DÉTERMINANTS ÉCOLOGIQUES DE LA SOCIALITÉ CHEZ LES FEMELLES RATONS LAVEURS (*PROCYON LOTOR*)

par

Karine Robert

mémoire présenté au Département de biologie en vue
de l'obtention du grade de maître ès sciences (M. Sc.)

FACULTÉ DES SCIENCES
UNIVERSITÉ DE SHERBROOKE

Sherbrooke, Québec, Canada, mars 2012

Library and Archives
Canada

Published Heritage
Branch

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque et
Archives Canada

Direction du
Patrimoine de l'édition

395, rue Wellington
Ottawa ON K1A 0N4
Canada

NOTICE:

The author has granted a non-exclusive license allowing Library and Archives Canada to reproduce, publish, archive, preserve, conserve, communicate to the public by telecommunication or on the Internet, loan, distrbute and sell theses worldwide, for commercial or non-commercial purposes, in microform, paper, electronic and/or any other formats.

The author retains copyright ownership and moral rights in this thesis. Neither the thesis nor substantial extracts from it may be printed or otherwise reproduced without the author's permission.

AVIS:

L'auteur a accordé une licence non exclusive permettant à la Bibliothèque et Archives Canada de reproduire, publier, archiver, sauvegarder, conserver, transmettre au public par télécommunication ou par l'Internet, prêter, distribuer et vendre des thèses partout dans le monde, à des fins commerciales ou autres, sur support microforme, papier, électronique et/ou autres formats.

L'auteur conserve la propriété du droit d'auteur et des droits moraux qui protege cette thèse. Ni la thèse ni des extraits substantiels de celle-ci ne doivent être imprimés ou autrement reproduits sans son autorisation.

In compliance with the Canadian Privacy Act some supporting forms may have been removed from this thesis.

While these forms may be included in the document page count, their removal does not represent any loss of content from the thesis.

Conformément à la loi canadienne sur la protection de la vie privée, quelques formulaires secondaires ont été enlevés de cette thèse.

Bien que ces formulaires aient inclus dans la pagination, il n'y aura aucun contenu manquant.

Canada

Le 29 mars 2012

le jury a accepté le mémoire de Madame Karine Robert

dans sa version finale.

Membres du jury

Professeure Fanie Pelletier
Directrice de recherche
Département de biologie

Professeur Dany Garant
Codirecteur de recherche
Département de biologie

Monsieur Denis Réale
Membre
Université du Québec à Montréal

Professeur Marco Festa-Bianchet
Président rapporteur
Département de biologie

À deux personnes exceptionnelles,

mes parents.

SOMMAIRE

En écologie comportementale, la compréhension des facteurs qui affectent la socialité des espèces est cruciale pour comprendre l'évolution des différents types d'organisations sociales. L'étude de la socialité nécessite cependant l'acquisition d'informations sur les taux de contacts entre les individus d'une même espèce. Les contacts et en particulier leur fréquence et leur durée sont importants dans l'évolution de la socialité puisqu'ils affectent, entre autres, la compétition, le succès reproducteur et le succès de quête alimentaire. Les contacts sont aussi reliés au taux de transmissions des maladies infectieuses. Il est donc nécessaire de déterminer les facteurs qui influencent la fréquence ainsi que la durée des contacts de manière à améliorer nos connaissances concernant, entre autres, l'évolution de la socialité et la propagation des maladies infectieuses.

L'objectif de ma maîtrise était d'étudier les déterminants écologiques du taux de contacts chez les femelles ratons laveurs (*Procyon lotor*). Pour atteindre cet objectif, j'ai capturé, marqué et effectué le suivi de 15 femelles ratons laveurs dans le parc national du Mont-Orford en 2010 et 2011. Lors de leur capture, j'ai installé à chacune des femelles un collier émetteur de type « proximity logger ». L'utilisation de ces colliers m'a permis d'obtenir des données concernant la fréquence ainsi que la durée des contacts des femelles.

Tout d'abord, j'ai utilisé les taux de contacts obtenus afin de vérifier l'efficacité du chevauchement des domaines vitaux comme méthode d'estimation du taux de contacts. J'ai vérifié la relation entre le chevauchement des domaines vitaux et le taux de contacts à l'aide de 5 indices de chevauchement couramment utilisés. Les résultats montrent que le chevauchement des domaines vitaux peut être un bon estimateur du taux de contacts. Ces résultats sont importants puisque des suivis télémétriques ont été effectués pendant plusieurs décennies sur une grande variété d'espèces. Ces données sont nombreuses et accessibles et pourraient donc être utilisées, par exemple, pour étudier les facteurs qui

influencent la structure sociale ou dans des programmes de prévention de propagations de maladies infectieuses.

Par la suite, j'ai effectué des analyses génétiques afin d'obtenir un indice de l'apparentement entre les femelles. J'ai utilisé les données de contacts issues du suivi des 15 femelles du printemps 2010 à l'automne 2011 de manière à étudier les facteurs environnementaux et individuels qui les influencent. J'ai découvert que les contacts variaient beaucoup entre les saisons, étant plus élevés durant l'hiver. Les facteurs qui influençaient les contacts étaient différents entre les saisons. L'été, l'apparentement avait un effet positif sur les contacts. À l'inverse, l'apparentement n'avait aucune conséquence sur les contacts durant l'hiver. Cependant, plus les températures étaient froides, plus les contacts étaient fréquents durant l'hiver. Ces résultats suggèrent que les femelles ratons laveurs utilisent la thermorégulation sociale durant l'hiver pour diminuer les coûts énergétiques liés au maintien de leur température corporelle.

En conclusion, j'ai montré que le chevauchement des domaines vitaux peut être un bon estimateur du taux de contacts. Mes résultats suggèrent que les températures froides de l'hiver ont une influence plus importante que l'apparentement sur la structure des femelles ratons laveurs au nord de leur distribution. Mes résultats suggèrent que des contraintes environnementales, telles que la température, pourraient avoir une influence importante sur la formation et le maintien des groupes chez certaines espèces. L'étude de facteurs environnementaux et individuels ainsi que de leurs impacts sur la structure sociale chez différentes espèces pourrait permettre d'améliorer notre compréhension de l'évolution de la socialité.

REMERCIEMENTS

J'aimerais tout d'abord remercier ma directrice, la Pre. Fanie Pelletier pour m'avoir fait confiance et pour m'avoir permis de me dépasser. Tu as toujours été d'une grande disponibilité et tu m'as toujours encouragée et appuyée dans mes divers projets. Tu es une personne passionnée et c'est stimulant, je n'arrêterai jamais de faire de la science. Merci Fanie. J'aimerais aussi remercier mon codirecteur, le Pr. Dany Garant. Merci pour ton temps et tes innombrables commentaires sur la multitude de versions préliminaires d'articles et de présentations. Merci aux membres de mon comité, Marco Festa-Bianchet et Denis Réale, pour vos conseils. Je voudrais aussi remercier tous les employés du parc national du Mont-Orford (Claudia Lascelle, Manon Paquette, et Frédérick Dagenais) ainsi que les employés du MRNF qui m'ont aidée (Sophie Plante, Robert Patenaude, Julien Mainguy et Sébastien Brisebois). Je tiens aussi à remercier tous les assistants qui m'ont aidée sur le terrain, particulièrement P-O et Sarah. Vous avez été nombreux à travailler avec moi, votre aide fut importante et appréciée! Un clin d'œil particulier à Léa, ce fut un super printemps en ta compagnie, même enlisée jusqu'au cou dans la boue! Jen, merci pour l'aide sur le terrain, en labo et pour ton écoute! Merci à mes collègues de bureau et aux membres des labos en écologie. Alex et Gab, merci pour votre aide et les moments de détente. Eric, thank you for your help and advices. Je voudrais remercier tout spécialement mes parents, Denise et Roger. Papa, maman, vous m'avez toujours dit : « Fais ce que tu aimes dans la vie », c'est ce que je fais et ce que je vais continuer à faire grâce à vous. Merci pour tout, je vous aime. Merci aussi à mon frère Christian, à tous les membres de ma famille et à mes amis : on ne se voit pas souvent, mais je pense à vous. Un clin d'œil tout spécial à Katia et Jérémie. J'aimerais aussi dire merci à Lise et Normand, vous avez souvent été d'une grande aide, merci d'être là! Finalement, un énorme merci à celui qui partage ma vie. Pascal, merci pour ta patience, ta compréhension et tes encouragements. Merci d'avoir accepté mes nombreuses absences. Tu es une des rares personnes qui arrive à apaiser mon caractère. Je t'aime. Mon projet de recherche a été rendu possible grâce au soutien financier du CRSNG, du FQRNT, du CSBQ, de la fondation canadienne pour l'innovation et de la Chaire de Recherche du Canada en Démographie Évolutive et Conservation, puis grâce également au soutien logistique du parc national du Mont-Orford.

TABLE DES MATIÈRES

LISTE DES TABLEAUX

CHAPITRE 4

LISTE DES FIGURES

Patience and tenacity of purpose are

worth more than twice their

weight of cleverness.

- Thomas Henry Huxley

CHAPITRE 1

INTRODUCTION

1.1 La socialité et l'importance de l'étude des contacts

La socialité est un thème important dans l'écologie comportementale des animaux (Hinde, 1976; Palla *et al.,* 2007; Frère *et al.,* 2010) puisqu'elle est étroitement liée aux stratégies de reproduction (Clutton-Brock, 1989), de quête alimentaire (White & Harris, 1994; Klaassen *et al.,* 2006), ainsi qu'à la propagation de maladies infectieuses (McCallum *et al.,* 2001). De plus, dans le règne animal, on observe une très grande variabilité de degrés de socialité. Chez les mammifères par exemple, on retrouve à un extrême des espèces solitaires comme le guépard (*Acinonyx jubatus*) et à l'autre des espèces eusociales telles que le rat-taupe nu (*Heterocephalus glaber*). La variabilité de socialité entre les espèces résulte d'un compromis entre les coûts et les bénéfices qui sont associés à la vie en groupe (Krause & Ruxton, 2002). Les bénéfices de la vie en groupe incluent une diminution du risque de prédation, par exemple par l'effet de dilution et une augmentation du succès de quête alimentaire par le biais de la chasse en groupe (Krause and Ruxton 2002). Cependant, la vie en groupe engendre aussi certains coûts tels que l'augmentation de transmission de maladies due aux interactions plus fréquentes et à l'augmentation de la compétition pour les ressources (Krause and Ruxton 2002). Bien que cette variabilité soit plus grande entre les espèces, on la retrouve aussi à l'intérieur des espèces (Lott, 1984). Chez le campagnol des prairies (*Microtus ochrogaster*) par exemple, on retrouve, selon la population, des individus solitaires, des paires d'individus ou même des groupes (McGuire & Getz, 1998). La socialité intraspécifique est influencée par plusieurs déterminants environnementaux (Lott, 1984) et individuels (Hamilton, 1964). Chez le chacal doré (*Canis aureus*) par exemple, la formation de groupes fluctue en fonction de l'abondance des ressources alimentaires : plus les ressources alimentaires sont nombreuses,

1

plus les groupes sont grands (Loveridge & Macdonald, 2001). Cependant, l'étude de la socialité d'une espèce et des facteurs qui l'influencent passe inévitablement par la connaissance des contacts (table 1.1) entre les individus. L'accessibilité des espèces est ainsi très importante pour l'obtention des connaissances concernant les contacts entre les individus puisqu'elle nécessite généralement l'observation des animaux. La majorité des connaissances concernant les facteurs déterminants le degré de socialité intraspécifique a donc été d'abord acquise par l'étude d'espèces grégaires (Alexander, 1974; Dunbar, 1988; Festa-Bianchet, 1991) via l'observation directe des individus. Les connaissances concernant les contacts des individus d'espèces solitaires (table 1.1), qui sont généralement plus difficiles à observer, ont été obtenues plus récemment à partir de suivis télémétriques, suite au calcul des domaines vitaux (Kenward & Hodder, 1998; Millspaugh et al., 2000; Böhm et al., 2008) et à l'aide de colliers émetteurs de type « proximity logger » (Prange et al., 2006). L'utilisation de ces techniques a permis de constater que les individus de certaines espèces de carnivores solitaires montrent de la flexibilité sociale, c'est-à-dire, de la variabilité dans leurs taux de contacts (Caro, 1994; Gehrt & Fritzell, 1998b; Hays & Conant, 2003).

Chez les carnivores, la flexibilité sociale serait un facteur important de l'évolution de la socialité (Dalerum et al., 2006) puisqu'elle aurait permis, sous l'influence de différentes contraintes environnementales, l'évolution de plusieurs formes d'organisations sociales. Bien que les espèces solitaires soient généralement caractérisées par un système social simple et soient donc considérées comme étant moins intéressantes pour l'étude de l'évolution de la socialité, on retrouve chez certaines d'entre elles des structures sociales plus complexes (Caro, 1994; Gehrt & Fritzell, 1998b; Hays & Conant, 2003). Chez le guépard par exemple, certains mâles forment de petits groupes pour défendre un territoire alors que d'autres vont s'en occuper seuls (Caro, 1994). Les espèces solitaires qui montrent de la flexibilité sociale sont donc d'un grand intérêt pour les études concernant l'évolution de la socialité puisqu'elles peuvent nous informer sur les facteurs écologiques qui influencent les contacts entre les individus.

2

Tableau 1.1 : Terminologie relative à la structure spatio temporelle des contacts chez le raton laveur et principaux termes utilisés dans ce mémoire.

Contact (Böhm, Hutchings *et al.*, 2009)
Évènement durant lequel des individus se retrouvent à proximité les uns des autres c'est-à-dire, à moins de 2 mètre.
Solitaire (Waser and Jones 1983)
Terme qui désigne la distribution spatiale des animaux relatives à leurs congénères et non à leur interactions sociales : les espèces solitaires sont celles dont les animaux sont généralement aperçu seul. Un individu qui chasse seul peut diminuer ses interactions avec ses congénères, mais peut quand même vivre à l'intérieur d'un réseau social complexe.
Apparentement (Hardy 2003)
Coefficient décrivant la similarité génétique entre des individus résultant d'ancêtres communs.
Domaine vital (Burt 1943)
Désigne la superficie du milieu qui est utilisée par un animal pour se nourrir, se reproduire et élever ses jeunes.

1.2 Plan du mémoire de maîtrise

Mon mémoire de maîtrise débute dans un premier chapitre par une introduction générale exposant les fondements théoriques sur lesquels mes travaux sont appuyés. Tout d'abord, je présente les objectifs ainsi que l'importance de mon projet. Par la suite, je présente les fondements théoriques concernant la relation et les implications des contacts avec socialité, les domaines vitaux et l'apparentement (table 1.1). Je termine par une description de mon site d'étude et de mon modèle animal, le raton laveur.

Mon mémoire est ensuite divisé en quatre grands chapitres. Le deuxième chapitre présente un article méthodologique dans lequel j'ai vérifié l'efficacité d'un mélange d'anesthésiant pour l'immobilisation chimique du raton laveur. Dans le troisième chapitre j'explore à l'aide de cinq indices la relation entre le chevauchement des domaines vitaux et le taux de contacts de manière à vérifier l'efficacité du chevauchement des domaines vitaux comme méthode d'estimation des taux de contacts. Le quatrième chapitre, porte sur les déterminants environnementaux et individuels du taux de contacts chez les femelles ratons laveurs afin d'explorer leurs impacts sur la socialité de cette espèce. Finalement, dans le cinquième chapitre, je présente un bref retour sur les principaux résultats de mon mémoire et je discute de l'importance de mon projet et de pistes de recherches futures concernant l'étude des contacts et des contraintes écologiques qui les influencent.

1.3 Objectifs et importance de mon projet

L'objectif principal de mon projet de maîtrise était de caractériser les déterminants écologiques des femelles ratons laveurs de la population du parc national du Mont-Orford, Québec, Canada. Pour ce faire, j'ai d'abord capturé 15 femelles ratons laveurs sur lesquelles j'ai installé des colliers de type « proximity logger ». J'ai ensuite effectué un suivi télémétrique des individus du printemps 2010 à l'automne 2011. Les captures effectuées m'ont aussi permis de vérifier les effets du mélange d'anesthésiant ketamine/médétomidine sur la survie et le succès reproducteur du raton laveur. Voici spécifiquement les deux objectifs de mon projet de maîtrise :

(1)   Explorer la relation entre le chevauchement des domaines vitaux et le taux de contacts.

(2)   Caractériser les déterminants environnementaux et individuels des taux de contacts.

