taux de déplacement pourrait potentiellement se solder en une population ayant une fréquence plus élevée d'infanticide sexuellement sélectionné, puisque des mâles se déplaçant davantage seraient possiblement plus enclins à rencontrer de nouvelles femelles pendant la période de reproduction. Quoi qu'il en soit, la chasse est une pression sélective importante dans la population d'ours brun scandinave autant

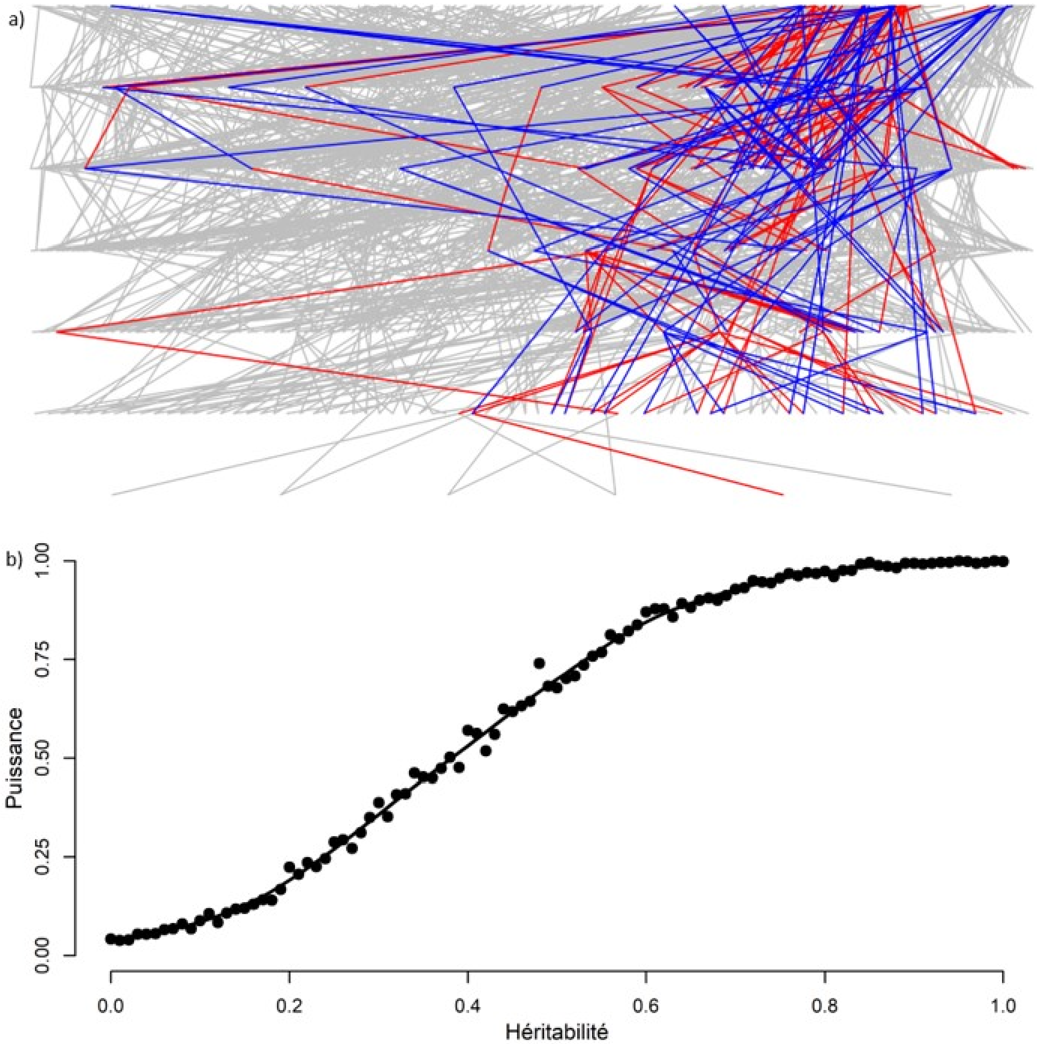

Figure 8.1 **Pedigree de la population d’ours brun scandinave (panneau a). Les liens maternels et paternels sont en bleus et en rouges, respectivement. Les liens en gris nous informent des liens maternels ou paternels entre les individus qui ne sont pas munis de collier GPS. Puissance du pedigree pour divers niveaux d’héritabilité (panneau b) selon des simulations de différent phénotypes basé à partir des liens d’apparentement observés dans le pedigree (voir la fonction « phensim » de la librairie « pedantics » du programme R 3.4.1).**

sur les traits comportementaux que les traits d'histoire de vie. Des études récentes montrent que la chasse a perturbé les relations entre la survie des individus et les facteurs environnementaux et a remodelé les bénéfices de différentes stratégies d'histoire de vie en sélectionnant pour des soins maternels plus longs (Bischof *et al.*, 2018; Van de Walle *et al.*, 2018). Quantifier l'héritabilité et l'évolution des traits phénotypiques et les possibles boucles de rétroaction écoévolutives dans cette population sont les prochaines étapes afin d'approfondir nos connaissances sur les effets évolutifs de la chasse.

Dans cette thèse, j'ai également essayé de favoriser les collaborations entre certains domaines d'études. En effet, dans le quatrième chapitre, en plus de quantifier la variabilité comportementale en sélection d'habitat, j'ai tenté de réduire les différences terminologiques en montrant les similitudes lexicales entre le domaine de la sélection d'habitat et de la variabilité comportementale. Cet article s'est positionné de manière opportune dans la littérature, alors que de nombreuses recherches se sont également intéressées au même sujet quelque temps après (Gaudry *et al.*, 2018; Spiegel *et al.*, 2017; Webber et Vander Wal, 2018). Considérant l'importance de la variabilité intra- et interindividuelle en sélection d'habitat pour l'écologie, l'évolution, mais également les programmes de conservation et de gestion, il y a fort à parier que le mouvement vers des études plus approfondies de la variabilité en sélection d'habitat va se poursuivre. Ensuite, dans le cinquième chapitre, j'ai explicitement formulé le souhait d'une approche collaborative entre le monde terrestre et le monde marin pour l'étude des effets sélectifs et évolutifs de la récolte (voir par exemple Kuparinen et Festa-Bianchet, 2017). Dans le sixième chapitre, j'ai prêché par l'exemple et testé des prédictions émises en milieu marin chez un grand carnivore en milieu terrestre. Les résultats obtenus m'ont permis de proposer un ajustement à un modèle conceptuel développé récemment afin de prédire la direction des pressions sélectives induites par la récolte sur le comportement. Sachant que les écosystèmes marins et terrestres sont fortement reliés entre eux (Gounand *et al.*, 2018; Soininen *et al.*, 2015), il serait intéressant de vérifier si les effets écologiques et évolutifs induits par la récolte en milieu marin peuvent se répercuter en des effets sur les milieux terrestres, ou l'inverse. Cette thèse est donc également un plaidoyer pour favoriser les collaborations entre des chercheurs de différents domaines afin de résulter en une vision holistique des effets anthropiques sur la faune.

Avant de conclure, j'aimerais apporter une réflexion sur la chasse sportive. Bien que l'Homme chasse depuis des millénaires (Sullivan *et al.*, 2017; Wilkins *et al.*, 2012), un mouvement social anti-chasse est présent et s'exprime de manière plus importante depuis quelques décennies. De Brigitte Bardot et Paul McCartney pour la protection des phoques (*Phoca groenlandica*) au tollé médiatique qu'a causé la mort de Cécil le lion au Zimbabwe en 2015 (Macdonald *et al.*, 2016), la société semble de plus en plus réfractaire à cette activité. Un autre exemple est l'interdiction récente de la chasse à l'ours brun en Colombie-Britannique en raison des pressions sociales, bien que le taux d'exploitation semblait être viable à long terme (Mclellan *et al.*, 2017). Cette décision politique a remis en question, pour certains, la gestion basée sur la science. Je crois cependant que le rôle de la science et des scientifiques dans le débat public est d'informer la société des conséquences des différentes options possibles et non de dicter les politiques à mettre en place (Darimont, 2017). Bien documenter les conséquences écologiques, évolutives et sociales (par exemple Angula *et al.*, 2018) de la chasse est donc primordial pour bien informer le débat public. Par conséquent, il est important de noter également que la chasse n'a pas que des effets négatifs sur les populations animales. En effet, lorsque bien encadrée (Brink *et al.*, 2016), la chasse peut améliorer la survie de certaines espèces (par exemple le Markhor (*Capra falconeri*); Michel et Rosen Michel, 2015) et même favoriser la biodiversité en général grâce à d'importants revenus qui sont réinvestis en conservation (Di Minin *et al.*, 2016). Ces exemples de bénéfices sont cependant souvent le résultat de la chasse au trophée et pourraient s'appliquer plus difficilement à d'autres modèles de chasse telle que la chasse de brousse. Quoi qu'il en soit, la chasse est une activité millénaire qui fait partie du développement des hominidés (McGuire et Hildebrandt, 2005; Sullivan *et al.*, 2017), mais dans un contexte où certaines alternatives sont envisageables, tel que l'écotourisme (Ripple *et al.*, 2016), nous devons nous questionner sur la valeur économique ajoutée et l'éthique des différentes formes et pratiques de cette activité.

Conclusion

Dans cette thèse, j'ai quantifié les effets écologiques et évolutifs de la chasse chez un grand carnivore. En utilisant une des rares bases de données à long terme d'une population chassée, j'ai montré que la chasse peut augmenter l'infanticide sexuellement sélectionné et agir comme pression sélective sur le comportement des ours bruns en Scandinavie. Ces connaissances pourront aider à affiner les stratégies de gestion et d'exploitation et, idéalement, permettre de mieux prévoir les effets des décisions prises par les gestionnaires. En effet, bien que la population d'ours brun scandinave ne soit pas menacée et que la taille de la population ait augmenté de 500 à 3000 individus au courant des 25 dernières années, il faut également souligner que les objectifs de gestion dans cette population sont rarement atteints (Swenson *et al.*, 2017).

De manière plus générale, cette thèse s'insère dans une optique où l'Homme perturbe de manière importante la biosphère et la lithosphère en plus de réduire la biodiversité planétaire (Dirzo *et al.*, 2014; Johnson et Munshi-South, 2017; Maxwell *et al.*, 2016; Ripple *et al.*, 2017; Steffen *et al.*, 2011; Sullivan *et al.*, 2017). Nous sommes maintenant au cœur de la sixième extinction massive, causée principalement par les activités anthropiques. Par conséquent, il est important de quantifier les conséquences des activités humaines sur l'écologie et l'évolution des espèces afin d'en minimiser les impacts. Il y va de la pérennité de la qualité de vie des populations humaines (Dirzo *et al.*, 2014; O'Bryan *et al.*, 2018).

ANNEXES

Annexes Chapitre 1

Annexe 1A: Liste des publications

Publications présentes dans cette thèse :

1. Gosselin, J., **Leclerc, M.,** Zedrosser, A., Steyaert, S.M.J.G., Swenson, J.E., and Pelletier, F. (2017). Hunting promotes sexual conflict in brown bears. J. Anim. Ecol. *86*, 35–42.
2. **Leclerc, M.,** Vander Wal, E., Zedrosser, A., Swenson, J.E., Kindberg, J., and Pelletier, F. (2016). Quantifying consistent individual differences in habitat selection. Oecologia *180*, 697–705.
3. **Leclerc, M.,** Van de Walle, J., Zedrosser, A., Swenson, J.E., and Pelletier, F. (2016). Can hunting data be used to estimate unbiased population parameters? A case study on brown bears. Biol. Lett. *12*, 20160197.
4. **Leclerc, M.,** Frank, S.C., Zedrosser, A., Swenson, J.E., and Pelletier, F. (2017). Hunting promotes spatial reorganization and sexually selected infanticide. Sci. Rep. *7*, 45222.
5. **Leclerc, M.,** Zedrosser, A., and Pelletier, F. (2017). Harvesting as a potential selective pressure on behavioural traits. J. Appl. Ecol. *54*, 1941–1945.

Manuscrit qui sera soumis pour publication et qui est présent dans cette thèse :

6. **Leclerc, M.,** Steyaert, S.M.J.G., Zedrosser, A., Swenson, J.E., and Pelletier, F. Hunter select for behavioral traits in a large carnivore. Sera soumis à Proceedings of the National Academy of Sciences of the U.S.A.

Publications qui ne sont pas incluses dans cette thèse et qui ont été effectuées dans le cadre de mes études doctorales :

7. Frank, S.C., Ordiz, A., Gosselin, J., Hertel, A., Kindberg, J., **Leclerc, M.,** Pelletier, F., Steyaert, S.M.J.G., Stoen, O.-G., Van de Walle, J., *et al.* (2017). Indirect effects of bear hunting: a review from Scandinavia. Ursus *28*, 150–164.
8. Frank, S.C., **Leclerc, M.,** Pelletier, F., Rosell, F., Swenson, J.E., Bischof, R., Kindberg, J., Eiken, H.G., Hagen, S.B., and Zedrosser, A. (2018). Sociodemographic factors modulate the spatial response of brown bears to vacancies created by hunting. J. Anim. Ecol. *87*, 247–258.
9. Steyaert, S.M.J.G., **Leclerc, M.,** Pelletier, F., Kindberg, J., Brunberg, S., Swenson, J.E., and Zedrosser, A. (2016). Human shields mediate sexual conflict in a top predator. Proc. R. Soc. B *283*, 20160906.
10. Steyaert, S.M.J.G., Zedrosser, A., Elfström, M., Ordiz, A., **Leclerc, M.,** Frank, S.C., Kindberg, J., Støen, O.-G., Brunberg, S., and Swenson, J.E. (2016). Ecological implications from spatial patterns in human-caused brown bear mortality. Wildlife Biol. *22*, 144–152.

Manuscrits qui seront soumis pour publication et qui ont été effectués dans le cadre de mes études doctorales :

11. Van de Walle, J., **Leclerc, M.,** Steyaert, S.M.J.G., Zedrosser, A., Swenson, J.E. and Pelletier, F. Spatial association with humans modulates the duration of maternal care in brown bear. Soumis à Ecology (ECY18-0533)
12. Hertel, A., **Leclerc, M.,** Warren, D., Pelletier, F., Zedrosser, A. and Mueller, T. Don't poke the bear: Using movement data to quantify behavioural syndromes in elusive wildlife. Une version révisée sera soumise de nouveau à Animal Behaviour.

Annexes Chapitre 2

Appendix 2A: Supplementary tables and figures

Table S2.1 Candidate models tested to determine the shape of the relationship (continuous or discontinuous with a breaking point) between distance to the closest killed male and litter before (*n* = 193), during (*n* = 185), and after (*n* = 125) the mating season in brown bears in Sweden during 1991-2011. All models are tested with Year and Female ID as random intercepts.

Model	Covariates
1	Distance of the closest killed male (km) + Food index[a] + Population density[a] + Age of female + Primiparity of female[b] + Litter size + Age of female × Primiparity of female[b]
2	Distance of the closest killed male when <10 km + Distance of the closest killed male when ≥10 km + Covariates model 1
3	Distance of the closest killed male when <15 km + Distance of the closest killed male when ≥15 km + Covariates model 1
4	Distance of the closest killed male when <20 km + Distance of the closest killed male when ≥20 km + Covariates model 1
5	Distance of the closest killed male when <25 km + Distance of the closest killed male when ≥25 km + Covariates model 1
6	Distance of the closest killed male when <30 km + Distance of the closest killed male when ≥30 km + Covariates model 1
7	Distance of the closest killed male when <35 km + Distance of the closest killed male when ≥35 km + Covariates model 1

8	Distance of the closest killed male when <40 km + Distance of the closest killed male when ≥40 km + Covariates model 1
9	Distance of the closest killed male when <45 km + Distance of the closest killed male when ≥45 km + Covariates model 1
10	Distance of the closest killed male when <50 km + Distance of the closest killed male when ≥50 km + Covariates model 1
11	Distance of the closest killed male when <55 km + Distance of the closest killed male when ≥55 km + Covariates model 1
12	Distance of the closest killed male when <60 km + Distance of the closest killed male when ≥60 km + Covariates model 1

[a] Scaled covariate where mean=0 and variance=1; [b] Primiparous or multiparous

Table S2.2 Candidate models tested to evaluate the effect of the number and timing of males killed during the hunting season, when distance to the closest killed male was < 25 km, on litter survival (*n* = 131) during the mating season in brown bears in Sweden during 1991-2011. Models are listed with their covariates, LogLikelihood (LL), number of parameters (K), difference in AICc to the most parsimonious model (ΔAICc) and model weight (ω_i).

Model	Covariates included	LL	K	ΔAICc	ω_i
A	Age of female + Primiparity of female[a] + Litter size + Age of female × Primiparity of female[a] + Distance to the closest killed male	-157.042	10	2.44	0.119
B	Model A + Timing[b]	-154.638	11	0.00	0.402
C	Model A + Number of killed males within 25 km	-155.399	11	1.52	0.188
D	Model B + Model C	-153.756	12	0.64	0.292

[a] Primiparous or multiparous, [b] closest male killed 0.5 or 1.5 years earlier

As all tested models were nested, we selected the model with the fewest parameters within ΔAICc < 2 of the top model (see methods for details). Therefore, we selected model B. Note that the coefficient of Timing = 1.5 years was -0.966 [-1.879 : -0.052]. Cub survival was 16.6% lower when the timing = 1.5 years earlier instead of 0.5 years earlier (prediction for multiparous female with litter size of 2 cubs and all numeric covariates fixed to the mean). Results obtained are similar to Swenson et al. 1997 *Nature,* 386, 450-451.

Please also note that the effect of the number of male killed (β= 0.210) in model D overlaps with 0 [CIs = -0.105 : 0.526].

Table S2.3 Candidate models tested to evaluate the effect of the number and timing of adult males killed, when the distance to the closest killed male was ≥ 25 km, on litter survival (*n* = 54) during the mating season in brown bears in Sweden during 1991-2011. Models are listed with their covariates, LogLikelihood (LL), number of parameters (K), difference in AICc to the most parsimonious model (ΔAICc) and model weight (ω_i).

Model	Covariates included	LL	K	ΔAICc	ω_i
A	Age of female + Primiparity of female[a] + Litter size + Age of female × Primiparity of female[a] + Distance to the closest killed male	-32.17	10	0.00	0.946
B	Model A + Timing	-34.16	11	7.10	0.027
C	Model A + Number of killed males within 25 km	-34.91	11	8.59	0.013
D	Model B + Model C	-33.25	12	8.52	0.013