Chez les espèces solitaires, il est généralement difficile d'observer les contacts entre les individus. En effet, certaines espèces sont nocturnes, vivent dans des milieux denses ou sont difficiles à capturer. Par conséquent, chez certaines espèces les contacts entre les individus

4

sont estimés à partir de différentes méthodes dont l'efficacité de certaines n'a jamais été vérifiée ou est impossible à étudier. Les contacts réels sont donc rarement quantifiés sur le terrain. De plus, les facteurs écologiques qui influencent les contacts, et donc la socialité, sont peu étudiés.

Mon étude est parmi les premières à vérifier l'efficacité du chevauchement des domaines vitaux comme méthode d'estimation des taux de contacts. De plus, si cette méthode s'avérait efficace, elle pourrait être utilisée pour estimer les contacts à partir de données issues de suivis télémétriques réalisés chez plusieurs espèces. J'innove aussi en obtenant des données concernant les taux de contacts réels chez une espèce de carnivore solitaire, ce qui demeure encore peu fréquent. Ces données me permettent aussi d'étudier un thème encore peu connu chez les espèces solitaires, c'est-à-dire les facteurs écologiques qui influencent les taux de contacts et donc la socialité. Les connaissances acquises permettront d'ailleurs d'améliorer les méthodes de préventions de maladies infectieuses. En effet, en ce qui concerne les maladies infectieuses qui nécessitent un contact pour se transmettre, le taux auquel une nouvelle infection se produit à l'intérieure d'une population est dépendant du taux de contacts (McCallum, Barlow *et al.,* 2001). La fréquence des contacts est donc un facteur fondamental de la transmission de maladies infectieuses (White & Harris, 1995) et une variable clé des modèles épidémiologiques. Bien que les contacts entre les animaux soient un facteur essentiel en épidémiologie (McCallum, Barlow *et al.,* 2001; Lloyd-Smith *et al.,* 2005), les études sur le sujet demeurent peu nombreuses. Finalement, mon projet de recherche est innovateur puisque j'ai utilisé des colliers spécialisés pour quantifier les taux de contacts réels sur le terrain.

1.4 Fondements théoriques

1.4.1 Les contacts et l'organisation sociale

Les contacts entre les individus sont cruciaux en écologie comportementale puisqu'ils définissent l'organisation sociale des populations, et donc leur socialité (Hinde, 1976). De plus, lors des interactions sociales, le choix des individus avec qui un individu aura des contacts n'est généralement pas effectué de façon aléatoire. En effet, la fréquence ainsi que la durée des contacts entre les individus sont influencées par différents facteurs individuels (Hamilton, 1964) et environnementaux (Leuthold, 1979; Rowell & Rowell, 1993). Il a d'ailleurs été montré que, chez des espèces grégaires, différents facteurs écologiques influencent l'organisation sociale des populations. Chez le mouflon d'Amérique (*Ovis canadensis*) par exemple, les groupes sont séparés en fonction du sexe et de l'âge. À l'âge de trois ans, la majorité des jeunes mâles quitte le groupe natal, formé de femelles adultes et de subadultes, pour rejoindre un groupe de mâles adultes (Festa-Bianchet, 1991). Les facteurs environnementaux tels que l'abondance de nourriture (Loveridge & Macdonald, 2001) et les températures froides (Willis & Brigham, 2007) peuvent aussi avoir des effets non négligeables sur l'organisation sociale. Chez la grande chauve-souris brune (*Eptesicus fuscus*) par exemple, les contacts entre les individus sont plus nombreux lorsque les températures sont plus froides (Willis & Brigham, 2007). À fine échelle, les contacts entre les individus sont aussi influencés par la manière dont les individus sont distribués dans l'espace (Wolf & Trillmich, 2007). Chez l'otarie des Galapagos (*Zalophus wollebaeki*) par exemple, plus la distance est élevée entre les animaux, moins les contacts sont fréquents. Cependant, en ce qui concerne les espèces solitaires, étant donné les problèmes logistiques liés à leur observation, il est difficile d'obtenir les taux de contacts réels. Par conséquent, les études concernant les déterminants écologiques des contacts sont peu fréquentes chez ces espèces. Il est donc nécessaire, pour obtenir des informations concernant l'organisation spatiale des individus, d'utiliser des méthodes qui permettent d'estimer les taux de contacts. Que ce soit à partir des données réelles ou d'estimations de celles-ci, il demeure essentiel d'obtenir des informations concernant les

6

contacts entre les individus pour effectuer des études fondamentales et appliquées de manière à comprendre l'évolution de la socialité et prédire la propagation de maladies infectieuses. Bien que les analyses de réseaux sociaux soient fréquemment utilisées dans la littérature (Borgatti, Everett *et al.*, 2002; Böhm, Hutchings *et al.*, 2009; Krause, Lusseau *et al.*, 2009) et spécialement en ce qui à trait à l'épidémiologie (Cauchemez, Bhattarai *et al.*, 2011), elles requièrent une taille d'échantillon élevée et une grande variabilité des caractéristiques individuelles (sexe, masse, âge, contact...). De plus, elles n'apportaient pas d'informations complémentaires pertinentes aux résultats obtenus à l'aide d'autres analyses durant cette étude, les analyses de réseaux n'ont donc pas été effectuées durant cette étude.

1.4.2 Le domaine vital reflet de l'organisation sociale

Le domaine vital, défini comme étant la superficie du milieu qui est utilisée par un animal pour se nourrir, se reproduire et élever ses jeunes (Burt, 1943; table 1), est un outil important en écologie comportementale puisqu'il permet d'obtenir des informations concernant les contacts entre les individus (Kenward & Hodder, 1998; Böhm, Palphramand *et al.*, 2008). En effet, le calcul du chevauchement des domaines vitaux est une méthode couramment utilisée pour obtenir une estimation des taux de contacts entre les individus (Kenward & Hodder, 1998; Böhm, Palphramand *et al.*, 2008; Habib *et al.*, 2011). L'utilisation fréquente de cette méthode pour estimer les taux de contacts, chez les espèces solitaires, s'explique par les difficultés logistiques à quantifier leurs contacts sur le terrain. Les facteurs qui influencent le chevauchement des domaines vitaux sont étroitement liés à ceux qui affectent leur taille puisque pour une superficie donnée, une augmentation de la taille des domaines vitaux, par exemple, va induire inévitablement un chevauchement plus élevé. Chez les carnivores, la disponibilité de nourriture et la variabilité de l'abondance de celle-ci dans le temps ont un effet substantiel sur la taille des domaines vitaux et par conséquent sur leur chevauchement (Maher & Lott, 2000). Des ressources très abondantes et très prédictibles ainsi que des ressources peu abondantes et peu prédictibles ont pour effet de diminuer la territorialité. À l'inverse des

7

ressources moyennement abondantes et prédictibles, ont pour effet de maintenir la territorialité (Maher & Lott, 2000). Cette variation serait expliquée par le fait que lorsque la nourriture est très abondante, ou à l'inverse très rare, les coûts associés à la défense des ressources sont plus élevés que leurs bénéfices (Maher & Lott, 2000). Cependant, les ressources essentielles à la survie des animaux ne se retrouvent généralement pas de façon homogène dans l'habitat, et la distribution spatiale des ressources a donc aussi un effet important sur le chevauchement des domaines vitaux (Maher & Lott, 2000). Chez les espèces se retrouvant dans un habitat fragmenté par exemple, le chevauchement des domaines vitaux est beaucoup plus élevé dans les zones où on retrouve les ressources essentielles (Atwood & Weeks, 2003). Toutefois, les facteurs qui influencent le chevauchement des domaines vitaux n'ont peut-être pas nécessairement des effets sur l'organisation sociale des individus. Bien qu'une augmentation de la superficie de la zone de chevauchement des domaines vitaux entraine une probabilité plus élevée de rencontre entre les individus, elle peut aussi entrainer de l'évitement temporel. En effet, deux individus montrant un fort chevauchement de leur domaine vital pourraient visiter les zones d'habitats partagées à des moments différents et n'avoir ainsi aucun contact. Il a d'ailleurs été montré, chez le cerf de virginie (*Odocoileus virginianus*), que le chevauchement des domaines vitaux n'étaient pas représentatif des contacts entre les individus (Schauber *et al.*, 2007). Les facteurs écologiques qui influencent le chevauchement des domaines vitaux n'aurait donc, pas nécessairement d'effet sur l'organisation sociale des animaux. C'est pourquoi il est important d'obtenir les taux de contacts réels, de manière à les utiliser pour étudier la relation entre le chevauchement des domaines vitaux et l'organisation sociale des populations animales.

1.4.3 L'influence de l'apparentement sur l'organisation sociale

Bien que moins évidentes que les facteurs environnementaux, certaines caractéristiques individuelles ont des effets sur l'organisation sociale des animaux. Le degré d'apparentement entre les individus est l'une de ces caractéristiques qui depuis la dernière décennie est de plus en plus étudiée (Bacon *et al.*, 1999; Pomeroy *et al.*, 2001; Spong *et al.*, 2002; Coltman *et al.*,

2003). L'intérêt de l'apparentement dans l'étude de la socialité est liée, entre autres, à la théorie de sélection de parentèle (Hamilton, 1964). Selon cette théorie, il y aurait des bénéfices indirects sur la valeur adaptative d'un individu à aider des individus avec lesquels il est apparenté (Hamilton, 1964). Par conséquent, le degré d'apparentement pourrait avoir une influence sur le choix des individus avec lesquels un animal a des contacts ainsi que la fréquence de ceux-ci. Un effet positif de l'apparentement sur les contacts entre les individus a d'ailleurs été montré chez différentes espèces. Chez le mouton domestique (*Ovis aries*) par exemple, le degré d'apparentement entre les individus qui ont des contacts plus fréquents est plus élevé qu'entre ceux qui ont peu ou pas de contacts (Nituch *et al.,* 2008). Le même phénomène a été observé chez des espèces sauvages d'animaux grégaires (Bacon, Dallas *et al.,* 1999; Pomeroy, Wilmer *et al.,* 2001; Buston *et al.,* 2009; Frère, Krützen *et al.,* 2010). En ce qui concerne les animaux solitaires, un effet positif de l'apparentement sur les contacts entre les individus a été observé chez certaines espèces (Schenk *et al.,* 1998; Ratnayeke *et al.,* 2002; Støen *et al.,* 2005). Chez l'ours brun (*Ursus arctos*) par exemple, on retrouve une structure matriarcale qui serait engendrée par la capacité des individus à reconnaître les individus avec lesquels ils sont apparentés (Støen, Bellemain *et al.,* 2005).

Bien que les études traitant de l'effet de l'apparentement sur la structure sociale soient nombreuses (Bacon, Dallas *et al.,* 1999; Ratnayeke, Tuskan *et al.,* 2002; Coltman, Pilkington *et al.,* 2003; McEachern *et al.,* 2007; Buston, Fauvelot *et al.,* 2009), la majorité d'entre elles utilisent le chevauchement des domaines vitaux comme proxy du taux de contact pour étudier son effet sur les contacts entre les individus. L'efficacité du chevauchement des domaines vitaux pour estimer les taux de contacts étant peu étudiée, il est d'autant plus important de documenter les effets de l'apparentement sur les contacts à partir de quantifications de ceux-ci sur le terrain.

1.5 Aire d'étude et population

Mon aire d'étude se situe dans le secteur du lac Stukely du parc du Mont-Orford en Estrie. Le parc du Mont-Orford a une superficie de 58,37 km^2 et est situé à environ 35 km à l'ouest de la ville de Sherbrooke. Le secteur du lac Stukely du parc du Mont-Orford comprend une aire de camping de 321 sites ouverte au public de mai à octobre. Le suivi de la population de ratons laveurs du parc national du Mont-Orford a débuté au printemps 2009. Depuis, 117 ratons laveurs ont été capturés. Puisque les animaux sont anesthésiés lors des captures, cela nous a permis de prendre plusieurs données morphologiques (masse, circonférence de la poitrine, circonférence du cou, longueur totale, etc.), comportementales et physiologiques (température corporelle). Dans le cadre de ma maîtrise, soit de 2009 à 2011, des colliers émetteurs ont aussi été installés sur les ratons laveurs.
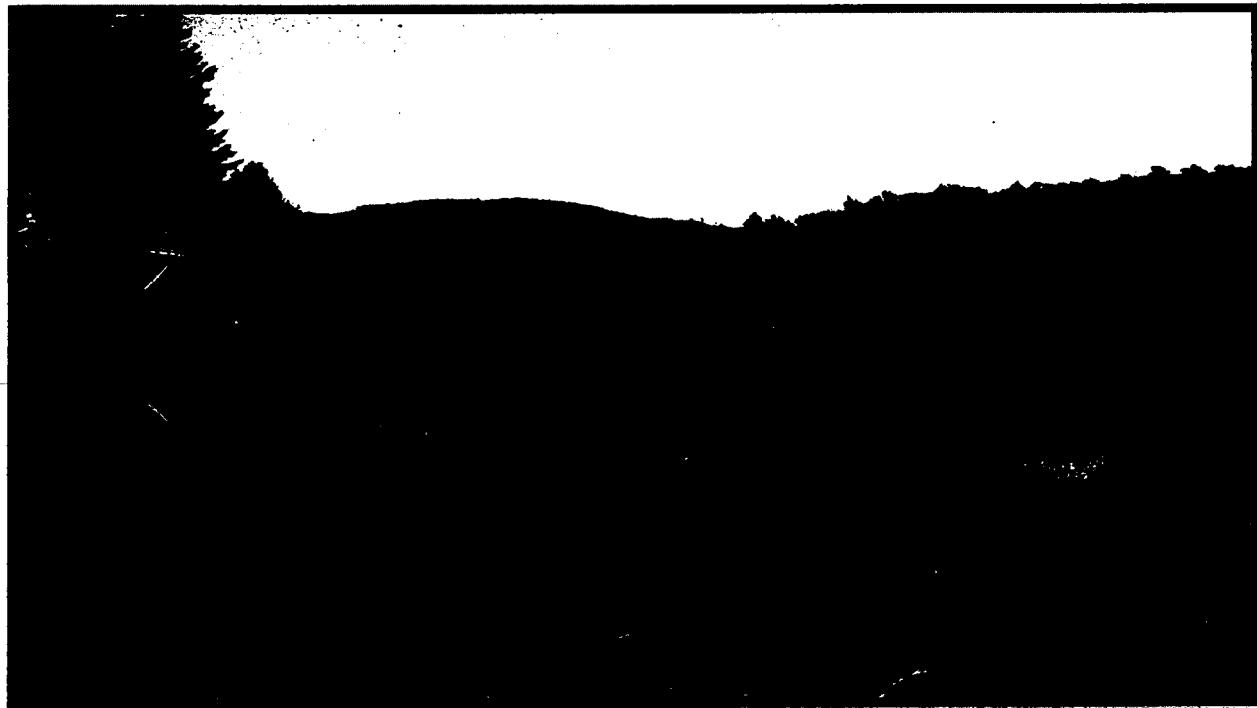
Figure 1.1 Étang Fer-de-Lance, Parc national du Mont-Orford. Crédit photo : Pierre-Olivier Benoit.

1.6 Le raton laveur comme sujet d'étude

Le raton laveur est un mammifère nocturne de taille moyenne de la famille des procyonidés, chez lequel la philopatrie est biaisée envers les femelles (Gehrt & Fritzell, 1998a). Sa distribution géographique s'étend de l'Amérique du Nord à l'Amérique centrale (Gehrt, 2003). Son régime se compose principalement d'aliments qui sont disponibles dans l'environnement selon la saison : crustacés, bivalves, poissons, œufs, fruits, noix, plantes et petits animaux (Johnson, 1970; Gehrt, 2003). Le raton laveur utilise principalement des arbres creux comme tanières de repos, mais lorsque ceux-ci se font rares, il utilise plutôt des terriers d'autres mammifères, des arbres, des cavités dans le sol ou dans le roc, des bâtiments ou simplement le sol (Zeveloff, 2002). En période de gestation (de février à avril), les femelles vont chercher une cavité, habituellement un arbre creux, pour mettre bas et pour y laisser les jeunes pendant les premières semaines. En Amérique du Nord, la reproduction s'effectue entre le mois de janvier et le mois de mars, ayant sont apogée au mois de février. La gestation est d'une durée moyenne de 63 jours, et la mise bas a lieu majoritairement pendant le mois d'avril. Les portées ont une taille variant entre 1 et 8 jeunes, et les jeunes pèsent entre 60 et 75 grammes à la naissance. Les femelles allaitent leurs petites pendant 8 à 16 semaines. Durant la période hivernale, les tanières sont généralement des cavités de grande taille partagées par plusieurs individus (Rosatte, 2000). Durant l'été, les ratons laveurs sont plutôt solitaire et utilisent principalement les arbres comme site de repos (Zeveloff, 2002).

Bien qu'il soit établi que le raton laveur est un carnivore solitaire (Fritzell, 1978), des groupes stables d'individus adultes ont été observés chez cette espèce (Gehrt & Fritzell, 1998a; Gehrt & Fritzell, 1998b; Chamberlain, 2002; Pitt *et al.*, 2008a). Cependant, les facteurs affectant la formation et le maintien de ces coalitions demeurent peu documentés (Gehrt & Fritzell, 1997; Pitt, Larivière *et al.*, 2008a). En ce qui concerne les femelles adultes, le comportement de philopatrie aurait comme effet d'augmenter la fréquence des contacts entre les individus apparentés. En effet, Ratnayeke (2002) a observé que chez le raton laveur la philopatrie entraine, à fine échelle, un apparentement plus élevé des individus voisins. Bien que

l'apparentement semble être un facteur important dans l'organisation sociale des ratons laveurs, les connaissances concernant la fluctuation des contacts entre les saisons et les facteurs écologiques qui les influencent demeurent encore limitées.

Le raton laveur est aussi une espèce intéressante en épidémiologie et en gestion de la faune puisqu'il est le principal hôte de la maladie de la rage. Au Québec, la variante du raton laveur du virus de la rage est présente seulement depuis 2006 (MRNF, 2009). Celle-ci a initialement été identifiée dans le sud des États-Unis (en Floride) en 1950 et s'est répandue dans le reste du pays entre les années 1970 et 1990 (Rupprecht *et al.,* 1995; Fu, 1997; Zeveloff, 2002). La dispersion de cette maladie aurait été entrainée, entre autres, par la translocation de milliers de ratons laveurs dans les États de la Virginie et de la Caroline du Nord (Rupprecht, Smith *et al.,* 1995; Zeveloff, 2002). La distribution rapide de cette maladie inquiète les autorités publiques puisqu'elle peut être mortelle chez l'homme (Rubin *et al.,* 1970). Les variations que l'on retrouve dans son organisation sociale ainsi que la maladie infectieuse dont il est le principal hôte font du raton laveur un modèle idéal pour étudier les déterminants écologiques des taux de contacts

CHAPITRE 2

IMMOBILISATION CHIMIQUE DE RATONS LAVEUR AVEC UN MÉLANGE DE KÉTAMINE-MÉDÉTOMIDINE

Introduction de l'article

Durant ma maîtrise, j'ai participé à la capture ainsi qu'à l'anesthésie de près de 117 ratons laveurs. Étant la première étudiante sur le projet ratons laveurs au parc du Mont-Orford, j'ai participé à l'élaboration des protocoles de captures et de suivis des individus. De plus, puisqu'il existe plusieurs types d'anesthésiants et que leurs impacts peuvent être différents entre les animaux, il est important de les explorer en fonction des espèces. Les effets du mélange d'anesthésiants utilisé lors de mon projet de maîtrise (Kétamine-médétominide) n'étant pas connus chez le raton laveur, nous avons récolté des données lors de chacune des captures en vue de les étudier. J'ai donc été en mesure de tester l'efficacité du mélange d'anesthésiants chez le raton laveur. De plus, j'ai exploré l'impact de l'anesthésie sur la survie à court terme, le succès reproducteur et l'habituation aux anesthésiants. L'article qui suit présente en détail le protocole de captures et les analyses. Ma contribution à cet article a été substantielle puisque j'ai effectué les analyses, écrit l'article et coordonné le processus de publication. J'ai été encadrée lors de ce projet par la Pre. Fanie Pelletier. De plus, plusieurs versions de chacun des articles ont été révisées par la Pre. Fanie Pelletier et par le Pr. Dany Garant.

13

Chemical immobilization of raccoons with ketamine-medetomidine mixture and reversal with atipamezole

Par

Karine Robert, Dany Garant et Fanie Pelletier

Abstract

Safe and reliable capture techniques for wild animals are important for ecologic studies and management operations. We assessed the efficiency of ketamine-medetomidine (K:M) injection and reversal with atipamezole. We anesthetized 67 raccoons (34 males, 33 females) 103 times (individuals captured between one and five times) from April 2009-October 2010 in Mont-Orford Provincial Park, Quebec, Canada. We administered a 1:1 mixture by volume of ketamine (Vetalar, 100 mg/ml, Bioniche Canada Inc., Belleville, Ontario, Canada) and medetomidine (Domitor, 1 mg/ml, Pfizer Canada Inc., Kirkland, Quebec, Canada) by intramuscular injection. Mean (±SD) induction times for males and females were 6.1±2.8 and 6.6±3.7 min, respectively. Mean induction time was 2 min longer for juveniles than adults (7.8±3.9 and 5.8±2.9 min, respectively) and longer in autumn than spring for adults (7.7±3.8 and 5.4±2.9 min, respectively). Recovery time after administration of atipamezole was 9.6±3.8 and 8.4±4.4 min for males and females, respectively. Recovery time was longer in spring than autumn (10.2±4 and 7.4±3.8 min, respectively) for adults. Induction time increased by 166 % after five captures of the same individual. Immobilization did not affect body mass, adult survival, or female reproductive success. We suggest the K:M mixture used is a safe and reliable method for anesthetizing raccoons in field conditions.

Key words: Immobilization, ketamine, medetomidine, *Procyon lotor*, raccoon.

Introduction

Chemical immobilization of wild mammals is frequently required in ecologic research and wildlife management. Several research programs depend upon safe handling procedures under field conditions to mark, measure, vaccinate, or sample wild animals (Gannon & Sikes, 2007). The efficacy of chemical immobilization depends on the type of drug, dosage, season, species, and characteristics including sex, age and size of target animals (Jalanka & Roeken, 1990). Drug mixtures may have synergistic effects on induction and recovery times compared to individual drugs and these effects may vary among species (Kreeger *et al.*, 2002). It is thus important to characterize the efficacy of each drug or drug mixture when used for a new species.

Potential consequences of capture, immobilization, and handling on individuals should also be assessed. There is mounting evidence that such manipulations may increase stress on animals (Harper & Austad, 2001; Fletcher & Boonstra, 2006; Lynn & Porter, 2008), which could lead to undesirable effects on individual performance on short and long-term scales. Several studies have reported negative consequences of capture and marking on behavior (Pelletier *et al.*, 2004), foraging efficiency (Saraux *et al.*, 2011), rates of production and abandonment of young (Ballard & Tobey, 1981; Côté *et al.*, 1998), and survival (Oosthuizen *et al.*, 2009). For example, Cattet *et al.*, (2008) found that repeated immobilization reduced mobility and body condition of grizzly bears (*Ursus arctos horribilis*) and black bears (*Ursus americanus*). Frequently, animals must be anesthetized more than once to change telemetry collars, download data, or measure growth. While the effects of repeated immobilization on the efficacy of anesthesia have often been studied in laboratory animals such as rats (*Rattus norvegicus*; Fassoulaki *et al.*, 1994; Hedenqvist *et al.*, 2000) or dogs (Bert *et al.*, 2008), they have rarely been assessed in wild species (Field *et al.*, 2002; Wheatley *et al.*, 2006). While there is no obvious reason to expect that drug effect would be different for captive versus wild animals of the same species, it is possible that the effect of repeated immobilization on the efficacy of anesthesia may be undetectable in the wild given that the number of repeated immobilizations for wild animals is typically lower than for captive animals. Although some

15

previous studies have found no effect of repeated immobilization on wild animals (Poole *et al.*, 1993; Thil & Groscolas, 2002; Storms *et al.*, 2005), others suggested that animals can become habituated to drugs (Field, McMahon *et al.*, 2002; Wheatley, Bradshaw *et al.*, 2006). However, it is unknown whether an increase in drug tolerance due to repeated use of anesthesia is applicable to a wide range of species.

Medetomidine hydrochloride is a selective α_2-adrenoreceptor agonist with dose-dependent muscle relaxant properties, as well as analgesic and sedative effects (Kreeger, Arnemo *et al.*, 2002). Its effects can be reversed by the antagonist atipamezole hydrochloride (Jalanka & Roeken, 1990). Ketamine hydrochloride is a dissociative anesthetic that reduces sensibility while keeping the animal immobile (Kreeger, Arnemo *et al.*, 2002). Used alone, it can cause superficial analgesia and muscle rigidity; however, when used in combination with medetomidine there is a reduction of side effects and overall drug volume required (Kreeger, Arnemo *et al.*, 2002). A ketamine-medetomidine mixture (K:M) has provided safe and effective immobilization of numerous species (Kreeger, Arnemo *et al.*, 2002). Although K:M mixture is apparently effective for immobilizing other carnivores, its efficacy to immobilize raccoons has not been examined.

Raccoons are widely distributed from Mexico to Canada (Gehrt, 2003), are common in urban areas (Roscoe, 1993), and frequently live in proximity to humans. As raccoons can carry several zoonoses, including rabies (McLean, 1975), and often occur at high densities (Zeveloff, 2002), several management programs and studies in Canada and the USA (Rosatte *et al.*, 2007) involve raccoon capture, which may also require anesthesia. It is thus important to have a safe, effective, and reliable immobilization method with as few short-term physiologic effects as possible and no consequences on reproductive success and survival of animals.

Several drugs have been used for immobilization of raccoons, including ketamine (Gregg & Olson, 1975; Beck, 1976; Norment *et al.*, 1994), succinylcholine chloride (Hoilien & Oates, 1981), saffan (Clutton & Duggan, 1986) and tiletamine-zolazepam (Pitt *et al.*, 2006). The use

16

of tiletamine-zolazepam mixture leads to an uncommon side effect that affected raccoon behavior (Pitt, Larivière *et al.*, 2006), leading them to frequently approach researchers during recovery, which can be problematic as raccoons may carry rabies (McLean, 1975). This behavior was also observed in arctic foxes (*Vulpes lagopus*) immobilized with tiletamine-zolazepam (Samelius *et al.*, 2003). Although some of these drugs, used alone or in combination, have been shown to provide safe and effective immobilization, they have yielded long recovery times due to the lack of a reversal agent (Belant, 2004). The ketamine-medetomidine mixture is currently one of the most commonly used drugs for immobilizing small carnivores (West *et al.*, 2007). It requires smaller doses, has quicker recovery times, and the availability of the antidote (atipamezole) allows reversing the effect of the medetomidine. We are not aware, however, of any study that has documented its use with raccoons.

We needed to capture and mark raccoons using live traps for a study of individually recognizable animals. Raccoon aggressive behavior and risk of rabies transmission made chemical immobilization essential. We report the effects of age, sex, season, and repeated immobilization on induction and recovery times of raccoons anesthetized using the K:M mixture. We also report the efficacy of reversal using atipamezole. Finally, we explored the consequences of capture, immobilization, and handling on short-term body mass changes and on short and long-term survival and reproductive performance of raccoons.

Study area and captures

We captured raccoons for 20 days in spring and autumn (April and October) 2009 and 2010. Raccoons were followed by radiotracking from April 2009 to October 2010 on a 58-km^2 study site in Mont-Orford Provincial Park, Quebec, Canada (72°14'18''W, 45°21'39''N). Raccoons were caught in live traps (Havahart® Products, Lititz, Pennsylvania, USA) baited with a mixture of fresh mackerel (*Scomber scombrusand*) or canned sardines (*Sardina pilchardus*) and canned corn (*Zea mays*). Traps were opened daily in late afternoon (5:00 PM-7:00 PM),

checked at sunrise, and closed during the day. During the four trapping sessions, we set 66 traps 100 m apart over a 1000 x 500-m grid.

Materials and methods

Captured raccoons were weighed in the trap, then immobilized with a 1:1 mixture by volume of ketamine (Vetalar, 100 mg/ml, Bioniche Canada Inc., Belleville, Ontario, Canada) and medetomidine (Domitor, 1 mg/ml, Pfizer Canada Inc., Kirkland, Quebec, Canada) administered by intramuscular injection with a hand syringe. We determined our starting dosage using those suggested by West et al., (2007): 5 mg/kg body weight of ketamine and 0.05 mg/kg of medetomidine. Following the observation that raccoons maintained some reflexes during anesthesia (ears twitching) at this dosage, we adjusted the dosage to 5.5 mg/kg of ketamine and 0.055 mg/kg of medetomidine. After drug injection, we left the raccoon in the trap in a quiet place until it was unresponsive to touch (induction time). If the raccoon was not immobilized after 10 min, we administered a second dose at half of the initial dose. If the animal was still not immobilized 10 min after the second injection, we again administered half of the initial dose. Once the animal was immobilized, we applied ophthalmic ointment to eyes to prevent desiccation. Raccoons were then sexed, measured, and marked with a pit tag (AVID Canada, Calgary, Alberta, Canada) and two colored plastic ear tags (Dalton ID Systems Ltd., Henley-on-Thames, Oxon, England). Adult raccoons (>5 kg) were fitted with a VHF collar (Sirtrack, Havelock North, Hawkes Bay, New Zealand or Holohil Systems Ltd., Carp, Ontario, Canada). For a subset of the captures (n=13), we monitored three physiologic parameters during the anesthesia: rectal temperature (C), heart rate (beats per min [bpm]), and respiration rate (breaths/min). These parameters were recorded at the beginning and end of the processing period while the animal was still immobilized. Pregnancy status was assessed by abdominal palpation and observation of developed mammae as a sign of lactation. The effect of medetomidine was reversed by an intramuscular injection of 0.375 mg/kg atipamezole (Antisedan, 5 mg/ml, Pfizer Canada) 30 min postinduction. After the atipamezole injection, we placed the raccoon back in the trap for recovery. 'Head-up' time was measured as the time

18

between atipamezole injection and when the animal first lifted its head. After recovery from anesthesia (approximately 1 hr), raccoons were released at their capture site. We waited at least six mo between immobilization events for the same animal and if the animal was recaptured within this period, it was weighed and released immediately on site. We collected repeated body mass data for 44 animals measured within 7 days of initial capture. We chose a time period of 7 days because, despite animals gaining mass rapidly in both spring and autumn, the mass gain of captured animals that were not drugged was negligible over 7 days ($t= 1.04$, df=43, $P=0.31$). We thus used that window of time to test whether capture and chemical immobilization have short-term effects on individual mass changes.

We assessed the effect of chemical immobilization on animal weight by comparing the weight measured the day of immobilization with a measurement within 7 days postimmobilization. To monitor survival, radio-collared animals were located one to five times per week for at least 3 mo after each chemical immobilization during capture sessions in 2009 and 2010. We followed every collared female daily by radio tracking and identified den location for females that were found in the same den for at least four consecutive days. We checked each den for cubs with a SeeSnake micro™ Inspection Camera (RIGID, Elyria, Ohio, USA). We used the presence of young as an index of the proportion of known pregnant females that successfully weaned their litter. All procedures were approved by the University of Sherbrooke's Wildlife Animal Care Committee (FP2008-02).

Statistical analyses

Multiple linear regressions were used to test whether induction and head-up times varied with age, sex, season (spring and autumn), drug dose, and number of immobilizations. We used a generalized linear mixed model with binomial error structure to determine if immobilization affected adult survival. Individual identity was included as a random effect in the model to avoid pseudoreplication. It is logistically unfeasible to compare survival of noncaptured animals with captured ones, as we cannot follow raccoons accurately without telemetry

19

equipment, which requires an initial capture and use of anesthesia. We thus assessed the effect of anesthesia on survival by comparing collared raccoons not anesthetized during a given capture session (spring/autumn 2009/2010) with collared raccoons that were anesthetized in a given session. Overall, 56 of the 67 raccoons captured were fitted with collars. Of those 56 raccoons, 23 were not immobilized during at least one trapping session and were used as reference individuals for survival and reproductive success analyses. We used a paired t-test to determine if anesthesia had an effect on individual body weight by comparing weight the day of the immobilization with weight measured within 7 days postimmobilization. If required, data were log transformed prior to analysis to respect the assumption of normality. All analyses were performed in the R statistical environment (version 2.10.0; R Development Core Team, 2009).