[a] Primiparous or multiparous, [b] closest male killed 0.5 or 1.5 years earlier

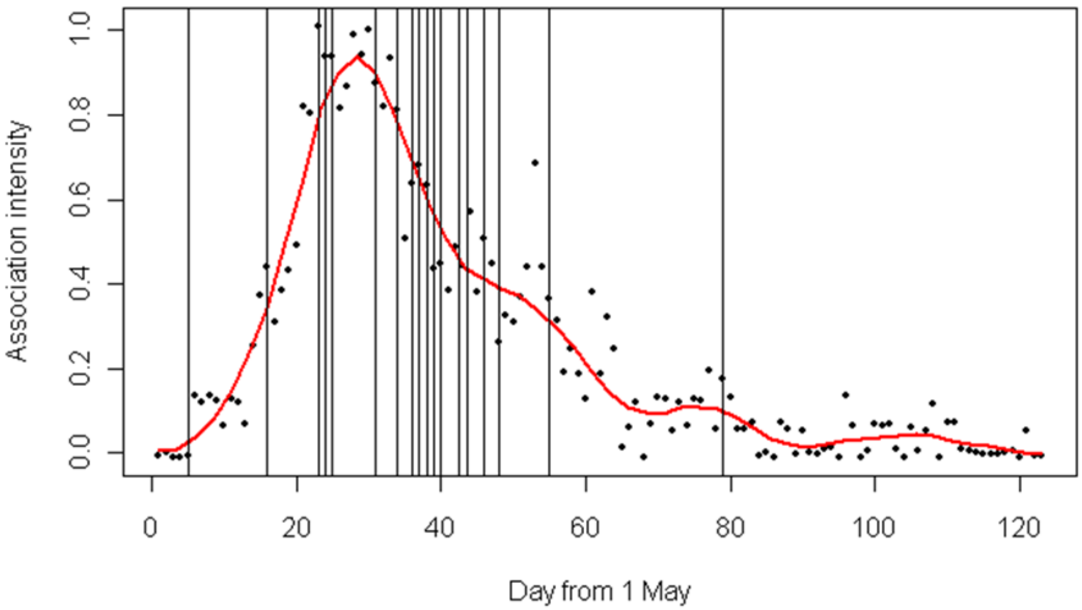

Figure S2.1 **Infanticide cases and attempts (vertical lines) in relation to the intensity of the mating season (red smoother). Black dots represent specific pairs of GPS marked adult male and female brown bears observed concurrently within 30 m of each other during a specific day in our study area in central Sweden (2008-2011). We scaled the observed number of male-female associations per day between 0 and 1 to calculate a relative 'association intensity', which we consider as a proxy for mating season intensity. Data from the infanticide cases were obtained from Steyaert (2012) and Bellemain, Swenson and Taberlet (2006).**

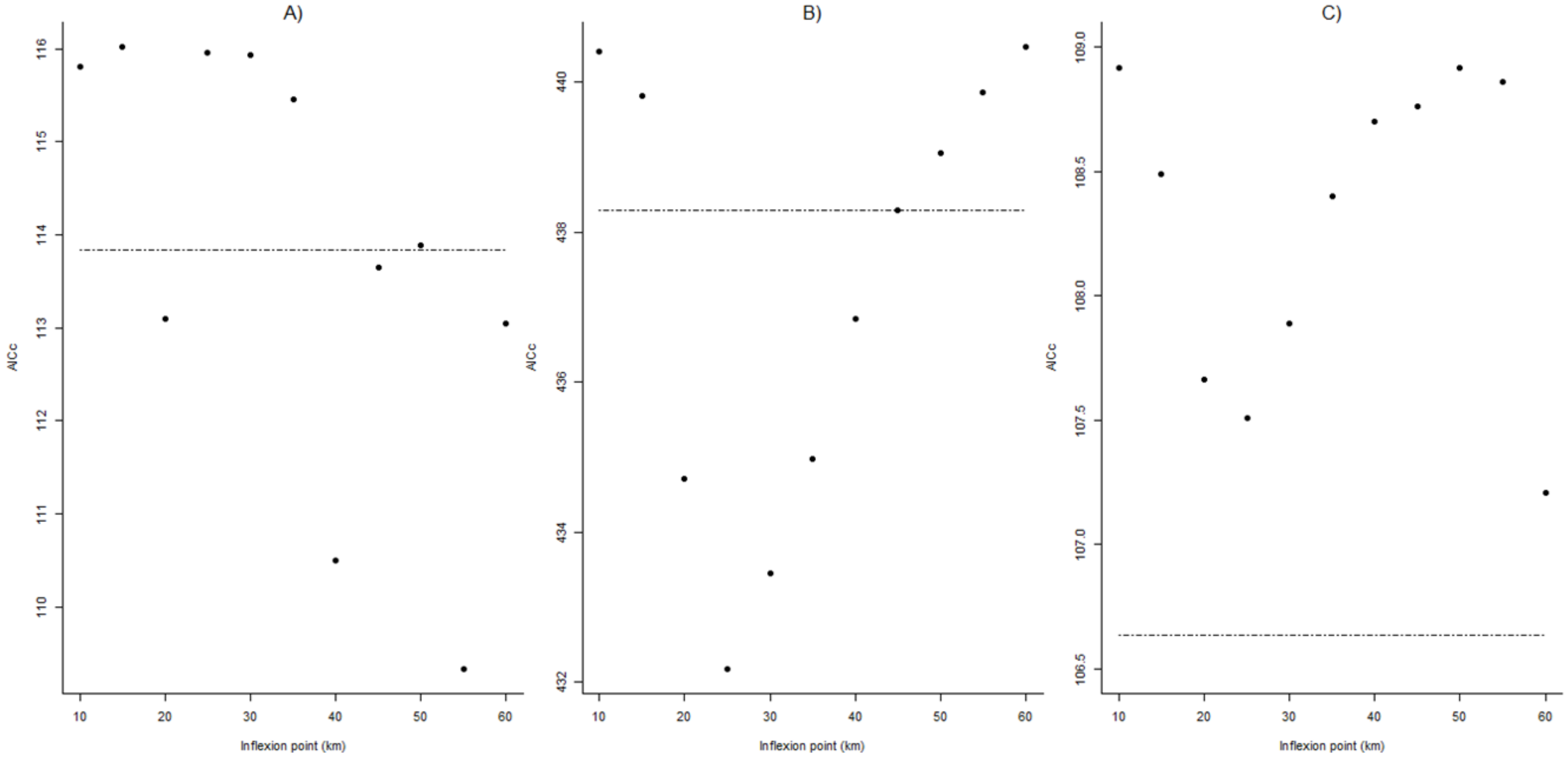

Figure S2.2 **Akaike Information Criterion corrected for small sample size (AICc) for piecewise regression models with varying breaking points that explain litter survival (a) before the mating season (*n* = 193), (b) during the mating season (*n* = 185), and (c) after the mating season (*n* = 125) in brown bears in Sweden during 1991-2011. The horizontal dotted line represents AICc value of the model when we did not allow any breaking point (model 1 in Table S2.1).**

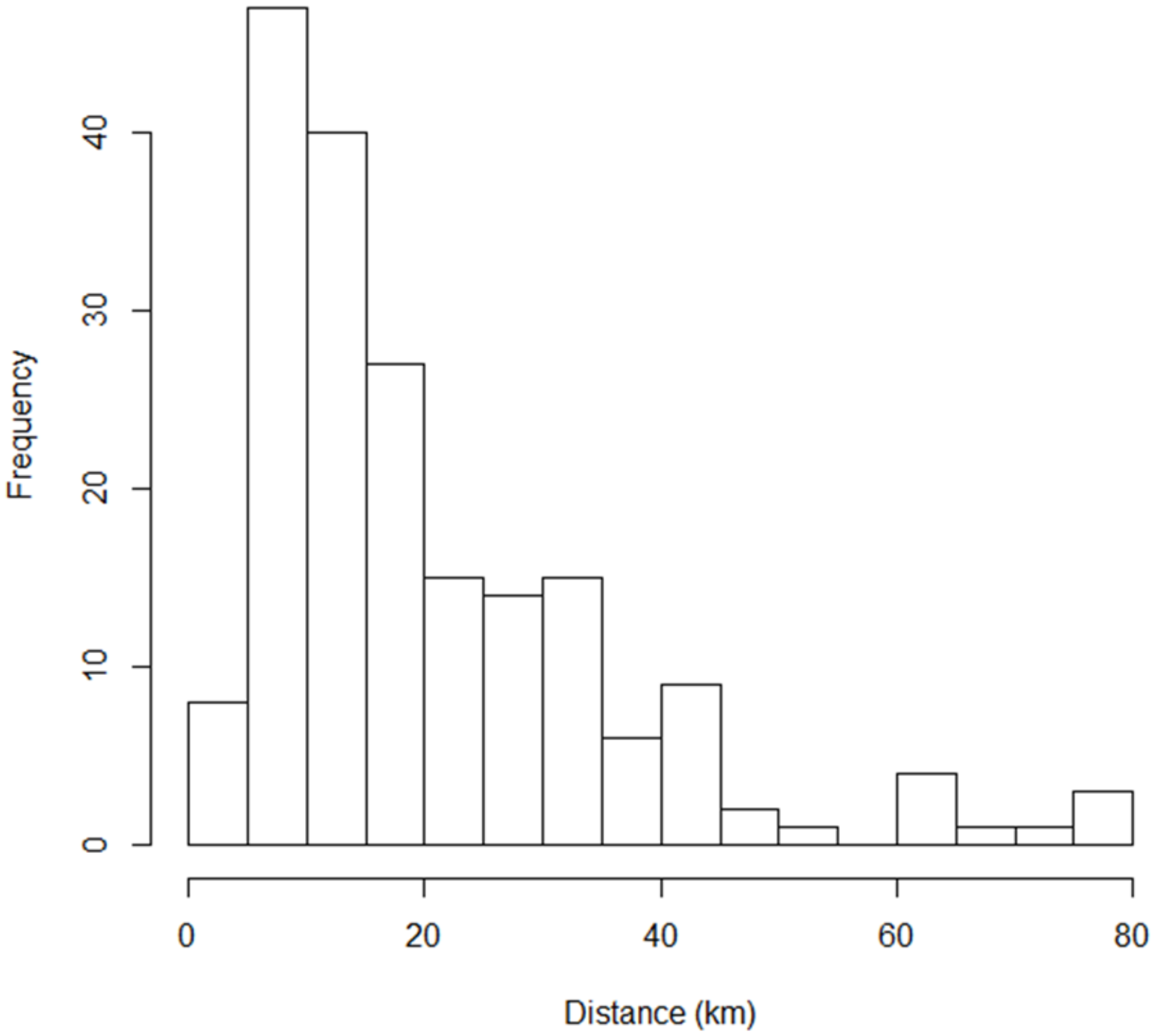

Figure S2.3 **Frequency of the distance to the closest adult male killed within the 1.5 previous years of a litter (n = 193) in brown bears in Sweden during 1991-2011.**

Annexes Chapitre 3

Appendix 3A: Supplementary tables and figures

Table S3.1 Candidate models tested to determine if surviving adult male brown bears shifted their home range use in response to the removal of a neighboring hunter-killed male. Candidate models included different combinations of 2 variables: if the relocation was inside or outside the hunter-killed male's home range (Inside) and if the relocations were 0, 1, or 2 years after the hunter-killed male's death (Period). All candidate models also included Year and survivor ID nested in the hunter-killed males' ID as random intercepts. Models are listed with their number of parameters (K), Log Likelihood (LL), difference in BIC relative to the most parsimonious model (ΔBIC), and model weight (ω).