Results

We captured 67 raccoons (34 males, 33 females) and performed 103 chemical immobilizations. Second and third injections were necessary for 15 (15%) and two (2%) immobilizations, respectively. We excluded immobilizations requiring repeated injections from data analysis on induction and head-up times, but included them in other analyses. Of the 86 immobilizations achieved with a single dose, 62 were performed on animals captured once, 12 on animals captured twice, 7 on animals captured three times, 4 on animals captured four times and 1 on an animal captured five times. Rectal temperature of immobilized raccoons ranged 36.2–39.4 C (mean±SD, 37.5±0.8 C) at induction time and 35.3–39.8 C (36.9±1.2 C) just prior to atipamezole injection. Heart rate ranged from 56–120 bpm (82.8±20.0 bpm) at induction time and 56–120 bpm (71.7±20.6 bpm) just prior to atipamezole injection. Respiration rate of anesthetized raccoons ranged 12–52 breaths/min (28.5±10.6 breaths/min) at induction time and 8–40 breaths/min (21.0±9.8 breaths/min) just prior to atipamezole injection. On average, induction time was 2 min longer for juveniles than for adults (t=2.55, df=77, P=0.01; Table 2.1). Season also affected induction time whereby autumn induction times were 2.6 min longer than those recorded in spring for adults and juveniles (t=-3.37,

df=77, P 0.01; Table 2.1). As the number of repeated immobilizations increased, we observed an increase in induction time (t=3.03, df=77 P<0.01; Figure 2.1), but no effect on the dose required to immobilize an individual (animal recapture more than one time did not required additional injection more often compare to animal capture only once, t=0.73, df=101, P=0.47). There was no effect of sex on induction time (t=-0.12, df=77, P=0.90). Head-up time averaged 2.8±0.9 min longer in spring than in autumn (t=3.15, df= 8, P<0.01). We found no effect of sex (t=1.30, df=78, P=0.20), age (t=-1.58, df= 8, P=0.12), number of immobilizations (t=-1.48, df=78, P=0.14) or dose (t=0.49, df=78, P=0.62) on head-up time.

Table 2.1 Weight, induction and head-up times of raccoons immobilized with a single dose of ketamine-medetomidine (K:M) mixture. Sample sizes (*n*) refer to the number of immobilizations in each category. Immobilizations were performed in April and October 2009-2010, at Mont-Orford Provincial Park, Quebec, Canada.

	Weight mean±SD (kg)	Induction time mean±SD (min)	Head-up time mean±SD (min)
All seasons			
Juveniles (*n*=25)	4.6±1.6	7.8±3.9	7.8±3.8
Adults (*n*=61)	5.9±1.6	5.8±2.9	9.4±4.2
Total (*n*=86)	5.5±1.7	6.4±3.3	9.0±4.2
Autumn			
Males (*n*=14)	5.4±2.4	7.7±3.2	9.3±4.1
Females (*n*=26)	6.4±2.1	7.7±4.2	6.4±3.3
Total (*n*=40)	6.0±2.2	7.7±3.8	7.4±3.8
Spring			
Males (*n*=22)	5.3±0.7	4.7±1.2	9.8±3.7
Females (*n*=24)	4.7±0.9	5.4±2.5	10.6±4.4
Total (*n*=46)	5.0±0.9	5.1±2.0	10.2±4.0

We did not observe short-term effects of chemical immobilization on body weight change (t=-1.04, df=43, P=0.31, *n*=44). Initial capture and subsequent capture mean weight ±SD were

5.02±1.6 kg and 5.05±1.6 kg, respectively. We did not observe any immobilization-induced mortality during captures. We found no effect of chemical immobilization on the survival of 56 collared raccoons immobilized during a given capture session compared to 23 animals not immobilized but monitored by telemetry (Generalized linear mixed model: (estimate ± SE) 20.7±270, z=0.08, P=0.94). Following anesthesia, the 11 collared females we identified as pregnant successfully weaned their litters.
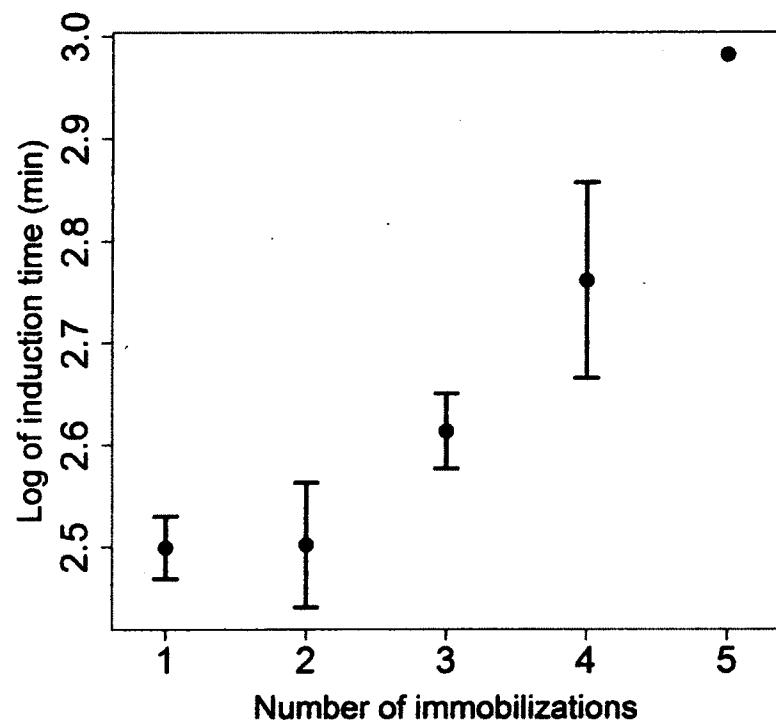
Figure 2.1 Relationship between log transformed induction time (min) and the number of immobilizations for 86 single dose anesthesias of 67 raccoons captured in April and October 2009-2010 at Mont-Orford Provincial Park, Quebec, Canada (effect: t=3.03, df=77, P<0.01).

Discussion

The K:M mixture provided reliable anesthesia of raccoons with predictable induction and recovery times, giving a handling time of at least 30 min. The high potency of medetomidine (Kreeger, Arnemo *et al.*, 2002) minimizes the volume of anesthetic required and the use of atipamezole provides complete reversal of medetomidine at completion of processing. Although no reversal agent is available for ketamine, animals recovered quickly once the atipamezole was administered.

An effect of age on induction time is often reported and is typically longer for adults (Jorgenson *et al.*, 1990; Travaini *et al.*, 1992; Dematteis *et al.*, 2009). However, in our study, we observed the inverse relationship, with juveniles showing a longer mean induction time. The reason for this difference is unclear but could be explained by juveniles having higher anxiety related to the capture and proximity of humans, since immobilization of nervous animals can be prolonged using alpha-adrenergic agonists like medetomidine (Kreeger, Arnemo *et al.*, 2002). The longer head-up time for juveniles compared to adults might be explained by a difference in sensitivity to drugs between age classes (Cline *et al.*, 1969; Roughton, 1975). The seasonal differences in induction and head-up times are likely due to the difference in subcutaneous fat deposits, which are greater in autumn (Mech *et al.*, 1968; Pitt *et al.*, 2008b). With thicker adipose tissue, there is a greater probability that some anesthetic will be injected into fat rather than muscle. Fatty tissues absorb anesthetics poorly (Kreeger, Arnemo *et al.*, 2002), which could lead to longer induction and shorter recovery times in autumn and the reverse in spring.

We did not observe any side effects of ketamine immobilization like convulsions, muscle rigidity, or excessive salivation during processing. Induction times were similar to those observed in previous studies where ketamine was used alone (Gregg & Olson, 1975; Norment, Elliott *et al.*, 1994). Although both ketamine and the K:M mixture appear to have slightly longer induction times than those observed previously with other anesthetics, it is unclear whether this is due to the drugs used, animal condition, trapping method, or trapping time, as

24

these factors greatly differed among studies (Norment, Elliott *et al.*, 1994; Belant, 2004). Because season affects efficiency of chemical immobilization, it is important to include this factor when comparing physiologic responses of animals. Furthermore, differences in the definition of recovery time among studies make comparisons of this parameter difficult. For example, some defined it as "the ability of an animal to maintain an upright position" (Belant, 2004), others as "standing and ambulating but with some minor, residual anesthetic-related ataxia" (Lewandowski *et al.*, 2002; Pitt, Larivière *et al.*, 2006), and in most cases recovery was not defined. Rectal temperatures and respiration rates of the raccoons immobilized in this study were similar to those obtained for small to medium carnivores also anesthetized with ketamine and medetomidine (Dzialak *et al.*, 2001; King *et al.*, 2008; Shilo *et al.*, 2010). However, the heart rate was found to be lower than those obtained for other carnivores of similar size anesthetized with the same drug mixture (Dzialak, Serfass *et al.*, 2001; King, Lapid *et al.*, 2008; Shilo, Lapid *et al.*, 2010) and lower than the normal heart rate for raccoons (Evans, 2002). This might be explained by the utilization of medetomidine which can lead to a decrease in cardiac rate (West, Heard *et al.*, 2007).

To our knowledge, only Field *et al.*, (2002) and Wheatley *et al.*, (2006) assessed the effect of repeated immobilization on induction and recovery times in wild animals. Wheatley *et al.*, (2006) suggested that frequent and repeated immobilizations might increase drug tolerance in the Weddell seal (*Leptonychotes weddellii*) and Field *et al.*, (2002) showed the same pattern in the elephant seal (*Mirounga leonina*). Our results support their findings, as we observed an increase in induction time with the number of immobilizations suggesting that individual tolerance increased with repeated exposure to drugs. The average difference in induction time between an individual's first and fifth immobilization was 10 min. Although longer induction times for animals first contained in a cage might not be a problem for safe handling, it could be important for other species that are immobilized using dart guns or other projectiles. Indeed, longer induction times might potentially increase the chances that an observer might lose sight of a targeted animal and increase the length of time over which the animal is stressed. The observation of drug tolerance might also be related to the type of anesthetics used. In the studies where an effect of the number of immobilizations on the induction or

recovery time was observed (Field, McMahon *et al.*, 2002; Wheatley, Bradshaw *et al.*, 2006), the drug mixture used always included at least one dissociative anesthetic. This is consistent with our observations, since ketamine is a dissociative anesthetic (Frey & Conover, 2007). Thus, possible effects of drug tolerance should be considered when repeated chemical immobilization of animals is required and dissociative anesthetics might be more prone to lead to tolerance.

Finally, we found no effects of anesthesia on short-term body weight, survival, or reproduction and we observed no noticeable effects of the immobilization with K:M on raccoon behavior, unlike what was reported following immobilization with tiletamine-zolazepam (Pitt *et al.*, 2006). We conclude that the K:M mixture is a safe and reliable method for anesthetizing raccoons for handling procedures under field conditions, although drug tolerance can be developed for animals who are frequently immobilized.

CHAPITRE 3

COMPARAISON DES INDICES DE CHEVAUCHEMENT DES DOMAINES VITAUX POUR L'ÉVALUATION DU TAUX DE CONTACTS INTRASPÉCIFIQUES CHEZ LE RATON LAVEUR.

Introduction de l'article

Puisqu'ils sont difficiles à quantifier sur le terrain, il existe plusieurs méthodes pour estimer les contacts entre les animaux. Une des méthodes les plus couramment utilisées est le chevauchement des domaines vitaux, mais les études portant sur la relation entre le chevauchement des domaines vitaux et le taux de contacts sont très peu fréquentes. Lors de ma maîtrise j'ai quantifié les taux de contacts réels chez les femelles ratons laveurs en utilisant des colliers de type contacts loggers. De plus, j'ai effectué un suivi télémétrique des individus durant l'été et l'hiver. Les données récoltées à l'aide des colliers et des suivis télémétriques m'ont permis d'explorer la relation entre le chevauchement des domaines vitaux et le taux de contacts. De plus, lorsque cette relation est étudiée dans la littérature, c'est généralement effectué avec seulement un indice de chevauchement des domaines vitaux, et ce, bien qu'il en existe plusieurs. Dans l'article qui suit, j'ai exploré la relation entre le chevauchement des domaines vitaux et le taux de contacts en utilisant les cinq indices de chevauchement des domaines vitaux les plus couramment utilisés. L'article présente la méthode de suivi télémétrique ainsi que la relation entre le chevauchement des domaines vitaux et le taux de contacts. Encore une fois, ma contribution à cet article a été importante puisque j'ai effectué le terrain, les analyses, écrit l'article et coordonné le processus de publication. La Pre. Fanie Pelletier et le Pr. Dany Garant m'ont encadré durant le projet et la préparation de cet article, et ont judicieusement commenté toutes les versions préliminaires.

27

Keep in touch: does spatial overlap correlate with contact rate frequency?

Par

Karine Robert, Dany Garant et Fanie Pelletier

Abstract

Quantifying animal contact rate is crucial both in fundamental and applied studies to understand the evolution of sociality and predict the spread of infectious diseases. Researchers typically use home range overlap among individuals as a proxy of contact rate, assuming a positive correlation. However, very few studies have assessed how the correlation of home range overlap and contact rate may vary with ecological context. We used proximity proximity loggers to quantify intraspecific contact rate among wild raccoons and explored the correlation between contact rate and home range overlap in different seasons. We monitored 15 female raccoons that formed 121 dyads during summer 2010 and winter 2011. We compared contact rate with the 5 most common overlap indices: home range overlap proportion (HRP), home range overlap probability (PHR), utilization distribution overlap index (UDOI), volume of intersection index (VI) and Bhattacharyya's affinity index (BA). Our results generally supported the contention of a positive and significant correlation between home range overlap and intraspecific contact rate in raccoons. The strength of the relationship differed among seasons and indices, being lower during winter than summer for HR and PHR. When contact rates were high, their frequency had stronger correlations with the UDOI and VI indices than with the other indices. Our results suggest that the UDOI performs better than other indices, as we obtained a good contact rate – home range overlap correlation with this index with animals both aggregated and randomly distributed in space.

Introduction

Understanding why animals live in groups and with whom they associate is a topic of great importance in behavioral ecology (Hinde, 1976, Madden *et al.,* 2009, Frère *et al.,* 2010). The identification of factors that affect animal contact rates is essential to understand the evolution of sociality. Recently, epidemiologists and population ecologists have also become interested in how animal contact rates may affect the dynamic of infectious diseases (Côté and Poulin, 1995, Dexter, 2003, Grear *et al.,* 2010). Transmission of disease such as rabies, hantavirus, lyme disease, brucellosis, or monkeypox often requires close contact between infected and susceptible hosts and should be faster within social than solitary species (Craft *et al.,* 2008). As a result, researchers are interested in quantifying contact rates under field conditions both in humans (Cauchemez *et al.,* 2011) and wild animal populations (Dexter, 2003, Böhm *et al.,* 2008, Habib *et al.,* 2011).

As intraspecific contact rates are very difficult to measure, several studies have used radiotracking data to estimate home range overlap as a proxy for contact rates (Kenward and Hodder, 1998, Millspaugh *et al.,* 2000, Böhm *et al.,* 2008). Although it seems reasonable to assume a positive correlation between home range overlap and contact rate, the strength of this association has rarely been assessed (but see Schauber *et al.,* 2007). The relationships between home range overlap and contact rates might vary among species and could be affected by season or sex-age class. For example, females of a species are often more solitary when lactating and more social during non-reproductive periods (Creel and Creel, 1991, Eberle and Kappeler, 2006). This change and others in social behaviour could affect the relationship between contact rate and home range overlap across different seasons and can vary by sex-age class.

29

A wide range of analytical techniques can be used to calculate home range overlap (reviewed by Fieberg and Kochanny 2005). There are 2 principal methods to calculate home range, one that takes into account the animal utilization distribution (UD) (Van Winkle, 1975), based on animal space use, and one that does not (Fieberg and Kochanny, 2005). Thus, the home range overlap that takes into account the UD should provides a better estimation of intraspecific contacts, as it gives a more accurate estimation of the overlapping area. The widespread use of kernel home range estimators has led to the development of multiple UD-based overlap indices (Fieberg and Kochanny 2005).

Proximity loggers (Prange *et al.*, 2006) now allow researchers to record when individuals come within a predefined distance from each other (Prange *et al.*, 2006). These devices can be used to test the assumption that home range overlap correlates with the rate of animal contacts. Collars with proximity loggers can efficiently record continuous contact data. Our objective was to assess the relationship between contact rates and home range overlap using raccoons as a model system. Raccoons are a good model species to assess whether the relationship between overlap and contact rate changes according to the level of sociality of a species, as some individuals use communal dens during winter (Prange, Gehrt *et al.*, 2011) which may lead to higher contact rate than during summer (Rosatte *et al.*, 2006). Raccoons are also of epidemiological concern as principal host of the raccoon variant of rabies (McLean, 1975). We also have good behavioral data suggesting that females are philopatric (Gehrt and Fritzell 1998), form associations (Gehrt and Fritzell 1998) and can have extensive overlap between home range (Gehrt and Fritzell 1998). Thus, exploring the correlations between home range overlap and contact rate in raccoons can bring additional information on their ecology as well as knowledge useful for wildlife managers.