Model	Variable	K	LL	ΔBIC	ω
1	None	4	-26524	893.6	0.00
2	Inside	5	-26077	9.6	0.01
3	Period	6	-26524	914.7	0.00
4	Inside × Period	9	-26051	0.0	0.99

Table S3.2 Candidate models tested to determine how intrinsic and extrinsic factors influenced shifts in home range use by surviving adult male brown bears in response to the removal of a neighboring hunter-killed adult male. Models include different combinations of 6 variables: if the relocation was inside or outside the hunter-killed male home range (Inside), if the relocations was 0, 1, or 2 years after the hunter-killed male's death (Period), the hunter-killed male's age (F_{age}), the surviving male's age (N_{age}), the harvest intensity (Harvest), and the population density index (Density). Models are listed with their number of parameters (K), Log Likelihood (LL), difference in BIC relative to the most parsimonious model (ΔBIC), and model weight (ω).

Model	Variable	K	LL	ΔBIC	ω
1	None	4	-26524	1206	0
2	Inside × Period	9	-26051	312	0
3	F_{age} × Inside × Period	15	-26044	361	0
4	N_{age} × Inside × Period	15	-25885	43	0
5	Harvest × Inside × Period	15	-25978	230	0
6	Density × Inside × Period	15	-25940	154	0
7*	F_{age} + N_{age}	21	-25865	67	0
8*	F_{age} + Harvest	21	-25961	260	0
9*	F_{age} + Density	21	-25921	180	0
10*	N_{age} + Harvest	21	-25858	53	0
11*	N_{age} + Density	21	-25847	31	0
12*	Harvest + Density	21	-25898	133	0
13*	F_{age} + N_{age} + Harvest	27	-25837	74	0
14*	F_{age} + N_{age} + Density	27	-25838	76	0
15*	F_{age} + Harvest + Density	27	-25857	115	0
16*	N_{age} + Harvest + Density	27	-25803	6	0.05
17*	F_{age} + N_{age} + Harvest + Density	33	-25768	0	0.95

* Each variable in models 7–17 is included with its interaction with the covariates "Inside" and "Period" as in models 3–6.

Table S3.3 Coefficients and 95% confidence intervals of the variables included in the most parsimonious model tested to determine if surviving adult male brown bears shifted their home range use in response to the removal of a hunter-killed adult male. See Table S3.1 for variable descriptions.

Variable	β	95 % Confidence intervals	
		Lower	Upper
Intercept	0.265	0.180	0.350
Inside = True	-0.852	-0.928	-0.775
Period = 1 year after male death	-0.001	-0.060	0.058
Period = 2 years after male death	-0.081	-0.142	-0.019
Inside = True × Period = 1 year after male death	0.028	-0.077	0.134
Inside = True × Period = 2 years after male death	0.349	0.242	0.455

Table S3.4 Coefficients (β) and 95% confidence intervals of the variables included in the most parsimonious model tested to determined how intrinsic and extrinsic factors influenced shifts in home range use by surviving adult male brown bears in response to the removal of a neighboring hunter-killed adult male. See Table S3.2 caption for variable descriptions.

Variable	β	95 % Confidence intervals	
		Lower	Upper
Intercept	0.250	0.159	0.341
F_{age}	-0.117	-0.218	-0.017
N_{age}	0.027	-0.043	0.097
Harvest	-0.118	-0.216	-0.020
Density	-0.024	-0.129	0.081
Inside = True	-0.947	-1.037	-0.857
Period = 1 year[a]	0.014	-0.052	0.080
Period = 2 years[b]	-0.085	-0.164	-0.005
Inside = True × Period = 1 year	-0.092	-0.224	0.039
Inside = True × Period = 2 years	0.473	0.351	0.594
F_{age} × Inside = True	-0.013	-0.123	0.098
F_{age} × Period = 1 year	0.089	-0.010	0.188
F_{age} × Period = 2 years	-0.050	-0.145	0.044
N_{age} × Inside = True	-0.653	-0.846	-0.459
N_{age} × Period = 1 year	0.005	-0.082	0.092
N_{age} × Period = 2 years	0.057	-0.027	0.140
Harvest × Inside = True	-0.220	-0.341	-0.098
Harvest × Period = 1 year	0.109	0.015	0.204
Harvest × Period = 2 years	-0.145	-0.246	-0.044
Density × Inside = True	0.375	0.254	0.496
Density × Period = 1 year	-0.067	-0.163	0.030
Density × Period = 2 years	0.124	0.028	0.221
F_{age} × Inside = True × Period = 1 year	-0.378	-0.545	-0.211
F_{age} × Inside = True × Period = 2 years	0.325	0.165	0.485
N_{age} × Inside = True × Period = 1 year	0.083	-0.174	0.341
N_{age} × Inside = True × Period = 2 years	0.114	-0.115	0.343
Harvest × Inside = True × Period = 1 year	-0.328	-0.501	-0.155
Harvest × Inside = True × Period = 2 years	0.564	0.403	0.726
Density × Inside = True × Period = 1 year	0.267	0.087	0.446
Density × Inside = True × Period = 2 years	-0.582	-0.750	-0.415

[a] 1 year after the hunter-killed male death, [b] 2 years after the hunter-killed male death

Annexes Chapitre 4

Appendix 4A: Supplementary tables and figures

Table S4.1 Random structures tested to assess the repeatability of habitat selection of cut blocks by brown bears in Sweden between 2007 and 2012. Models are listed with their random intercepts, random coefficient, log likelihood (LL), differences in Akaike Information Criterion in relation to the best-supported model (Δ AIC), and Akaike weight (w_i).

MODEL	Random intercept	Random coefficient	LL	Δ AIC	w_i
A	Bear-year nested in BearID	–	-92170	1410	0
B	Bear-year nested in BearID	% cut blocks	-91462	0	1

Table S4.2 **Candidate models tested to assess repeatability of habitat selection of cut blocks by brown bears in Sweden between 2007 and 2012. Models are listed with their fixed effects covariates, log likelihood (LL), differences in Akaike Information Criterion in relation to the best-supported model (Δ AIC), and Akaike weight (w_i). All models were tested with bear-year nested in BearID as a random intercept and % cut blocks as a random coefficient (model B from Table S4.1).**

MODEL	VARIABLES INCLUDED	LL	Δ AIC	w_i
Base	% cut blocks + % cut blocks in the annual home range + % cut blocks × % cut blocks in the annual home range	-98294	13652	0
Elevation	Base model + mean elevation + coefficient of variation of elevation	-96905	10877	0
Natural	Elevation model + % water + % mixed–deciduous + % bog	-93384	3841	0
Full	Natural model + % young forest + road density	-91462	0	1

Table S4.3 Coefficients (β) and 95% confidence intervals of the fixed effect covariates of the most parsimonious model to assess the repeatability of cut blocks habitat selection by brown bears in Sweden between 2007 and 2012. This model also included bear-year nested in BearID as a random intercept and % cut blocks as a random coefficient (model B from Table S4.1).

Variable	β	95% Confidence Interval	
		Lower	Upper
Intercept	-0.070	-0.115	-0.026
% cut blocks	0.264	0.194	0.334
% cut blocks within annual home range	-0.125	-0.158	-0.091
Mean elevation	-0.131	-0.148	-0.114
Coefficient of variation of elevation	0.073	0.060	0.085
% water	-0.483	-0.503	-0.464
% mixed–deciduous	0.022	0.011	0.033
% bog	-0.433	-0.447	-0.419
% young forest	0.182	0.170	0.194
Roads length	-0.306	-0.317	-0.294
% cut blocks × % cut blocks within annual home range	0.014	-0.046	0.073

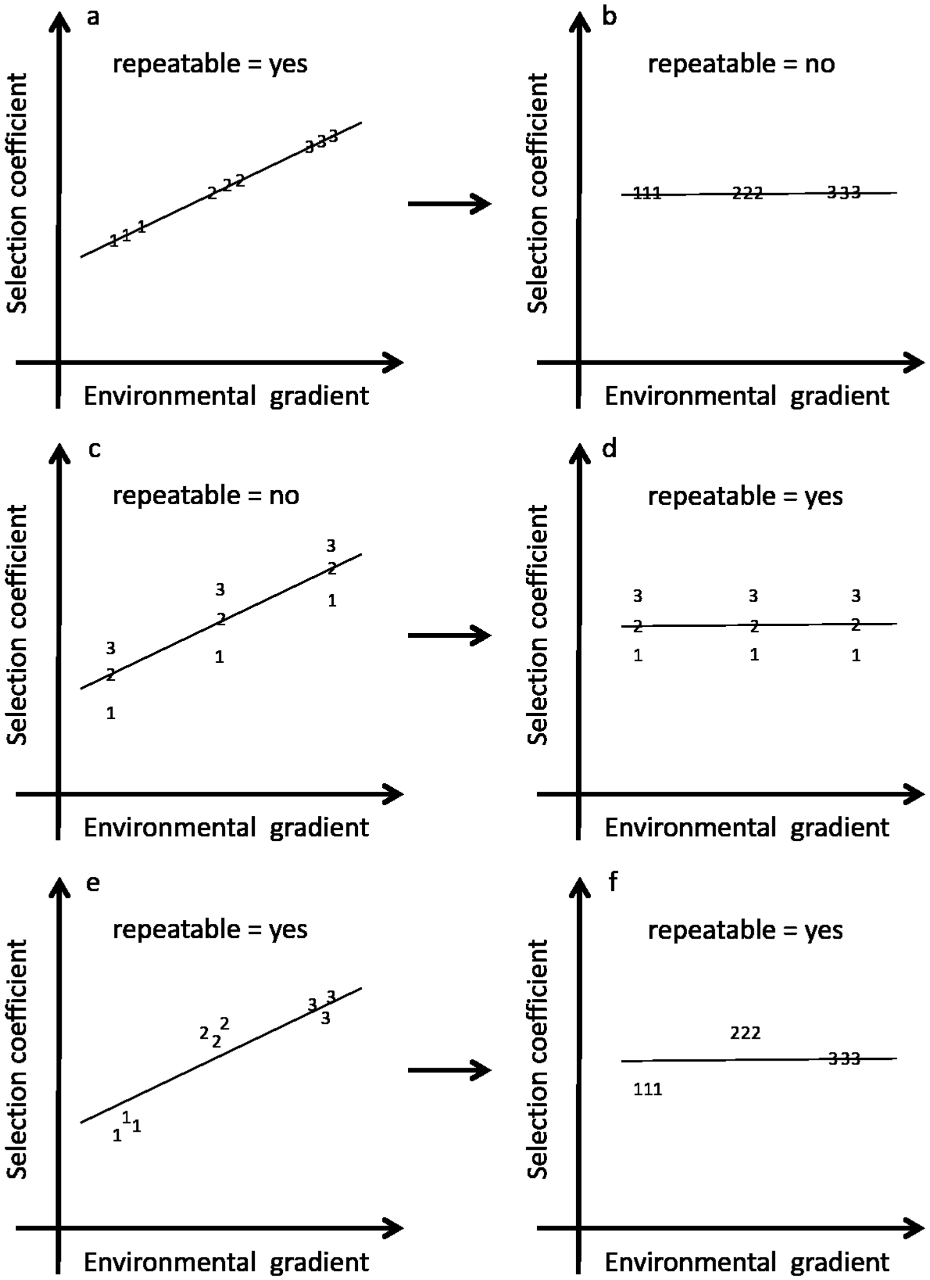

Figure S4.1 Schematic representation showing that biased estimates of repeatability of habitat selection can be obtained if we do not account for functional responses in habitat selection. Results from the left panel (a, c, and e) do not account for functional response in habitat selection while panel on the right panel (b, d, and f) account for functional response in habitat selection. Note that different numbers refer to different individuals.

Appendix 4B: R code of simulations

```
# R-Script by Martin Leclerc
# For Leclerc et al. –Quantifying consistent individual differences in habitat selection–
Oecologia

# Simulations of consistent individual variation in habitat selection
# Simulations of 5 individuals followed for 3 years
# Each individual-year exist in similar landscapes
# Habitat use differ between individual and individual-year

#######
# Simulation 1
# Habitat X non-significant at the population level
# but high among and low within individual variation

# Create the landscape
random=as.data.frame(cbind(bearID=c("a","b","c","d","e"),
                           year=c(rep(1,2500),rep(2,2500),rep(3,2500)),
                           y=0))
random$bearyear=paste(random$bearID,random$year,sep="")
random$value=rnorm(7500,mean=100,sd=30)

# Create habitat use pattern for each individual-year
# with high among and low within individual variation
inda1=rnorm(500,mean=60,sd=10)#individual1-year1
inda2=rnorm(500,mean=70,sd=10)#individual1-year2
inda3=rnorm(500,mean=80,sd=10)#individual1-year3
indb1=rnorm(500,mean=85,sd=10)#individual2-year1
indb2=rnorm(500,mean=88,sd=10)#individual2-year2
```

```
indb3=rnorm(500,mean=90,sd=10)#individual2-year3
indc1=rnorm(500,mean=90,sd=10)#individual3-year1
indc2=rnorm(500,mean=100,sd=10)#individual3-year2
indc3=rnorm(500,mean=110,sd=10)#individual3-year3
indd1=rnorm(500,mean=110,sd=10)#individual4-year1
indd2=rnorm(500,mean=112,sd=10)#individual4-year2
indd3=rnorm(500,mean=115,sd=10)#individual4-year3
inde1=rnorm(500,mean=120,sd=10)#individual5-year1
inde2=rnorm(500,mean=130,sd=10)#individual5-year2
inde3=rnorm(500,mean=140,sd=10)#individual5-year3
loc=as.data.frame(cbind(bearID=c(rep("a",1500),rep("b",1500),rep("c",1500),rep("d",1500)
,rep("e",1500)),
year=c(rep(1,500),rep(2,500),rep(3,500)),y=1))
loc$bearyear=paste(loc$bearID,loc$year,sep="")
loc$value=c(inda1,inda2,inda3,indb1,indb2,indb3,indc1,indc2,indc3,indd1,indd2,indd3,ind
e1,inde2,inde3)

# Merging database and RSF model
str(loc)
str(random)
Final=rbind(random,loc)
library(lme4)
Sim1=glmer(y~value+(value|bearID/bearyear),family="binomial",Final)
summary(Sim1)

# Extract variances component and estimate repeatability
repSim1= VarCorr(Sim1)$bearID[4] / (VarCorr(Sim1)$bearID[4] +
VarCorr(Sim1)$bearyear[4])
repSim1
```

```
####################################################################
# Habitat type not selected nor avoided at the population level
# and highly repeatable (0.8-0.9 depending on rnorm values)
####################################################################

#######
# Simulation 2
# Habitat X non-significant at the population level
# and low among and high within individual variation

# Create the landscape
random=as.data.frame(cbind(bearID=c("a","b","c","d","e"),
                           year=c(rep(1,2500),rep(2,2500),rep(3,2500)),
                           y=0))
random$bearyear=paste(random$bearID,random$year,sep="")
random$value=rnorm(7500,mean=100,sd=30)

# Create habitat use pattern for each individual-year
# with low among and high within individual variation
inda1=rnorm(500,mean=90,sd=30) #individual1-year1
inda2=rnorm(500,mean=100,sd=30)#individual1-year2
inda3=rnorm(500,mean=110,sd=30)#individual1-year3
indb1=rnorm(500,mean=90,sd=30 )#individual2-year1
indb2=rnorm(500,mean=100,sd=30)#individual2-year2
indb3=rnorm(500,mean=110,sd=30)#individual2-year3
indc1=rnorm(500,mean=90,sd=30 )#individual3-year1
indc2=rnorm(500,mean=100,sd=30)#individual3-year2
indc3=rnorm(500,mean=110,sd=30)#individual3-year3
indd1=rnorm(500,mean=90,sd=30) #individual4-year1
indd2=rnorm(500,mean=100,sd=30)#individual4-year2
```

```
indd3=rnorm(500,mean=110,sd=30)#individual4-year3
inde1=rnorm(500,mean=90,sd=30) #individual5-year1
inde2=rnorm(500,mean=100,sd=30)#individual5-year2
inde3=rnorm(500,mean=110,sd=30)#individual5-year3
loc=as.data.frame(cbind(bearID=c(rep("a",1500),rep("b",1500),rep("c",1500),rep("d",1500)
,rep("e",1500)),
year=c(rep(1,500),rep(2,500),rep(3,500)),y=1))
loc$bearyear=paste(loc$bearID,loc$year,sep="")
loc$value=c(inda1,inda2,inda3,indb1,indb2,indb3,indc1,indc2,indc3,indd1,indd2,indd3,ind
e1,inde2,inde3)

# Merging database and RSF model
str(loc)
str(random)
Final=rbind(random,loc)
library(lme4)
Sim2=glmer(y~value+(value|bearID/bearyear),family="binomial",Final)
summary(Sim2)

# Extract variances component and estimate repeatability
repSim2=VarCorr(Sim2)$bearID[4] / (VarCorr(Sim2)$bearID[4] +
VarCorr(Sim2)$bearyear[4])
repSim2
####################################################################
# Habitat type not selected nor avoided at the population level#
# and low repeatability (>1.0e-5)
####################################################################
```

```
#######
# Simulation 3
# Habitat X selected at the population level
# and low among and high within individual variation

# Create the landscape
random=as.data.frame(cbind(bearID=c("a","b","c","d","e"),
year=c(rep(1,2500),rep(2,2500),rep(3,2500)),y=0))
random$bearyear=paste(random$bearID,random$year,sep="")
random$value=rnorm(7500,mean=100,sd=30)

# Create habitat use pattern for each individual-year
# with low among and high within individual variation
inda1=rnorm(500,mean=90+40,sd=30) #individual1-year1
inda2=rnorm(500,mean=100+40,sd=30)#individual1-year2
inda3=rnorm(500,mean=110+40,sd=30)#individual1-year3
indb1=rnorm(500,mean=90+40,sd=30) #individual2-year1
indb2=rnorm(500,mean=100+40,sd=30)#individual2-year2
indb3=rnorm(500,mean=110+40,sd=30)#individual2-year3
indc1=rnorm(500,mean=90+40,sd=30) #individual3-year1
indc2=rnorm(500,mean=100+40,sd=30)#individual3-year2
indc3=rnorm(500,mean=110+40,sd=30)#individual3-year3
indd1=rnorm(500,mean=90+40,sd=30) #individual4-year1
indd2=rnorm(500,mean=100+40,sd=30)#individual4-year2
indd3=rnorm(500,mean=110+40,sd=30)#individual4-year3
inde1=rnorm(500,mean=90+40,sd=30) #individual5-year1
inde2=rnorm(500,mean=100+40,sd=30)#individual5-year2
inde3=rnorm(500,mean=110+40,sd=30)#individual5-year3
loc=as.data.frame(cbind(bearID=c(rep("a",1500),rep("b",1500),rep("c",1500),rep("d",1500)
,rep("e",1500)),
```

```
year=c(rep(1,500),rep(2,500),rep(3,500)),y=1))
loc$bearyear=paste(loc$bearID,loc$year,sep="")
loc$value=c(inda1,inda2,inda3,indb1,indb2,indb3,indc1,indc2,indc3,indd1,indd2,indd3,ind
e1,inde2,inde3)

# Merging database and RSF model
str(loc)
str(random)
Final=rbind(random,loc)
library(lme4)
Sim3=glmer(y~value+(value|bearID/bearyear),family="binomial",Final)
summary(Sim3)

# Extract variances component and estimate repeatability
repSim3=VarCorr(Sim3)$bearID[4] / (VarCorr(Sim3)$bearID[4] +
VarCorr(Sim3)$bearyear[4])
repSim3
##################################################################
# Habitat type selected at the population level
# and low repeatability (>1.0e-5)
##################################################################
```

Annexes Chapitre 6

Appendix 6A: Supplementary tables and figures

Table S6.1 Candidate models tested to explain variation in rates of movement (log-transformed) of brown bears in Sweden (2003-2016). All models included "Bearyear" nested in "Bear ID" as random intercepts and a AR1 temporal autocorrelation function. Models are listed with their variable, log likelihood (LL), and difference in AICc to the most parsimonious model (ΔAICc).