We compared the relationship between spatial overlap and contact rate using different home range overlap indices. As several home range overlap indices have been proposed, we calculated all indices reviewed by (Fieberg and Kochanny, 2005). We also tested the

relationship between contact rate and overlap among seasons. Raccoon sociality ranges from largely solitary during summer to highly gregarious in winter dens (Gehrt, 2003). As raccoons considerably reduce their activities during winter (Gehrt, 2003), their space use also differs greatly among seasons. We therefore expected that seasonality in space use may influence the relationship between contact rate and home range overlap.

Study area

Our study area 55 km2 Mont-Orford Provincial Park, Québec, Canada (72° 14' 18''W, 45°21'39''N). The climate was characterized by relatively short summers, long and cold winters, with a mean low of -13.4° C, and mean high of 20.9° C (Environment Canada, 2011). The study area consisted of a continuous mature forest dominated by sugar maple (Acer saccharum) with a campground of more than 300 sites.

Methods

We captured raccoons during spring (April 2010 and April 2011) and autumn (October 2010) using cage traps (Havahart® Products, Pennsylvania, USA) baited with fresh mackerel or canned sardines and canned corn. Traps were opened daily in late afternoon (1700-1900), checked at sunrise and closed during the day during. During each trapping session (April 2010, October 2010 and April 2011), 66 traps were set 100 m apart over a 1000 m x 500 m grid and opened during 30 nights. We concentrated our trapping and monitoring efforts in the Stukely sector of the park using the trapping grid, in order to capture every raccoon and to install a radiocollar to every adult female residing in that zone. Once we did not capture new individual we expanded our trapping to peripherals zones, in order to install remaining collars. Captured raccoons were weighed in the trap, then immobilized with a 1:1 mixture by volume of ketamine (Vetalar® 100 mg/ml, Bioniche Canada Inc., Belleville, Ontario, Canada) and

medetomidine (Domitor® .1 mg/ml, Pfizer Canada Inc., Kirkland, Québec, Canada) administered by intramuscular injection with a hand syringe (details in Robert et al., 2012). Once the animal was immobilized, we applied ophthalmic ointment to eyes to prevent desiccation. Raccoons were then sexed, measured, and marked and 2 colored plastic ear tags (Dalton ID Systems Ltd., Henley-on-Thames, Oxon, England). All animals also received a pit tag (AVID Canada®, Calgary, Alberta, Canada) which was injected subcutaneously on the left shoulder with a syringe applicator. Adult females (> 5 kg) were fitted with a proximity data logger placed within a VHF collar (Sirtrack©, Havelock North, Hawkes Bay, New Zealand). After processing (30 min post-induction), medetomidine was reversed by an intramuscular injection of 0.375 mg/kg atipamezole (Antisedan® 5 mg/ml, Pfizer Canada Inc., Kirkland, Québec, Canada). Following antidote injection, the raccoon was placed back in the trap until recovery and then released at its capture site. All procedures were approved by the Université de Sherbrooke's Animal Care Committee (FP2008-02).

We programmed proximity loggers were programmed to register every time an animal was within 1.87 m (± 0.20) of another animal with a logger. The collar settings are not flexible, the 2 smallest distances were 0.50 m and 1.87 m. We chose 1.87 m since raccoons are able to see each other and interact at that distance. A new encounter was logged when 2 units were separated for at least 30 seconds by > 1.87 m. The logger recorded the collar ID, date, time, count and duration of the contacts. Data were stored in the collar until the animal was recaptured. They were then downloaded for analyses. The contact rate was defined as the number of contacts per week for a given dyad. Also, since most raccoons had their collars installed on different days, the total number of contacts of a given dyad was divided by the number of weeks when both individuals were simultaneously collared.

Proximity data loggers were equipped with VHF transmitters, which permitted weekly relocations during summer 2010 (April through August) and winter 2010-2011 (November through March). During summer, we located radiocollared raccoons at least 5 times a week (once during day time and 4 times during the night) for 32 ± 1.1 mean ± SE locations per individual. During the day, we located raccoon on foot with a portable 3-element Yagi antenna

(ATStrack, Minnesota) and receiver (Communications specialists inc., California). Daytime locations were taken with a GPSmap 76CSx (Garmin®). At night, we located raccoons from 1 hour after sunset until 1 hour before sunrise by triangulation (White and Garrott, 1990) from 3 fixed stations. The 2 or 3 directional bearings were taken within 5 minutes. We used the program LOCATE III to determine each location of an individual (Nams, 2006). We obtained 1 nighttime location per day for every animal during 4 days per week systematically. During summer, 2 nighttime locations per week were taken between 1 hour after sunset and midnight and the other 2, between midnight and 1 hour before sunrise. The order in which animals were tracked was randomly changed every day. To ensure biological independence (Lair 1987) of the location data, we recorded only one daytime and nighttime location per raccoons per day. Summer home range were calculated from at least 1 daytime location per week and 2 nighttimes location per week for a mean ± SE of 32 ± 0.3 number of locations. During winter, we located radiocollared individuals on foot once a week at their den with a portable antenna for a mean ± SE number of locations of 19 ± 0.6. Bearing precision was estimated to be SD = 3.52° based on 75 bearings on 5 test transmitters placed randomly in the radiotracking zone. We conservatively estimated error associated with locations to be <8 m for daytime locations and <100 m for nighttime locations.

We estimated summer and winter home ranges using the fixed kernel (h_{ref}) (Worton, 1989). It have been shown that using kernel estimator it is possible to obtain accurate estimate using as few as 10 fix per month (Börger, Franconi *et al.*, 2006), we thus used 10 locations per month/individual. However, as the females did not always had their collars at the same time and that some individual died during the study the mean number of locations for the summer period we used a minimum of 30 locations as the criterion for home-range estimation during summer and 19 during winter. We calculated home ranges with the Adehabitat package (Calenge, 2006) for R software (version 2.10.0, R Development Core Team 2009) at 95% and 50 % isopleths. The 50 % and 95 % isopleths are most widely used in the literature and represents respectively the core area and the full home range.

All 5 indices reviewed by Fieberg and Kochanny (2005) typically range between 0 (no overlap) to 1 (complete overlap) unless stated otherwise. Below, we briefly describe each index (but see Fieberg and Kochanny, 2005). The Home Range overlap proportion (HR) is equal to the proportion of home range overlap area of animal A and B divided by the home range area of animal A. This index is calculated for each individual of the dyad. The Home range overlap probability (PHR) index estimates the probability finding animal A in animal's B home range according to the animals UD. This index is also calculated for each individual of the dyad. The Utilization distribution overlap index (UDOI) quantifies overlap based on the product of the UD of 2 individuals. It generally ranges between 0 (no overlap) and 1 (100 % uniform distribution), but it can be >1 if the UDs of the 2 individuals are aggregated in space and show much overlap (Fieberg and Kochanny, 2005). The Volume of intersection index (VI) assesses overlap by comparing the shape and the location of the UD of 2 individuals and calculating the volume of intersection from the 3-dimensional surface of the home ranges (Seidel, 1992). This method provides a single measure of overlap that is calculated from the full UD of both individuals. Finally, Bhattacharyya's affinity (BA) index estimates the extent of overlap by measuring the similarity between the UD of 2 animals (Bhattacharyya, 1943, Fieberg and Kochanny, 2005). We calculated home range overlap indices were using the Adehabitat package (Calenge, 2006) for R software (version 2.10.0 R Development Core Team 2009).

Statistical analyses

We first tested the difference in contact rates between winter and summer using a linear mixed-effects model with Gaussian error distribution. As the contact rate differed greatly among seasons, we standardized contacts data (zero mean and unit variance) prior to analysis. As an individual can be represented in several dyads we included dyad identity as a random effect in each mixed model. We also used a linear mixed-effects model with dyad identity as a random effect to test for seasonal changes in the relationship between contact rate and home

34

range overlap by fitting an interaction between overlap and season. We conducted Mantel tests between contact rates and home range overlap indices to test the strength of the relationship between contact rate and the overlap index at each isopleths during each season. To assess whether an overlap index performed better than others, we compared the Mantel test correlation coefficients using pairwise comparisons. We used the same approach to assess, for each index, whether the correlation differed according to the percentage of the localizations used to calculate the home range (core area or home range). We also determined if the slope of the contact rate – home rage overlap relationships differed among indices and according to the percentage of the localizations used to calculate the home range (core area or home range). We used a Bonferroni correction to account for multiple comparisons (Rice 1989). All analyses were performed in the R statistical environment.

Results

During the trapping sessions conducting in April 2010, October 2010 and April 2011, we captured 26, 34 and 16 raccoons respectively. On average 92 % of the marked adult female raccoons were fitted with a proximity logger. During the study, 87 % (23/27) of the proximity logger were recovered with data we did not observe any logging errors or battery failure (Table 3.1).

Table 3.1 Proximity loggers utilization installed on 15 female raccoons during summer 2010 (April through August) and during winter 2010-2011 (November through March) in the Mont-Orford provincial park, Québec, Canada.

	Loggers used	Loggers recovered	Loggers with data
Summer 2010	12	11	11
Winter 2010-2011	15	12	12
Total	27	23	23

We monitored contacts and space use of 15 females throughout the year, including 55 dyads during summer and 66 during winter. Each collar recorded between 7 and 16383 contacts, for a mean (± SE) of 4332 ± 1051. Contact rates were higher in winter (35.0 ± 4.21) than summer (15.0 ± 2.58) (linear mixed model:[estimate ± SE] 0.71 ± 0.23, t = 3.07, P < 0.01). We found a significant interaction between season and home range overlap for HR (Table 3.2a) and PHR (Table 3.2b) at 50 isopleths (core area) as a predictor of contact rate, suggesting that the correlation between contact rate and home range overlap was lower in winter than summer for these 2 indices at this isopleths. The interaction was not significant for the HR and PHR indices at the 95% isopleths (home range) and for the other 3 indices at 50 and 95% isopleths (see Table 3.4 and 3.5 for results).

Table 3.2 Effects of home range overlap on contact rates (contacts/week) obtained from 55 dyads of female raccoons during summer 2010 (April through August) and from 66 dyads during winter 2010-2011 (November through March) in the Mont-Orford provincial park, Québec, Canada. Parameter estimates were from a linear mixed effect model including dyad identity as a random effect and are presented for the home range overlap proportion (HR) and home range overlap probability (PHR) at core area (isopleths 50), for which we found an interaction between season and home range overlap. Sample size was 121 dyad from 15 female raccoons.

	Coefficient	SE	t value	P value (adjusted)
a) HR				
Intercept	-0.36	0.14	-2.55	0.012
Season (winter)	0.20	0.20	1.03	0.313
Home range overlap	2.83	0.54	5.22	<0.001
Season x overlap	-2.19	0.66	-3.30	0.003
b) PHR				
Intercept	-0.49	0.14	-3.47	0.001
Season (winter)	0.06	0.21	0.29	0.777
Home range overlap	4.92	0.84	5.82	<0.001
Season x overlap	-3.24	0.94	-3.46	0.002

In summer, Mantel tests revealed a positive relationship between contact rate and home range overlap regardless of the index used (Table 3.3a). The percentage of locations used to calculate home range that were also used to estimate home range overlap had little influence on the relationship between contact rate and home range overlap. The correlation coefficient was similar among isopleths for a given index (Table 3.3a).

During winter, the correlation between contact rate and home range overlap was lower using the HR index at core area (Table 3.3b) and higher using the VI and UDOI indices at home range. During winter, the isopleths at which the home range overlap was estimated affected the correlation only if the index used did not account for animal space use (HR index), being lower at core area (3.3b).

Table 3.3 Mantel tests for the correlations between contact rate (contacts/week) and home range overlap calculated using 5 methods: home range overlap proportion (HR), home range overlap probability (PHR), utilization distribution overlap index (UDOI), volume of intersection (VI) and Bhattacharyya's affinity (BA)at core area (50%) and full home range (95%). Data were obtained from 55 dyads of females raccoons during summer 2010 (April through August) and from 66 dyads during winter 2010-2011 (November through March) in the Mont-Orford provincial park, Québec, Canada. The correlation coefficients ($\pm$ SE) (r) are reported and values in bold were statistically significant. Differences among correlation coefficients are indicated by a letter.

	Seasons	Isopleths	
		50%	95%
A)	Summer		
	HR	**0.64^a** (0.11)	**0.59^a** (0.08)
	PHR	**0.65^a** (0.11)	**0.55^a** (0.08)
	UDOI	**0.59^a** (0.11)	**0.63^a** (0.10)
	VI	**0.65^a** (0.08)	**0.65^a** (0.08)
	BA	**0.62^a** (0.08)	**0.62^a** (0.08)
B)	Winter		
	HR	0.10^a (0.03)	**0.40^b** (0.06)
	PHR	**0.45^b** (0.06)	**0.37^b** (0.06)
	UDOI	**0.50^{bc}** (0.16)	**0.82^c** (0.11)
	VI	**0.58^{bc}** (0.12)	**0.58^{bc}** (0.12)
	BA	**0.49^b** (0.12)	**0.49^b** (0.12)

Table 3.4. Linear mixed effect models of the effects of season, the home range overlap calculated using 5 indices: home range overlap proportion (HR), home range overlap probability (PHR), utilization distribution overlap index (UDOI), volume of intersection (VI) and Bhattacharyya's affinity (BA) on contact rate of females raccoons at Mont-Orford provincial park, Québec, 2010-2011, giving estimates, standard errors and t value. Sample size was 191 observations from 93 different dyads. Dyad identity had significant effect and was included as a random term.

	Coefficient	SE	t value	P value (adjusted)
HR 95				
Intercept	-0.66	0.17	-3.91	< 0.001
Season (winter)	0.08	0.25	0.31	0.759
Home range overlap	2.33	0.43	5.39	< 0.001
Season x overlap	-0.75	0.61	-1.24	0.228
PHR 95				
Intercept	-0.60	0.17	-3.60	< 0.001
Season (winter)	-0.01	0.26	-0.04	0.966
Home range overlap	1.83	0.36	5.09	< 0.001
Season x overlap	-0.43	0.52	-0.83	0.416
UDOI 50				
Intercept	-0.29	0.12	-2.36	0.021
Season (winter)	0.10	0.16	0.63	0.533
Home range overlap	10.61	1.99	5.33	< 0.001
Season x overlap	-1.75	2.53	-0.69	0.494
UDOI 95				

Intercept	-0.44	0.11	-3.91	< 0.001
Season (winter)	0.09	0.14	0.59	0.560
Home range overlap	1.99	0.29	6.78	< 0.001
Season x overlap	-0.57	0.33	-1.73	0.095
VI 50				
Intercept	-0.57	0.14	-3.98	< 0.001
Season (winter)	0.22	0.18	1.22	0.233
Home range overlap	2.83	0.47	6.02	< 0.001
Season x overlap	0.73	0.77	0.95	0.349
VI 95				
Intercept	-0.57	0.14	-3.98	< 0.001
Season (winter)	0.22	0.18	1.22	0.233
Home range overlap	2.83	0.47	6.02	< 0.001
Season x overlap	0.73	0.77	0.95	0.349
BA 50				
Intercept	-0.64	0.16	-3.92	< 0.001
Season (winter)	0.27	0.21	1.30	0.206
Home range overlap	1.93	0.35	5.45	< 0.001
Season x overlap	0.19	0.58	0.33	0.742
BA 95				
Intercept	-0.64	0.16	-3.92	< 0.001
Season (winter)	0.27	0.21	1.30	0.206
Home range overlap	1.93	0.35	5.45	< 0.001
Season x overlap	0.19	0.58	0.33	0.742

Table 3.5 Slopes of the Mantel tests results for the correlations between the overlap of home ranges calculated using 5 different indices: home range overlap proportion (HR), home range overlap probability (PHR), utilization distribution overlap index (UDOI), volume of intersection (VI) and Bhattacharyya's affinity (BA) at calculated at 2 isopleths core area (50%) and full home range (95%) and the contact rate (contacts/week) obtained from 55 dyads of females raccoons during summer 2010 (April through August) and from 66 dyads of females raccoons during winter 2010-2011 (November through March) in the Mont-Orford provincial park, Québec, Canada. The slopes (± SE) are reported. Values in bold are significant. Differences among slope are indicated by a letter.