		Male (*n*=41)		Female (*n*=37)	
Model	Variable*	LL	ΔAICc	LL	ΔAICc
1	None	-65091.0	5457.5	-68781.3	6496.3
2	Age	-65080.9	5441.3	-68774.5	6486.7
3	Age + Time of day	-62506.9	297.3	-65690.7	323.2
4	Age + Time of day by hunting season fate	-62423.5	134.5	-65668.2	282.1
5	Age + Julian date	-65038.4	5360.4	-68676.8	6295.5
6	Age + Julian date by hunting season fate	Did not	converged	-68675.4	6296.5
7	Age + Number of years to live	-65079.1	5441.6	-68772.7	6487.2
8	Model 3 + Model 5	-62444.9	177.2	-65549.9	45.4
9	Model 3 + Model 6	-62443.0	177.6	-65548.6	47.0
10	Model 3 + Model 7	-62504.8	297.1	-65690.1	325.9
11	Model 4 + Model 5	-62360.3	12.0	-65526.6	3.0
12	Model 4 + Model 6	-62358.1	11.7	-65525.2	4.1
13	Model 4 + Model 7	-62421.0	133.5	-65667.5	284.7
14	Model 8 + Model 7	-62437.7	166.9	-65546.5	42.8
15	Model 9 + Model 7	-62438.1	171.8	-65546.7	47.1
16	Model 11 + Model 7	**-62352.2**	**0**	**-65523.2**	**0**
17	Model 12 + Model 7	-62352.7	4.9	-65523.2	4.1

* All variables were fitted with smoothing splines which allows flexible specification of the relationships, instead of forcing them to be linear, quadratic or cubic.

Table S6.2 Candidate models tested to explain variation in activity pattern of brown bears in Sweden (2003-2015). All models included “Bearyear” nested in “Bear ID” as random intercepts and a AR1 temporal autocorrelation function. Models are listed with their variable, log likelihood (LL), and difference in AICc to the most parsimonious model (ΔAICc).

		Male (*n*=38)		Female (*n*=37)	
Model	Variable*	LL	ΔAICc	LL	ΔAIC
1	None	-33.3	53.3	524.0	61.1
2	Age	-24.3	39.3	526.1	60.9
3	Age + Julian date	-7.1	9.0	**558.5**	**0**
4	Age + Julian date by hunting season fate	-6.4	11.6	557.4	6.3
5	Age + Number of years to live	-18.1	31.1	527.0	63.1
6	Model 3 + Number of years to live	**-0.6**	**0**	559.4	2.3
7	Model 4 + Number of years to live	-1.4	5.6	558.5	8.1

* All variables, except hunting season fate. were fitted with smoothing splines which allows flexible specification of the relationships, instead of forcing them to be linear, quadratic or cubic.

Table S6.3 Candidate models tested to explain variation in the daily mean distance to roads of brown bears in Sweden (2003-2016). Models are listed with their variable, log likelihood (LL), and difference in AICc to the most parsimonious model (ΔAICc).

		Male (*n*=31)		Female (*n*=35)	
Model	Variable*	LL	ΔAICc	LL	ΔAICc
1	None	-1097.1	13.3	-1358.2	37.7
2	Home range road density + Age	-1094.2	11.5	-1353.1	31.4
3	Model 2 + Julian date	-1092.5	10.3	-1343.0	13.2
4	Model 2 + Julian date × Hunting season fate	-1089.1	7.4	-1337.5	6.3
5	Model 2 + Number of years to live	-1088.9	3.0	-1346.5	20.4
6	Model 3 + Number of years to live	**-1086.4**	**0.0**	-1335.4	0.04
7	Model 4 + Number of years to live	-1085.6	2.5	**-1333.3**	**0.0**

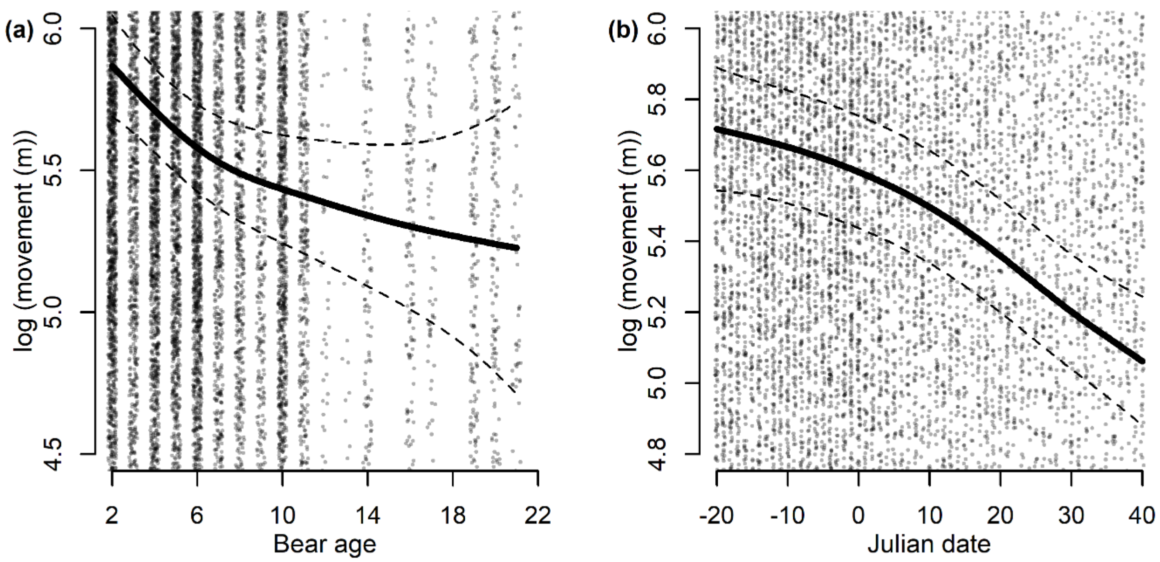

Figure S6.1 **Predicted variation in rates of movement (log-transformed) for the most parsimonious model tested for male (n = 41 bears, 32,849 movements) brown bears in Sweden. Shown are the effect of bear age (panel a, estimated degree of freedom = 2.174) and Julian date (panel b, estimated degree of freedom = 2.542), where 0 represents the start of the hunting season.**

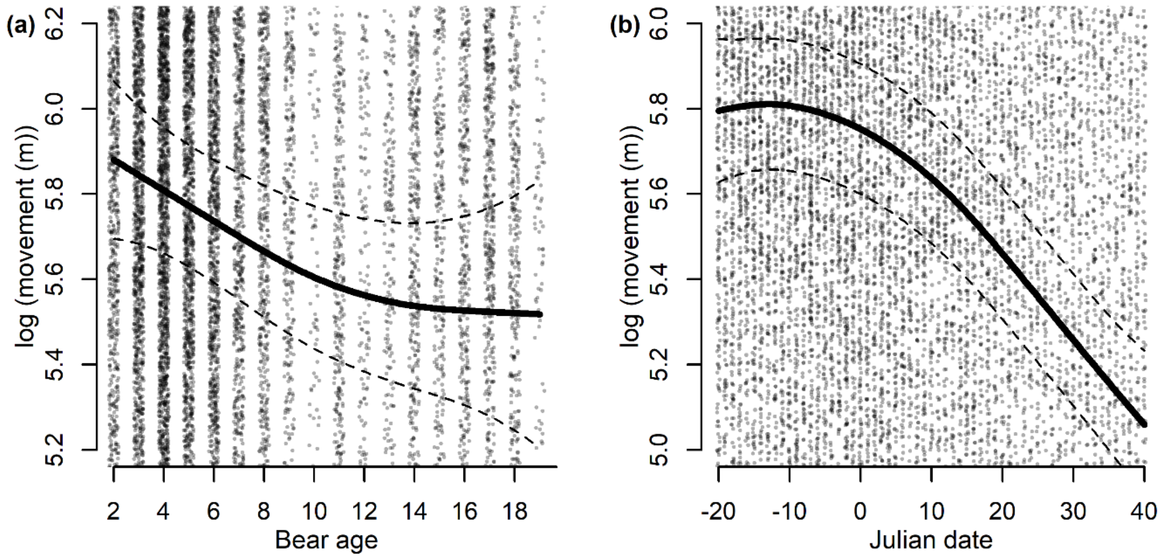

Figure S6.2 **Predicted variation in rates of movement (log-transformed) for the most parsimonious model tested for female (n = 37 bears, 35,821 movements) brown bears in Sweden. Shown are the effect of bear age (panel a, estimated degree of freedom = 1.724) and Julian date (panel b, estimated degree of freedom = 3.357) where 0 represents the start of the hunting season.**