	Season	Isopleths	
		50%	95%
a)	Summer		
	HR	**0.17^{ab} (0.04)**	**0.14^{ab} (0.03)**
	PHR	**0.29^{a} (0.06)**	**0.11^{b} (0.02)**
	UDOI	**0.62^{a} (0.25)**	**0.12^{ab} (0.13)**
	VI	**0.17^{ab} (0.03)**	**0.17^{ab} (0.03)**
	BA	**0.11^{b} (0.02)**	**0.11^{b} (0.02)**
b)	Winter		
	HR	0.66^{b} (0.68)	**2.72^{a} (0.70)**
	PHR	**3.03^{a} (0.80)**	**2.41^{ab} (0.79)**
	UDOI	**3.82^{a} (0.53)**	**42.46^{d} (6.94)**
	VI	**6.13^{ac} (2.11)**	**6.13^{ac} (2.11)**
	BA	**3.66^{ab} (1.35)**	**3.66^{ab} (1.35)**

Discussion

Quantifying contacts rate in the field is often difficult, thus proxies such as home range overlap can be useful to estimate contact rates. However, the relationship between home range overlap and contact rate have rarely been assess in the field (but see Schauber *et al.*, 2007). We found that contact rate is positively and significantly correlated with home range overlap. However seasonality had a strong effect on the magnitude of this relationship, which changed with the distribution of animals in space. We observed higher contact rates during winter than in summer, supporting observations that female raccoons are more gregarious in winter (Gehrt, 2003). We also found that when raccoons were widely spaced (summer), the 5 indices performed similarly as predictors of contact rates. However, when the animals were more gregarious (winter), VI and UDOI were better predictors of contact rate than other indices.

Two indices were more influenced by the distribution of the animals in space: HR and PHR. Since HR index is an area-based measure and does not take into account the UD (Fieberg and Kochanny, 2005) the HR home range overlap estimation will be similar for 2 overlapping zone of a same area regardless of the animals overlapping utilization. Although raccoons had larger overlap in winter than in summer, according to their home range they were more aggregated in space. Thus, the estimation of the home range overlap with the HR index did not take into account the higher probability of contact in winter, which has probably led to a weaker home range overlap – contact rate relationship in winter. The PHR index is based on the probability to find animal A in animal's B home range (Fieberg and Kochanny, 2005). The PHR index is not an quantification of the space use sharing but an estimation of the probability to find animal A in animal's B home range and thus, might be more influenced by the distribution of animals in space.

To our knowledge, only one study (Schauber *et al.*, 2007) explored the relationship between home range overlap and contact rate in the field. They reported that home range overlap, estimated from VI index, was not a good estimator of direct contacts among white tailed deer. Our results do not support their finding as we found a strong relationship between home range overlap estimated from VI index and contact rates in raccoons. There are 2 potential explanations for these contrasting results. First, the biology of the species (an ungulate versus a medium-size carnivore) might lead to difference in the correlation between contact rates and spatial overlap. Although sociality among raccoons and white tailed deer seems different, they share many similarities as they are more solitary in summer (Nixon *et al.*, 1992, Bertrand *et al.*, 1996, Gehrt, 2003) and gregarious in winter (Hirth, 1977, Gehrt, 2003). Thus, we suggest that the difference among species is unlikely to explain the differences among results. The second explanation is methodological. Schauber *et al.*, (2007) used GPS collars to estimate contact rates. With this approach, direct contact rates were estimated from distances ranging from 10 m to 100 m with a median positioning error of 8.8 m. In addition, contacts rates obtained using GPS collars were based on hourly data recordings, which do not account for frequency of relocations. Thus, not every dyadic contact was recorded which might have led to a weaker estimation of contact by the joint space use. In contrast, proximity loggers allowed us greater resolution in space and time by recording contacts every time 2 raccoons were within less than 2 m and the duration of the contacts in second. More studies are required to evaluate the strength of the relationship between home range overlap and contact rate for different species.

During summer, animals were less aggregated than in winter and the 5 indices performed equally well. This suggests that when space use is relatively uniform, the correlation between contact rate and home range overlap is little affected by the method used. This suggestion is supported by our results comparing the HR index to other indices. As the HR index does not account for animal distribution in space (Fieberg and Kochanny, 2005), it will provide a home range overlap results similar to those estimated by other indices if space use is uniform (Fieberg and Kochanny, 2005). The contact rate – home range overlap relationships were also

equivalent among isopleths for each index, suggesting that when individuals are well distributed in space, the size of the home range used to calculate overlap had little influence on the estimation of contact rate.

In winter, when animals were aggregated, the correlation obtained between home range overlap and contacts rate was stronger using the VI and UDOI indices. Although the correlation between home range overlap and contact rate was not statistically different using these 2 indices, the correlation coefficient was 24% higher with the UDOI index at home range, but was 8 % lower at core area. Thus, when estimated over the entire home range our results support the suggestion by Fieberg and Kochanny (2005) that the UDOI index was a better estimator of space use sharing than VI. We also found that the degree of space use can affect the correlation between contact and overlap, but only when using the HR index, which does not account for the UD (Fieberg and Kochanny, 2005).

Our results are surprising for a largely solitary animal as raccoon as we would expect avoidance among congeners during summer. These results however could be explained by female biased philopatry in raccoons. Previous studies have shown that females often share dens and forage together (Gehrt 1994) and that they exhibit extensive overlap (Gehrt and Fritzell 1998; Gehrt and Fritzell 1998). Social tolerance in female raccoons probably occurs between related individuals (Gehrt and Fritzell 1998) which are generally found in their neighborhood following philopatry.

Our results could be affected by different environmental and individual factors. In fact, the size of the home range and the overlapping zone are influenced different environmental factors such as resources abundance and distribution (Maher and Lott 2000) and landscape fragmentation (Atwood and Weeks 2003). Scarce resources will generally lead to extensive home range overlap (Maher and Lott 2000), thus to an higher probability of encounter.

Moreover individual characteristics such as genetic relatedness can influence social tolerance among individuals (Gehrt and Fritzell 1998). It have been reported in solitary mammal species that individuals were more tolerant toward their kins than unrelated individuals (Rogers 1987; Koprowski 1996; Gehrt and Fritzell 1998). In gregarious species others factors might affect contact rate among individuals (Vander Wal, Yip *et al.*, In press). It has been shown in elk, for example, that density affected differently male and female contact rate (Vander Wal, Yip *et al.*, In press). At high density male contact rates were higher than at low density in contrast, female contact rate did not differ (Vander Wal, Yip *et al.*, In press). Although the factors that affect contact rate and the home range size are different as we move along the continuum from solitary to gregarious species we expect to find similar results as ours.

Management Implications

Home range analyses are widely used in field studies (White *et al.*, 1994, Dexter, 2003, Böhm *et al.*, 2008). Our results support the assumption that increase in home range overlap lead to higher contact rate and thus, in absence of detailed behavioral data, home range overlap can be used as a proxy of contact rate among animals. This is an important result because standard telemetry data have been collected for decades and are more widely available than contact rates data. However, our results also showed much variability in contact rate (summer : CV = 193%; winter : CV = 231%) between individuals as well as seasonal variation. Researchers should therefore be cautious when making inference about contact rate based on indices of home range overlap alone. The choice of the overlap index as proxy of contact rate must be done thoroughly according to the purpose or the study, the species, the environment and the period of the year. Thus, we suggest that home range overlap can be use as a proxy of contact rate for wildlife disease management, but managers should also be aware of the large error margin.

Acknowledgments

CHAPITRE 4
DÉTERMINANTS INDIVIDUELS ET ENVIRONNEMENTAUX DU TAUX DE CONTACTS CHEZ LES FEMELLES RATONS LAVEURS

Introduction à l'article

L'objectif de cet article était d'explorer les facteurs environnementaux et individuels qui influencent la structure sociale chez les femelles ratons laveurs. Pour ce faire, j'ai vérifié comment les taux de contacts changeaient en fonction des saisons. Par la suite, j'ai étudié les effets de la température et de l'apparentement sur les taux de contacts. Cette étude est parmi les premières à étudier l'impact des effets écologiques sur le taux de contacts en utilisant les colliers de type « contacts loggers » pour quantifier les contacts. Les résultats de cette étude permettent d'apporter des indices sur les facteurs, tels que des contraintes environnementales, qui pourraient avoir une influence sur la variabilité de socialité que l'on observe entre les populations animales. Ma contribution à cet article a été considérable puisque j'ai effectué la récolte des données, les analyses, et la rédaction. J'ai été encadrée lors de ce chapitre, comme pour les précédents, par la Pre. Fanie Pelletier et par le Pr. Dany Garant qui ont également révisé plusieurs versions de cet article. Eric Vander Wal, étudiant au post-doctorat dans le laboratoire de la Pre. Fanie Pelletier, m'a fournit des codes du logiciel statistiques R qui m'ont permis d'organiser et d'analyser mes données.

Environmental and individual determinants of contact rate in female raccoons.

Par

Karine Robert, Dany Garant, Eric Vander Wal et Fanie Pelletier

Abstract

Animals are organized in a wide range of social structures. Variability in sociality is found both within and among species and is influenced by environmental and individual factors. To identify the factors influencing sociality in wild species, it is crucial to obtain quantitative data on animal interactions, including their frequency and duration, over long periods of time. While the majority of mammals are solitary, studies on pairwise interactions have generally been conducted on gregarious species. Mammals considered solitary, however, often exhibit context-specific social behaviours; although these social behaviours are less common and harder to observe than within gregarious species. In this article, we used proximity-logging biotelemetry collars to quantify intraspecific contact rate among raccoons. We tested the effect of extrinsic (season and temperature) and intrinsic (individual relatedness) variables on contact rate. We monitored 15 female raccoons from April 2010 to August 2011 which comprised 120 dyads. We found that female raccoons had higher contact rates during winter (mean $\pm$ SE: 24.1 $\pm$ 4.2) than summer (3.0 $\pm$ 2.6). We also found a negative relationship between ambient temperature and contact rate, which suggested that female raccoons use social thermoregulation as a mechanism to reduce energetic costs in cold environments. Finally, we found that relatedness was positively correlated with contact rate during summer and winter. Studies on solitary species that show social flexibility, such as raccoons, provide insights on factors that might play a major role in the evolution of sociality.

Introduction

Animal social systems range from predominantly solitary to eusocial species. For decades, researchers have been interested to identify the factors shaping sociality at the inter-specific level (Eberhard 1975; Schwarz *et al.,* 2007) as well as quantifying the costs and benefits of social behaviours. Social structures of animal populations are closely linked to conspecifics interactions (Krause and Ruxton 2002). Thus, animal interactions can be used to explore how variation in sociality affects specific behaviours, such as mating (Clutton-Brock 1989; Gehrt and Fritzell 1999) and foraging (Beauchamp 2005; White and Harris 1994). Interactions and contact rates are also very important factors in epidemiology (Lloyd-Smith *et al.,* 2005; White and Harris 1995) as infectious diseases will spread more rapidly in gregarious species that in solitary one (Begon *et al.,* 2002). Thus, understanding the factors affecting the degree of sociality is crucial for both fundamental and applied research.

There are many benefits associated with group living, such as dilution of predation risk (Hamilton 1971), reduction of heat lost (Hwang *et al.,* 2007), increase in foraging success (Giraldeau and Caraco 2000) and reduced movement costs (Krause and Ruxton 2002). However, group living also involves a number of costs: increase of transmission of pathogens and parasites (Côté and Poulin 1995) and of competition for resources (Krause and Ruxton 2002). Thus, sociality has evolved as a result of a trade-off between the benefits and the costs of grouping for the fitness of the animals (Silk 2007). Intraspecific variation in sociality, also known as social flexibility, occurs in a wide range of species (Lott 1984). Context-specific variation in sociality has been observed in solitary species. For example, complex social structure was observed in mammals known to be solitary such as cheetahs (Caro 1994), small Indian mongoose (*Herpestes javanicus*) and raccoons (Gehrt and Fritzell 1998a, b).

Environment variability (Lott 1991) and individual genetics characteristics (Hamilton 1964) have been posited to explain intraspecific variation in social systems. For endotherms, such as mammals, variable temperatures have been shown to influence social structure (Hwang *et al.*, 2007; Willis and Brigham 2007b). Endotherms need to maintain high and constant internal body temperature (McNab 2002), which leads to greater energetic costs especially at low temperatures. The cost of maintaining high and constant body temperature is reduced when the animals group (Hwang *et al.*, 2007; Willis and Brigham 2007b). Indeed, communal denning can lead to a reduction of thermal conduction and body fat lost (Hwang *et al.*, 2007; Merritt and Zegers 2002). Thus, in cold environment animals that den communally potentially save energy that can be allocated into survival and/or reproduction. The occurrence of communal denning should increase with a decrease of ambient temperature (Ebensperger 2001). Thus, group formation of solitary species in cold temperature could therefore be explained, at least partially, by social thermoregulation.

Kin selection theory predicts that relatedness is a major factor in the evolution of sociality (Eberhard 1975; Hamilton 1964). Fitness advantages are accorded to individuals that cooperate with related conspecifics in activities such as foraging and alloparenting. Cooperating individuals also receive indirect fitness benefits via the reproductive success of their kin. However, for sociality to persist both direct and indirect fitness benefits need to outweigh the costs of cooperating. Related individuals have been observed to cooperate more frequently than unrelated individuals, and thus have more interactions, in a wide range of mammals, such as rodents (Lacey and Wieczorek 2004; Viblanc *et al.*, 2010), carnivores (Gompper *et al.*, 1997; Packer *et al.*, 1991) and ungulates (Nituch *et al.*, 2008).

Although more species of mammals are solitary than gregarious (Jarman and Kruuk, 1996), group-living mammals have been the focus of most studies of social behaviours, as they are more easily observed (Alexander 1974; Dunbar 1988; Festa-Bianchet 1991). The aim of this article is to investigate the environmental (extrinsic) and individual (intrinsic) factors affecting

sociality in a meso-carnivore, the raccoon. Raccoons are typically solitary carnivores (Kaufmann 1982), where the peaks of their activity is thought to involve infrequent contacts with other adult conspecifics (after Waser and Jones 1983). However, raccoons are known to form family groups consisting of a female and her yearling (Gehrt 2003). Raccoons have also been observed forming winter denning groups consisting of adults and juveniles of both sexes (Whitney 1952). Furthermore, exclusive male coalitions have been observed in raccoons (Gehrt and Fritzell 1998b; Pitt *et al.*, 2008). Thus, raccoon social structure appears to be more complex than previously reported.

Radiotelemetry data revealed that raccoon dispersal occurs predominantly in males (Gehrt and Fritzell 1998) while females are more philopatric. Several studies have shown extensive overlap between female's home range, females associations (denning and traveling together) and behavioral tolerance (Gehrt and Fritzell 1998). Females associations and tolerance could be explained by genetic relatedness and spatial proximity of related individuals as it have been shown that females that were more related were more spatially closer (Côté *et al.*, 2012) and that genetic similarities was positively correlated with home range overlap (Ratnayeke *et al.*, 2002).

In this study, we specifically assess the social flexibility of female raccoons by investigating factors affecting their contact rates among seasons and by assessing whether they form kinship associations during winter. Quantifying the level of sociality for a species or a population can be done using different approaches. One of them is to measure fine-scale interaction rates (hereafter contact-rates) (Frère *et al.*, 2010; Hinde 1976; Palla *et al.*, 2007). Due to advances in biotelemetry technology, it has recently become possible to quantify pairwise animal contacts using proximity-based data-logging biotelemetry collars. This technology is an objective and accurate method to quantify contact rate within a predefined range, which has been successfully employed on various species including raccoons (see Prange *et al.*, 2006, Goodman 2007, Walrath *et al.*, 2011, Vander Wal *et al.*, 2012). As raccoons den communally

at low temperatures we expect to find higher contact rates during winter than summer. Because temperature is variable during winter we also predict that contact rate will vary within that season, increasing at lower temperatures. Given the probability of kin-based social groups, we further predict that contact rate will increase among relatives, particularly during winter. As raccoons are solitary during summer, however, we do not expect relatedness to influence contact rate during this season.

Materials and methods

Study area and captures

We radiotracked female raccoons from April 2010 to April 2011 on a 58 km^2 study site in Mont-Orford Provincial Park, Québec, Canada (72° 14' 18"W, 45°21'39"N). We captured raccoons on three occasions: spring (April 2010 and 2011) and autumn (October2010). During each trapping session (lasting for 20 days), 66 traps were set 100 m apart over a 1000 m x 500 m grid. Traps were opened daily in late afternoon (1700-1900), checked at sunrise, and closed during the day. Raccoons were caught in live traps (Havahart® Products, Pennsylvania, USA) baited with a mixture of fresh mackerel and/or canned sardines and/or canned corn.