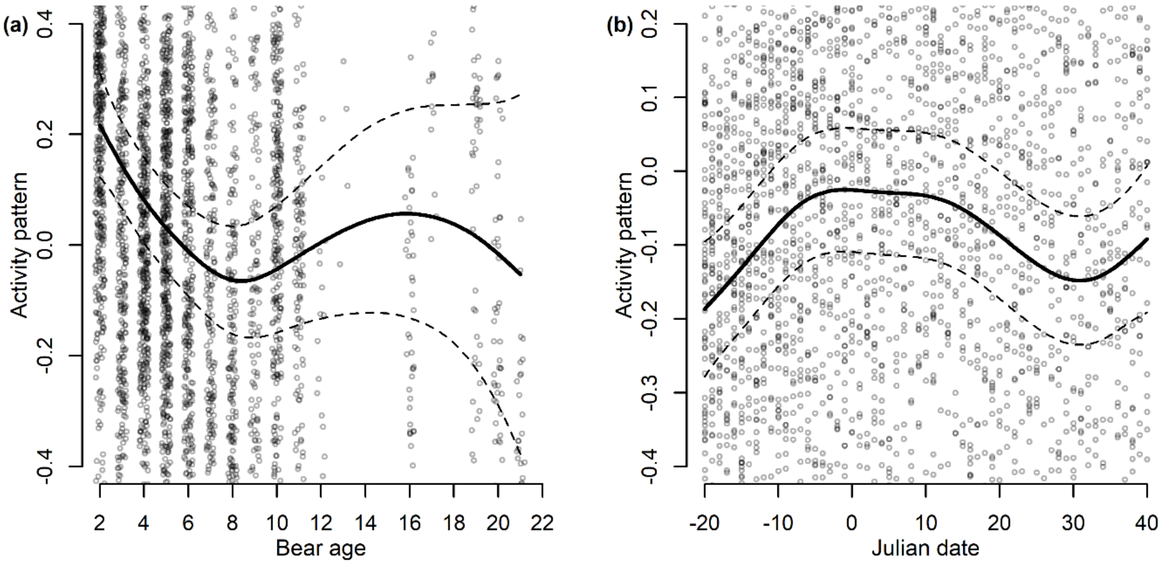

Figure S6.3 **Predicted variation of male brown bears (n = 38 bears, 3,356 daily values) activity pattern from the most parsimonious model tested. Shown is the relationship between activity pattern and bear age (panel a, estimated degree of freedom = 3.507) and Julian date (panel b, estimated degree of freedom = 5.038), where 0 represents the start of the hunting season. Activity pattern values of -1 and 1 indicates that all activity occurred during nonhunting and hunting hours, respectively.**

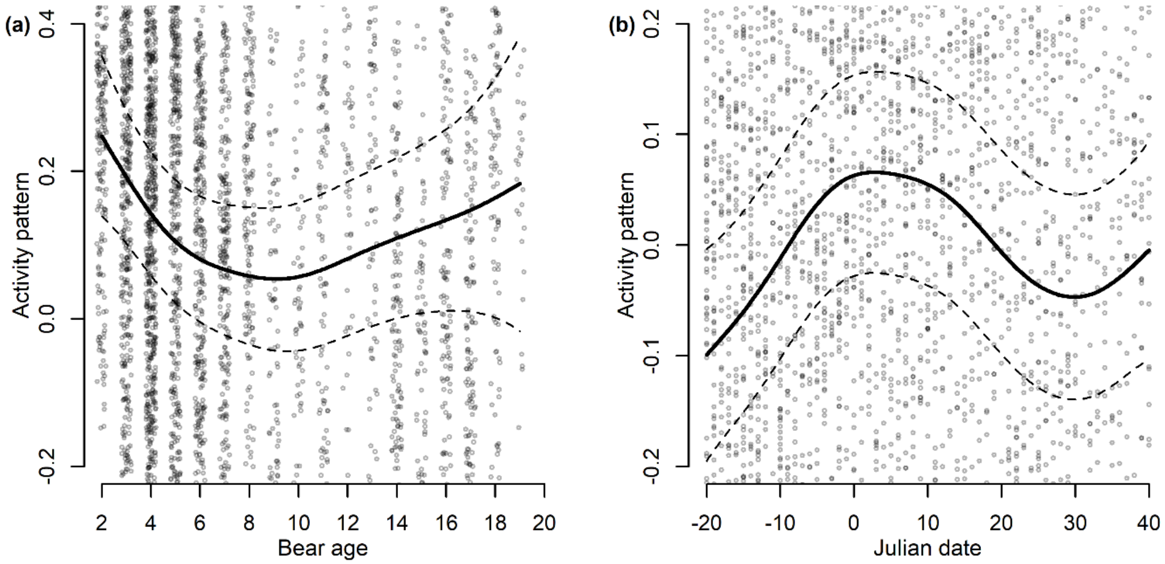

Figure S6.4 **Predicted variation of female brown bears (n = 37 bears, 4,145 daily values) activity pattern from the most parsimonious model tested. Shown is the relationship between activity pattern and bear age (panel a, estimated degree of freedom = 3.039) and Julian date (panel b, estimated degree of freedom = 5.165), where 0 represents the start of the hunting season. Activity pattern values of -1 and 1 indicates that all activity occurred during nonhunting and hunting hours, respectively.**

Annexes Chapitre 7

Appendix 7A: Details of the monitoring protocol

Females without young and females accompanied by yearlings were immobilized with a dart gun from a helicopter. Females with cubs of the year were not captured for animal welfare reasons. Captures were carried out after den emergence from mid-April to early May. Because all bears were captured within a 2-week period, we did not adjust body size for capture date. All females were marked individually with tattoos (inside the upper lip), and passive integrated transponder (PIT) tags under anesthesia. Females were fitted with radio transmitters, radio-implants (Telonics, model IMP/40/L HC), or both. Females were originally fitted with VHF radio transmitters (Telonics, model 500). However, since 2003, most (gradually from 6% to 90%) females captured or recaptured were fitted with GPS–GMS transmitters (GPS Plus, Vectronic Aerospace GmbH). A vestigial premolar tooth was collected from all females not captured as a yearling to estimate age based on the cementum annuli in the root (Mattson's Inc., Milltown, MT). Approximately 50–80% of the females in the study area were monitored annually (Scandinavian Brown Bear Project, personal communication). For further information about capture and handling of bears, see Arnemo et al. (2011) and Zedrosser et al. (2007).

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Appendix 7B: Supplementary tables and figures

Table S7.1 Means of parameters used, 95% confidence intervals [lower : upper], and number of observations of brown bears in the monitored dataset and hunting records in Sweden, 1996-2013.

	Monitored dataset	Hunting records
Mean ratio of yearlings to adult females	1.32	0.71
Mean yearling mass (kg)	22 [10:37] (*n*=266)	54 [31:79] (*n*=108)
Mean adult female mass (kg)	84 [48:112] (*n*=205)	125 [78:177] (*n*=157)
Mean age of females	9 [4:20] (*n*=205)	8 [4:17] (*n*=157)

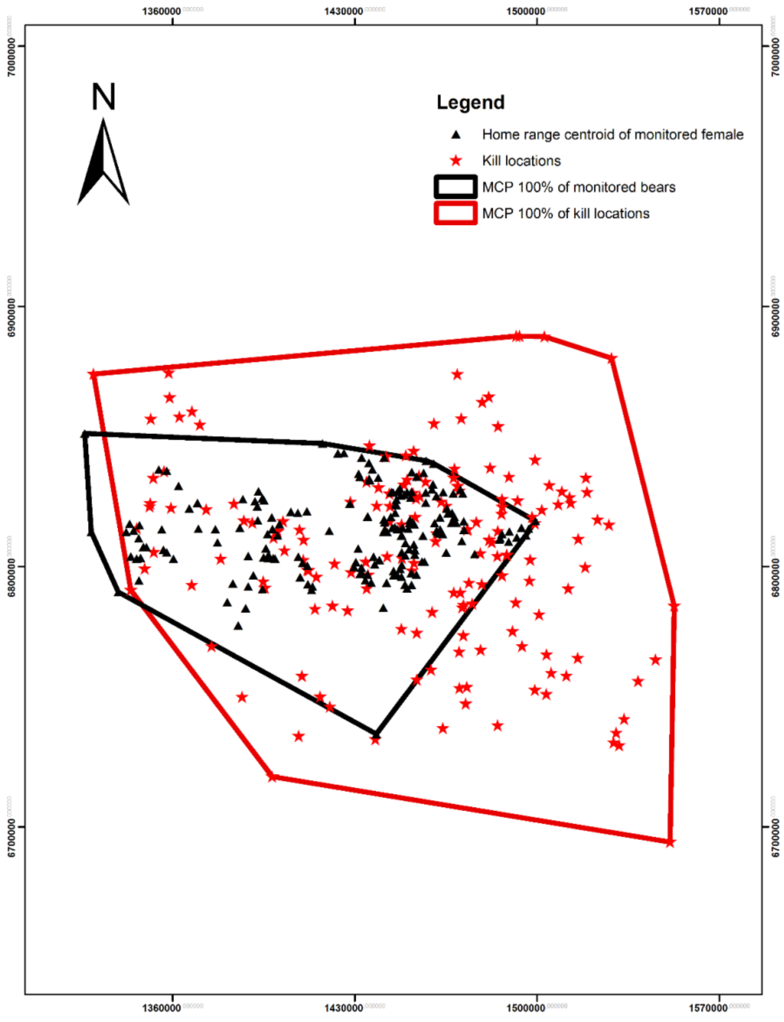

Figure S7.1 Map of the distribution of monitored (black triangles) and kill locations of hunter-killed (red stars) brown bears in Sweden, 1996-2013. More than 95% of the area covered by monitored bears is within the area of hunter-killed bears. The MCP centroids are 43 km apart. Note that we only show the home range centroids of the monitored bears (black triangles), but the bears' actual home ranges often extended beyond the MCP of monitored bears in the figure below, and thus, the spatial overlap is underestimated.