Captured raccoons were weighed in the trap, then immobilized with a 1:1 mixture by volume of ketamine (Vetalar® 100 mg/ml, Bioniche Canada Inc., Belleville, Ontario, Canada) and medetomidine (Domitor® 1 mg/ml, Pfizer Canada Inc., Kirkland, Québec, Canada) administered by intramuscular injection with a hand syringe (For more details on the capture procedures see (Robert *et al.*, 2012). Females raccoons (> 5 kg) were fitted with a proximity data-logging biotelemetry collars (hereafter, proximity collars; Sirtrack©, Havelock North, Hawkes Bay, New Zealand) allowing us to register fine-scale contact rates and to relocate animals for spatial analyses (see below). During the anaesthesia, ear tissue was taken from all

individuals for genetics analyses with a 2 mm diameter punch plier (Maun industries, England) and kept in ethanol 95% until analyses. After the manipulations (30 min post-induction), the effect of medetomidine was reversed by an intramuscular injection of 0.375 mg/kg atipamezole (Antisedan® 5 mg/ml, Pfizer Canada Inc., Kirkland, Québec, Canada). All procedures were approved by the University of Sherbrooke's Wildlife Animal Care Committee (FP2008-02).

Contact rates and duration

We used proximity collars to collect data on contact rates and durations. We programmed the proximity data-loggers to register data every time an animal was within 1.87 m (± 0.20, SE) of another collared animal. We choose 1.87 m for technical and biological reasons. First, raccoons can detect conspecifics in a forest environment at that distance. Second, using such range prevents from recording small distance movement (within a den) during winter, thus avoiding to fill up the collars memory quickly and allowing us to have continuous recording data. A new encounter was logged every time two units were separated for at least 30 seconds at a distance > 1.87 m. When the loggers were within this range, the logger recorded the other collar identity, date, time, count, and duration of the contacts. Contact rate was defined as the number of contacts/day for each dyad by season. Also, since most raccoons had their collars installed on different days, the total number of contacts of a given dyad was divided by the number of days during which both individuals had an active collar simultaneously. Contact duration was defined as the total duration of the contacts/day for each dyad by season. Contact duration was also divided by the number of days during which both individuals of a dyad had an active collar simultaneously. We defined two principal seasons based on raccoon biology and radio-tracking constraints: summer (May-August) and winter (November-April).

Air temperature

We used temperature data-loggers (Thermochron iButton DS1921, Dallas Semiconductor, Dallas, TX, USA; accuracy±0.5°C; 17 mm × 6 mm, 3•0 g) to record ambient temperatures at our study site every 4 hours. We placed data-loggers (n = 20) at five recording sites randomly selected on our trap grid. At each recording site two data loggers were installed in a tree cavity and two were attached on the exterior of the tree. We determine the average daily temperature by calculating the mean for all loggers per day.

Home range

We obtained estimates of the summer and winter home range via fixed kernel analysis (h_{ref}) (Worton 1989). According to Börger et al (2006), this method is accurate, robust and does not overestimate home range size at low sample size. Home ranges were calculated with the adehabitat package (Calenge 2006) for R software (version 2.10.0, R Development Core Team 2009) at 95% isopleths. Home range overlap was calculated using the utilisation distribution overlap index *(UDOI)* which quantifies overlap based on the product of the utilisation distribution (UD) of two individuals. It generally ranges between 0 (no overlap) and 1 (100 % uniform distribution), but it can be >1 if the UDs of the two individuals are not uniform in space and show much overlap (Fieberg and Kochanny 2005).

Genetic data

We performed DNA extraction using a modified version of the salting-out method as described in Chambers and Garant (2010). Microsatellite loci amplification was obtained by

55

employing primer sets chosen from (Siripunkaw *et al.*, 2008) (PLM 6, PLM 10, PLM 20), (Cullingham *et al.*, 2006) (PLO2-14, PLO2-117, PLOM 2, PLOM 3, PLOM 15, PLOM 17, PLOM 20) and (Fike *et al.*, 2007) (PLOT-5). Amplifications were performed in a GeneAmp PCR System 9700 thermocycler (Applied Biosystems). Amplification products were visualized using an AB 3130 capillary DNA sequencer (Applied Biosystems) (For details on the amplification conditions and procedures (see Côté *et al.*, 2012).

Microsatellites polymorphism and relatedness coefficients

We tested all loci for departure from Hardy-Weinberg equilibrium and linkage disequilibrium using the software GENEPOP version 4.0 (Raymond and Rousset, 1995). We used CERVUS version 3.0.3 (Marshall *et al.*, 1998; Kalinowski *et al.*, 2007) to assess the presence of null alleles. Finally, we used SPAGEDI version 1.3 (Hardy and Vekemans, 2002) to estimate pairwise genetic relatedness (Rxy) between studied females using Wang's estimator (Wang, 2002).

Statistical analyses

Environmental determinants

We assessed the correlation between contact rate and duration using a Pearson correlation. To identify the environmental determinants affecting contact rate, we used the daily contact rate to test the difference in contact rate among season using a linear mixed-effect model with Gaussian error distribution. We also used a linear mixed-effect model to test the effect of the season (summer/winter) and the period of the day (daytime/nighttime) on contact rate. We

then used a generalised mixed-effect models with binomial error distribution to test the effects of temperature on contact rate during winter. We used a generalised mixed-effect models with quasi Poisson error distribution (controlling for overdispersion) to test the effects of temperature on contact rate only among dyad that had contacts during winter. As an individual can be represented in several dyads, we included dyad identity as a random effect in each models. All the mixed-effects models analyses were conducted in Genstat (version 8.0, VSN International, Oxford, UK, 2005).

Individual determinants

We used mean contact rate per dyad to conduct multiple regression matrices (MRM) (Lichstein 2007) to assess the relationship between contact rate and home range overlap, and home range overlap and relatedness. To investigate individual determinants of contact rate and duration, we also used MRM from mean contact rate per dyad to establish the strength and significance of the correlations between relatedness, home range overlap, and the contacts rates among dyads. We build matrices with the mean contact rate per dyad defined as the total number of encounters divided by the number of days that the individuals of the dyads had a collar at the same time. We also used the mean contact duration for each dyad to conduct the MRM with the contact duration as the response variable. All the MRM analyses were conducted in R (version 2.10.0, R Development Core Team 2009).

Results

Thirty-two proximity collars have been recovered from 120 dyads over two years. We estimated that 92% of the females that have been marked in our study area had a collar. During the study, all 15 collared females had an encounter with at least two other females.

Each collar recorded between 53 and 16383 contacts (9799 ± 2376) (mean ± SE). There was a strong correlation between contact rate and duration (r = 0.883, P < 0.001; Figure 4.1) and thus analyses on these two variable yielded similar results. We thus only report the results for contact rate in the main text.
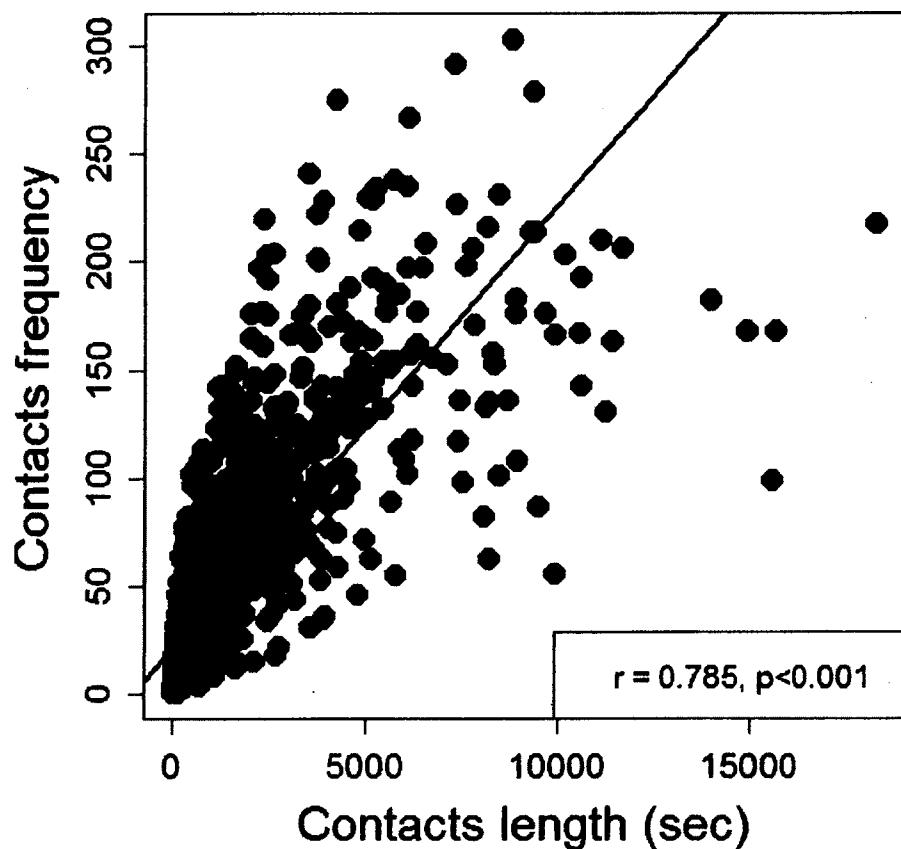
Figure 4.1 Relationship between the contact rate (per day) and duration (s) among 120 dyads of female raccoons sampled in the Mont-Orford provincial park, Québec, Canada in 2010 and 2011.

The sampled raccoons were genotyped at eleven microsatellites. No significant deviation from Hardy–Weinberg equilibrium or linkage disequilibrium was detected after Bonferroni correction. Null alleles were found at low frequencies within our data (<5%). The relatedness among members of dyads had a normal like distribution (mean ± SD : 0.008 ± 0.183; Figure 4.2).
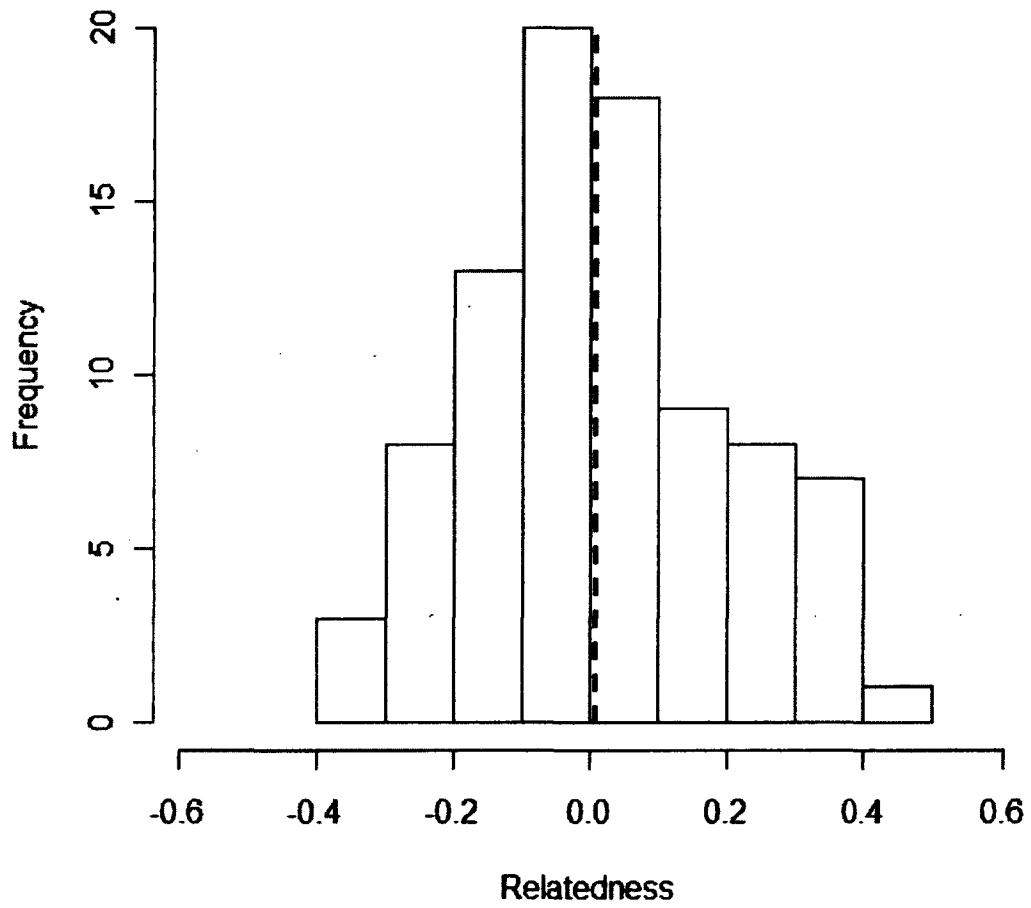
Figure 4.2 Distributions of estimates of pairwise relatedness among female raccoons sampled from April 2010 to April 2011 in the Mont-Orford provincial park, Québec, Canada. Mean relatedness is represented by the dashed line.

Environmental determinants

Results obtained from analysis made with daily contact rate showed that contact rate differed among seasons being significantly higher in winter (mean ± SE: 24.07 ± 4.21) than in summer (3.02 ± 2.58) (linear mixed model: [estimate ± SE] 0.70 ± 0.13, t = 5.46, P < 0.001). There was no time-of-day effect on contact rate during the summer (linear mixed-model: [estimate ± SE] 0.09 ± 0.05, t = 1.66, P = 0.10). During winter, however, raccoons had higher contact rate during nighttime (linear mixed-model: [estimate ± SE] 0.27 ± 0.07, t = 3.79, P < 0.001).

During winter, daily contact rate was best explained by a model including temperature only as contact rate was higher when the temperature was low (generalized linear mixed-model: [estimate ± SE] -0.02 ± 0.01, t = 12.9, P < 0.001). Our model predicted that a decrease of 1 °C results in a gain of one contact per day. However, when only the dyads that had contacts were taken into account we did not found any effect of temperature (generalized linear mixed-model: [estimate ± SE] -0.002 ± 0.004, t = 0.16, P = 0.69).

Individual determinants

Multiple regression matrices analysis made from dyads mean contact rate revealed a positive correlation between home range overlap and relatedness during summer and winter (Table 4.1). During summer females raccoons had more encounters with females with whom they were more related (Table 4.2). Multiple regression matrices conducted with contact rate and home range overlap showed a positive correlation; however, the effect disappeared when the relatedness variable was added to the model. Multiple regression analysis revealed that during winter there was also a positive effect of home range overlap and relatedness on contact rate among female raccoons (Table 4.2).

61

Table 4.1 Multiple regression matrices results for the correlations between the relatedness and the home range overlap among females raccoons sampled in the Mont-Orford provincial park, Québec, Canada.

	Explanatory variable	β	r^2	P-value
Summer 2010	Relatedness	0.049	0.338	0.001
Summer 2011	Relatedness	0.719	0.120	0.020
Winter 2010-2011	Relatedness	23.103	0.079	0.028

Table 4.2 Multiple regression matrices results for the correlations between the relatedness and the home range overlap with the mean contact rate for female raccoon dyads sampled in the Mont-Orford provincial park, Québec, Canada.

r^2	Explanatory variable	β	P-value
Summer 2010 (r^2= 0.373)	Relatedness	0.041	0.003
	Home range overlap	0.012	0.201
Summer 2011 (r^2= 0.121)	Relatedness	0.734	0.026
	Home range overlap	-0.027	0.874
Winter 2010-2011 (r^2= 0.491)	Relatedness	17.933	0.021
	Home range overlap	0.003	0.004

Discussion

Environmental determinants

The higher contact rates observed during winter support the observations that raccoons are more gregarious in winter than in summer (Gehrt 2003; Mech and Turkowski 1966). Our results are also consistent with a recent study by Prange *et al.*, (2011) which shows that

contacts were affected by seasons and that they were higher in winter and spring than in summer and autumn. However, the mean female contacts rates we obtained during winter were much higher than the one reported in Prange *et al.*, (2011); they observed less than 1 contact/day among female dyads and we recorded over 24 contacts/day. Variation between populations in contact rate could be explained by difference in winter strategy due to the difference in climatic constraints between study sites. Our study was conducted in southern Québec – at the northern edge of the raccoon range distribution – whereas Prange *et al.*, (2011) study was performed in northern Illinois, which is located much farther south (Prange *et al.*, 2011). In southern Québec winters are relatively long and cold, with a mean low temperature of -13.4° C in January (Environment Canada 2011). In contrast, mean January low temperature in Illinois is -2.9° C (National climatic data center, 2012). As the climate is colder in our study site it could be more advantageous for an individual to share dens with several raccoons to keep a warmer body temperature. Thus, the social thermoregulation hypothesis (Ebensperger 2001; Kerth 2008) may explain the apparent variation in social behaviours observed among study sites. According to this hypothesis, winter aggregations should occur in cold environments and the frequency of groupings should show a negative relationship with ambient temperature (i.e., increase with decreases in ambient temperature) (Ebensperger 2001).