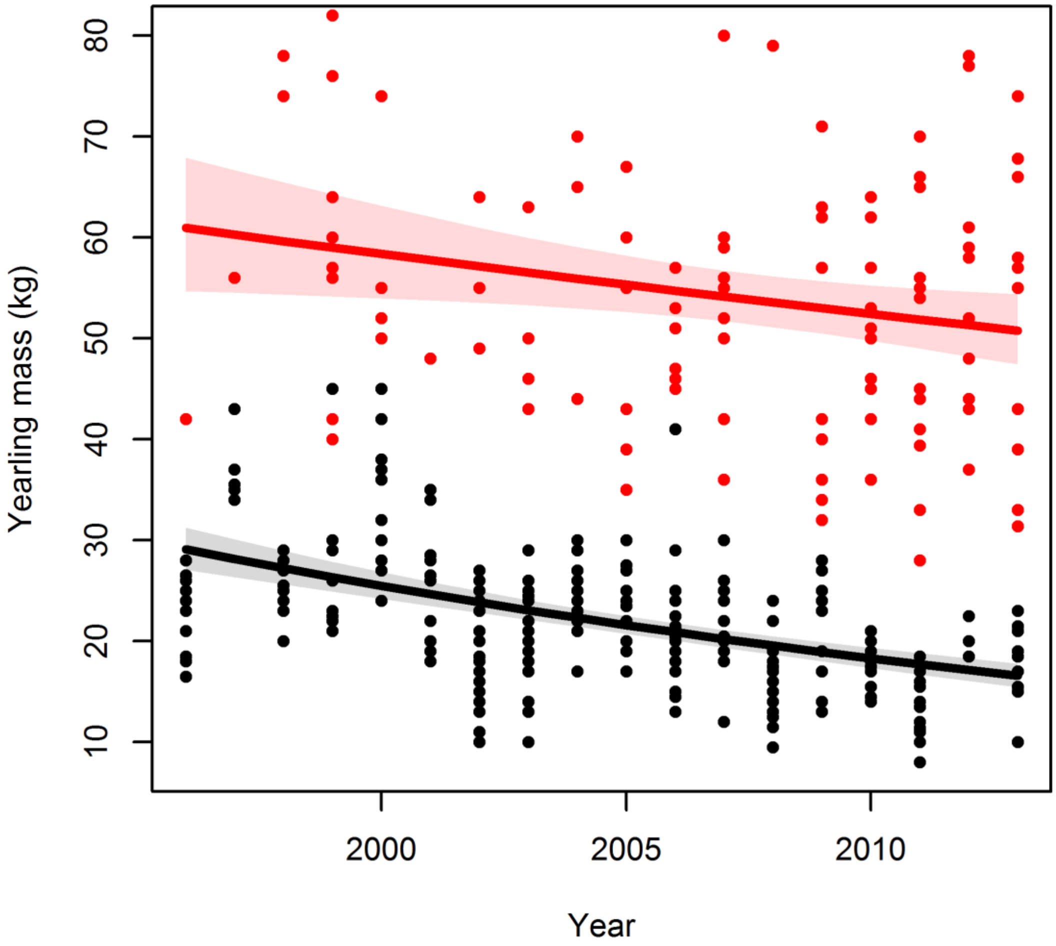

Figure S7.2 **Predictions for the mass of yearling male brown bears (solid line) and the 95% confidence intervals of the final model (transformed back to the original scale) suggesting bias in the data from hunter-killed brown bears in Sweden, 1996-2013. We investigated bias in yearling mass in the data from hunting records (red line and dots) in comparison to data from bears monitored by the Scandinavian Brown Bear Project (black line and dots).**

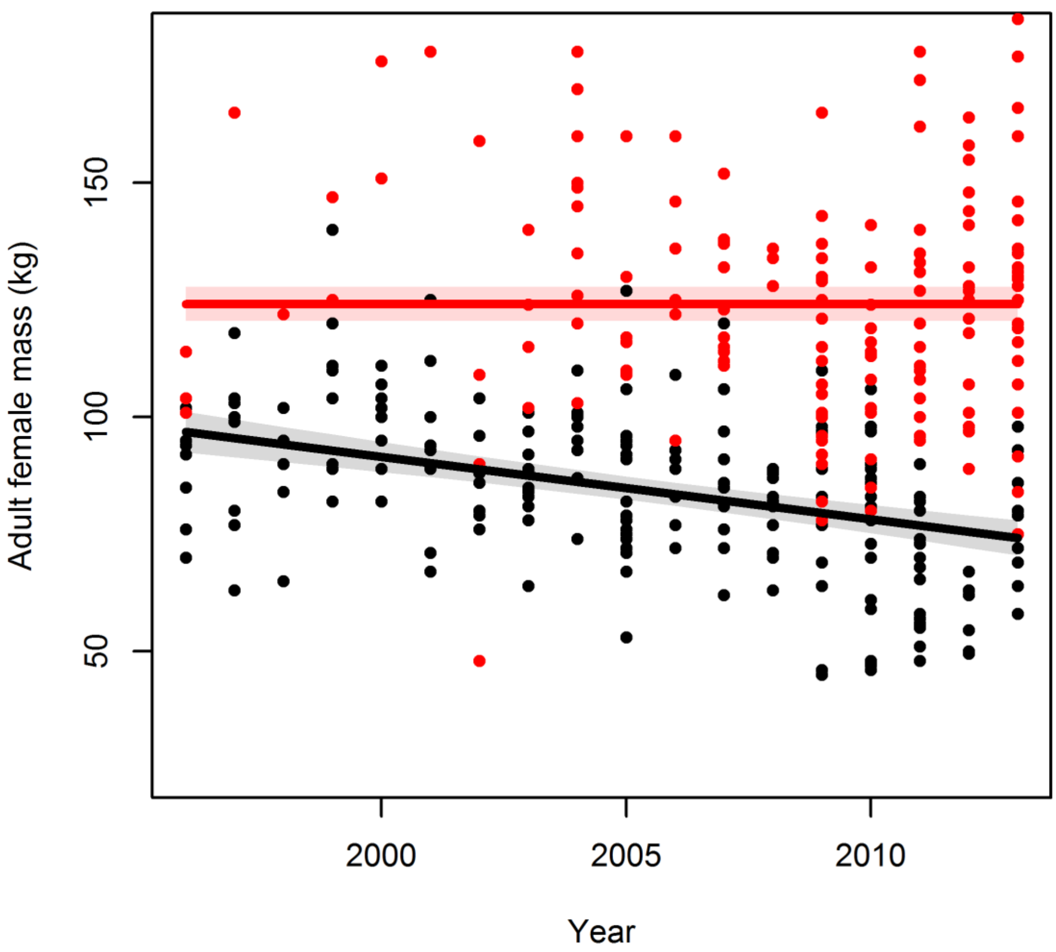

Figure S7.3 **Predictions (solid lines) for 8 year-old females and 95% confidence intervals of the final model (transformed back to the original scale) showing bias in data from hunter-killed brown bears in Sweden, 1996-2013. We investigated bias in adult female mass from the harvest records (red line and dots) in comparison to data from bears monitored by the Scandinavian Brown Bear Project (black line and dots).**

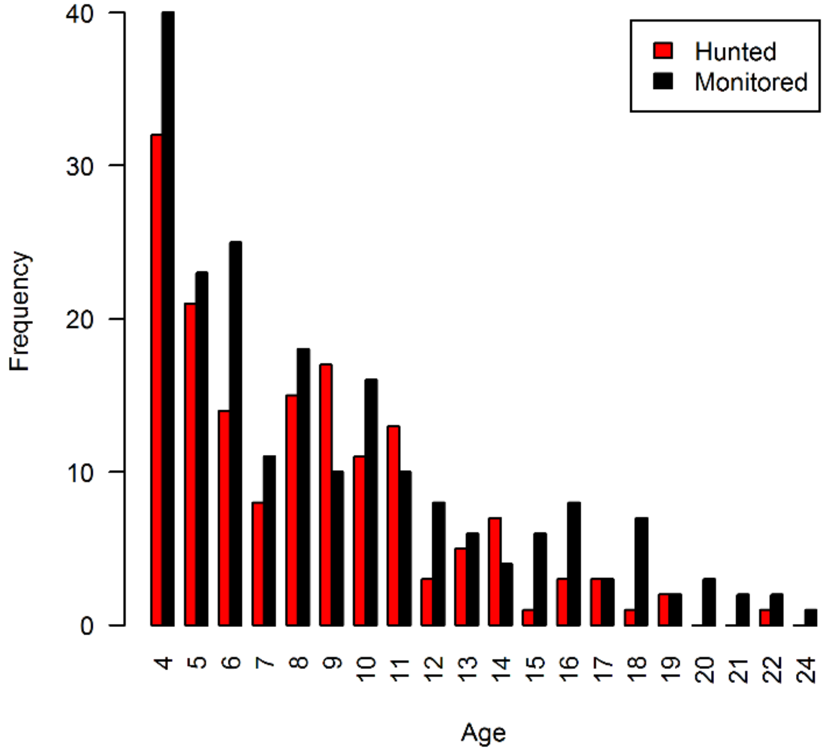

Figure S7.4 Age class distribution of bears from the harvest records (red bars) and the bears monitored by the Scandinavian Brown Bear Project (black bars).

Appendix 7C: Supplementary analyses

Supplementary analyses showing that our results were not driven by 1) the fact that body mass was recorded during spring for monitored females and during autumn for hunter-killed females, or by 2) different age structures between monitored and hunter-killed datasets.

The difference in temporal trends between the monitored and hunter-killed female mass could potentially be affected by the fact that they were recorded at different times of the year. We therefore carried out a post-hoc analysis using only females that were monitored in spring and killed in autumn during the same year (n=20). We obtained a significant correlation of $r = 0.87$ ($p < 0.001$) between the mass in autumn (hunting dataset) and the mass in spring (monitoring dataset). The mass in spring explained 74.5% of the mass variation in autumn and this relationship was not driven by female age ($p = 0.102$ and VIF=1.56), suggesting that a small female in spring would also be small in autumn. Consequently, we argue that the different temporal trends observed between datasets were not caused by the fact that bears were weighed at different times of the year.

The observed difference in temporal trends in female mass between the monitored and hunter-killed datasets could potentially have been a result of a different age structure between the datasets. However, a post-hoc analysis showed that age class distribution was similar between the two datasets ($X^2 = 21.839$, df = 19, $p = 0.29$, see figure S7.4).

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