Social thermoregulation has been observed in other species: agile Antechinus (*Antechinus agilis*) (Fisher *et al.*, 2011), Abert's squirrels (*Sciurus aberti*) (Edelman and Koprowski 2007) and big brown bats (Willis and Brigham 2007a). Social thermoregulation results in decreased water loss and energy costs associated with thermoregulation (Hwang *et al.*, 2007; Merritt and Zegers 2002). For example, in skunks (*Mephitis mephitis*), individuals that participated in social thermoregulation during winter had a higher percentage of fat reserves at den emergence than solitary individuals (Hwang *et al.*, 2007). The percentage of fat at den emergence is also important for raccoons as their food resources are scarce during that period (Farley and Robbins 1995). It might be especially important for females because of their higher reproductive costs incurred during pregnancy (i.e., gestation and lactation). Our results

suggest the social thermoregulation hypothesis may have shaped the evolution of sociality among female raccoons at the northern range of their distribution.

Individual determinants

In raccoons, females are philopatric (Gehrt 2003). Based on observations of home range overlap (Kaufmann 1982) and the persistence of females in their natal habitat (Ratnayeke 1997), previous studies suggest that females raccoons are more related to neighbouring females. Molecular evidences also revealed patterns of isolation by distance such that females who shared space or were proximally located were also closely related (Ratnayeke *et al.*, 2002; Côté *et al.*, 2012). However, unrelated or weakly related females have also been observed having extensive home range overlap (Ratnayeke *et al.*, 2002). Our results are consistent with findings supporting a positive relationship between home range overlap and relatedness during summer and winter. Our results also suggest that during summer females raccoons might show temporal avoidance at fine spatial scales, as we found a positive effect of relatedness on contact rate, but no effect of home range overlap. Thus, our results suggest that for similar shared areas female raccoons might avoid encounters with unrelated females during summer. According to the kin selection theory (Hamilton 1964) it would be more beneficial for an individual's fitness to share food resources or shelter, for example, with related individuals than unrelated individuals. Although contacts were infrequent during summer, these results could be explained by a higher tolerance of related individuals, which is reinforced by philopatry as we observed that kin were more aggregated in space.

Female raccoons are known to form groups with their yearling(s) during winter (Gehrt 2003). Anecdotal observations of adult raccoons in winter dens suggest that raccoons may also form family groups (Gehrt and Fritzell 1998b). The results obtained from the mean contact rate per dyad show a positive effect of relatedness on contact rate. Relatedness has been shown to affect communal nesting in some species (Ebensperger *et al.*, 2004; Thorington and Weigl

65

2011). Consistent with our results, however, communal nesting in Abert squirrels was more common among unrelated individuals during the cold season (Halloran and Bekoff 1994). Again, at colder temperatures the benefits of social thermoregulation on fitness might outweigh the indirect fitness benefits obtained by forming denning groups consisting exclusively of related individuals. For example, in big brown bats, the energy savings related to social thermoregulation was positively correlated with the number of individual that was found in the cavity (Willis and Brigham 2007a). To benefits from communal denning at the northern limit of their range, raccoons might require more individuals than are available from their kin alone. Thus, as the energetic demand on females are higher due to gestation and lactation, benefits from forming larger groups might exceed the individual-level benefits that would be predicted based solely on kin selection theory. Furthermore, such benefits must outweigh the costs incurred by increased competition or probability of contracting infectious diseases.

Conclusions

Our results suggest that ecological factors, such as temperature, may affect the evolution of sociality in female raccoons. They also suggest that female raccoons showed social flexibility (Lott 1991) as observed in a wide range of species (Caro 1994; Loveridge and Macdonald 2001; McGuire and Getz 1998). We encourage future work to be conducted on the factors that influence the formation of coalitions among male raccoons. Explicit tests of fitness related cost/benefit trade-offs resulting from social thermoregulation among communally denning species would also help to bring new insights on the effect of environmental variation on the evolution of sociality in mammals. In carnivores, it has been suggested that sociality has evolved from socially flexible solitary ancestors (Dalerum *et al.*, 2006). Thus, studies on solitary species that show context-dependent social flexibility, such as raccoons, provide insights into factors that shape the evolution of sociality in other more gregarious species. We encourage future work to be conducted on the factors that influence the formation of coalitions among male raccoons and explicit tests of fitness related cost/benefit trade-offs resulting from social thermoregulation among communally denning species.

Acknowledgments

CHAPITRE 5

CONCLUSION

5.1. Retour sur les résultats du mémoire

Mon projet de maîtrise a permis dans de vérifier l'efficacité du chevauchement des domaines vitaux comme méthode d'estimation des taux de contacts. Bien que les études sur le sujet demeurent très peu fréquentes (Schauber, Storm *et al.*, 2007), on suppose qu'il existe une corrélation positive entre le chevauchement des domaines vitaux et le taux de contacts. Contrairement à la seule étude qui, à ma connaissance, a exploré cette relation chez le cerf de virginie (Schauber, Storm *et al.*, 2007), mes résultats suggèrent que le chevauchement des domaines vitaux et le taux de contacts sont positivement corrélés. Bien que les études aient été effectuées avec deux espèces différentes (un ongulé vs un carnivore solitaire). Les deux espèces sont plutôt solitaires durant l'été (Nixon, Hansen *et al.*, 1992; Bertrand, DeNicola *et al.*, 1996; Gehrt, 2003) et grégaires durant l'hiver (Hirth, 1977; Gehrt, 2003). Il est donc peu probable que la différence observée soit expliquée par des différences dans le niveau de socialité entre les espèces. La non-concordance des résultats serait plutôt expliquée par le matériel utilisé. Dans l'étude de Schauber *et al.*, (2007), des colliers GPS ont été utilisés pour quantifier les contacts. Avec ces colliers, un contact direct est estimé à partir de distances pouvant être très grandes (variant de 10 m à 100 m). De plus, il n'est pas possible d'obtenir des données sur chacun des contacts puisque les colliers contraignent la prise de données à des intervalles de temps donnés. Il est donc possible que ce ne soit pas tous les contacts qui aient été enregistrés, ce qui aurait pu mener à l'absence de corrélation entre le chevauchement des domaines vitaux et le taux de contacts. Les colliers utilisés lors de mon étude (de type « proximity logger ») permettent, au contraire, d'obtenir des données sur chaque contact, puisqu'un enregistrement s'effectue chaque fois que deux individus ou plus se retrouvent à moins de deux mètres. Nos résultats suggèrent que le chevauchement des domaines vitaux

68

peut être un bon estimateur du taux de contacts. Ces résultats sont importants puisque plusieurs données issues de suivis télémétriques effectués sur différentes espèces sont disponibles, et ce, depuis plusieurs décennies. Ces données pourraient donc être utilisées de manière appliquée lors de programmes de prévention de maladies infectieuses ou lors d'études concernant l'évolution de la socialité chez les animaux.

Mon projet de maîtrise a permis, dans un deuxième temps, de mieux comprendre les déterminants environnementaux et individuels des taux de contacts chez les femelles ratons laveurs. Mes résultats montrent que les femelles ratons laveurs montrent de la flexibilité sociale (Lott, 1991) puisqu'elles ont des contacts très peu fréquents durant l'été et à l'inverse très fréquents durant l'hiver. De plus, les températures froides de l'hiver semblent avoir une influence déterminante sur les taux de contacts. En effet, mes résultats montrent que plus les températures sont froides, plus les contacts entre les individus sont fréquents, ce qui supporte l'hypothèse de la thermorégulation sociale (Ebensperger, 2001). La thermorégulation sociale a été observée chez plusieurs espèces (Edelman & Koprowski, 2007; Willis & Brigham, 2007; Fisher, Nuske *et al.*, 2011) et procure certains bénéfices tels qu'une diminution de la perte en eau et une réduction des coûts associés à la thermorégulation (Merritt & Zegers, 2002; Hwang, Larivière *et al.*, 2007). Chez la moufette par exemple, les individus qui pratiquent la thermorégulation sociale durant l'hiver ont des réserves de graisse plus importantes à l'émergence du terrier que ceux qui ont passé l'hiver seuls (Hwang, Larivière *et al.*, 2007). Chez les ratons laveurs, les avantages de la thermorégulation sociale sont particulièrement importants pour les femelles puisque, durant l'hiver, les coûts associés à la reproduction sont plus élevés étant donné la gestation, la mise bas et l'allaitement. De plus, mes résultats supportent les hypothèses selon lesquelles il y aurait formation de groupes familiaux chez les ratons laveurs adultes durant l'hiver (Gehrt & Fritzell, 1998b) puisqu'ils montrent un effet de l'apparentement sur les contacts. Mes montrent suggèrent que des facteurs écologiques tels que les températures hivernales ont aussi un impact dans l'évolution de la socialité chez les femelles ratons laveurs au nord de leur distribution. Mes résultats suggèrent que les ratons laveur forment des groupes familiaux durant l'hiver et que leur tolérance aux individus non

69

apparentés peut être influencée par des facteurs environnementaux tels que la température. Durant l'été, les taux de contacts sont influencés positivement par l'apparentement des individus. Bien que les contacts demeurent très peu fréquents durant cette période, ces résultats pourraient être expliqués en partie par le comportement de philopatrie (Gehrt, 2003) et par la sélection de parentèle (Hamilton, 1964). En effet, puisque selon la théorie de sélection de parentèle (Hamilton, 1964) il serait plus avantageux pour la valeur adaptative d'un individu de partager des ressources ou des abris, par exemple, les individus pourraient être plus tolérants avec des individus apparentés que non apparentés.

5.2. Importance du projet

Mes travaux ont un impact autant au niveau fondamental qu'appliqué. Tout d'abord, les résultats obtenus lors de mon projet de maîtrise montrent l'importance de l'étude des contacts chez les espèces solitaires puisqu'elle nous permet d'identifier des facteurs ayant un rôle primordial dans la structure des contacts entre les individus ayant possiblement des effets importants dans l'évolution de la socialité. De plus, mes résultats montrent une structure sociale plus complexe que celle attendue chez un animal solitaire. Ce type de structure a aussi été observé chez plusieurs autres espèces solitaires (Caro, 1994; Sterling & Richard, 1995; Hays & Conant, 2003). L'étude des espèces solitaires semble donc avoir plus d'importance que ce que l'on croyait en ce qui a trait à notre compréhension de l'évolution de la socialité.

Ensuite, mes travaux permettent d'effectuer des avancées en épidémiologie puisqu'ils apportent des connaissances sur les taux de contacts intraspécifiques d'une population d'animaux sauvages. En fait, il existe actuellement plusieurs modèles épidémiologiques élaborés pour les populations humaines qui sont utilisés pour prédire le potentiel de propagation des maladies infectieuses chez les populations d'animaux sauvages (Anderson, 1995; Grenfell & Dobson, 1995; Fromont *et al.*, 1998; Fromont *et al.*, 2003; Gudelj & White,

2004). Cependant, le taux de transmissions des maladies infectieuses est une variable essentielle pour la modélisation de leur propagation et est très difficile à quantifier empiriquement sur le terrain. Pour la majorité des maladies toutefois, le taux de contacts est corrélé au taux de transmissions, spécialement en ce qui concerne les maladies qui nécessitent un contact direct pour se transmettre telles que le virus de la rage (Haydon *et al.*, 2003). Le taux de contacts est donc utilisé dans les modèles épidémiologiques comme une estimation du taux de transmissions. Cependant, les taux de contacts réels demeurent encore peu fréquemment quantifiés dans les populations sauvages. Ils sont souvent obtenus, eux aussi, à partir d'une méthode d'estimation. Il en résulte donc des modèles épidémiologiques simplifiés dont les résultats obtenus sont plus ou moins représentatifs de la réalité. Pour améliorer les modèles et générer des résultats plus réalistes, il est nécessaire de quantifier les taux de contacts réels des populations d'animaux sauvages et de les intégrer aux modèles (Diekmann *et al.*, 1995; Grenfell & Dobson, 1995). Les résultats issus de mon projet de maîtrise pourront être intégrés dans un modèle plus général visant à modéliser le potentiel de la propagation de la rage au Québec et dans l'Est du Canada. Mes résultats sont donc particulièrement importants dans le cas du raton laveur puisque c'est une espèce se retrouvant souvent à proximité de l'homme et qui est l'hôte d'une maladie pouvant avoir des répercussions tragiques chez l'humain. En effet, les résultats que j'ai obtenus pourront contribuer à générer des résultats plus réalistes concernant la propagation de la maladie de la rage dans l'Est du Canada et de cette manière améliorer les méthodes de prévention.

5.3. Perspectives futures

Les résultats obtenus laissent la porte ouverte à d'autres études dans lesquelles il serait pertinent d'explorer de nouvelles pistes de recherche. En effet, il serait important d'étudier, entre autres, les fluctuations des taux de contacts chez les mâles et les facteurs qui les influencent. De plus, il a été montré récemment que les mâles ratons laveurs forment des coalitions (Pitt, Larivière *et al.*, 2008a). Il serait donc pertinent de vérifier les facteurs qui influencent la formation de ces coalitions de manière à vérifier si les facteurs qui affectent la

71

socialité diffèrent entre les sexes. Comme les températures hivernales semblent avoir un effet important sur les contacts des femelles ratons laveurs, il serait pertinent d'étudier comment la thermorégulation sociale influence leur valeur adaptative. Puisqu'il y a de la variabilité dans la formation des groupes durant l'hiver, il serait possible, par exemple, de comparer le succès reproducteur des femelles qui montrent de la thermorégulation sociale avec celui des femelles qui passent l'hiver seules. De plus, il a été montré chez la moufette, une espèce de taille similaire au raton laveur, que certains individus montraient de la torpeur et d'autres de la thermorégulation sociale. Il serait donc pertinent de voir si certains individus chez les ratons laveurs montrent aussi de la torpeur, puis d'étudier les conditions sous lesquelles ce comportement est observé. Il serait aussi intéressant d'explorer la socialité à plus grande échelle et à différentes latitudes de manière à explorer l'effet des différentes contraintes environnementales sur les taux de contacts, et ce, dans différents climats.

BIBLIOGRAPHIE

Alexander, R. D. (1974). The evolution of social behavior. Annu. Rev. Ecol. Syst. *5*, 325-383.

Anderson, R. M. (1995). Evolutionary pressures in the spread and persistence of infectious agents in vertebrate populations. Parasitology *111*, S15-S31.

Atwood, T. and J. Weeks, HP (2003). Spatial home-range overlap and temporal interaction in eastern coyotes: the influence of pair types and fragmentation. Can. J. Zool. *81*, 1589-1597.

Bacon, P. J., J. F. Dallas and S. B. Piertney (1999). Spatial distribution of genetic relatedness in a moorland population of red grouse (*Lagopus lagopus scoticus*). Biol. J. Linn. Soc. *68*, 317-331.

Ballard, W. and R. Tobey (1981). Decreased calf production of moose immobilized with anectine administered from helicopter. Wild. Soc. B. *9*, 207-209.

Beauchamp, G. (2005). Does group foraging promote efficient exploitation of resources? Oikos *111*, 403-407.

Beck, C. (1976). Vetalar® (Ketamine Hydrochloride) a unique cataleptoid anesthetic agent for Multispecies Usage. J. Zoo Anim. Med. *7*, 11-38.

Begon, M., M. Bennett, R. Bowers, N. French, S. Hazel and J. Turner (2002). A clarification of transmission terms in host-microparasite models: numbers, densities and areas. Epidemiol. Infect. *129*, 147-153.

Belant, J. (2004). Field immobilization of raccoons (*Procyon lotor*) with telazol and xylazine. J. Wild. Dis. *40*, 787-790.

Bert, B., I. Hartje, J. P. Voigt, G. Arndt, H. F. Ulbrich, H. Fink and P. Hauff (2008). Repeated anaesthesia with isoflurane and xylazine/levomethadone/ fenpipramide premedication in female Beagle dogs: Influence on general health and wellbeing. Lab. Anim. *42*, 473-482.

Bertrand, M. R., A. J. DeNicola, S. R. Beissinger and R. K. Swihart (1996). Effects of parturition on home ranges and social affiliations of female white-tailed deer. J. Wild. Manage. *60*, 899-909.

Bhattacharyya, A. (1943). On a measure of divergence between two statistical populations defined by their probability distributions. Bull. Calcutta Math. Soc *35*, 99-109.

Böhm, M., K. L. Palphramand, G. Newton Cross, M. R. Hutchings and P. C. L. White (2008). Dynamic interactions among badgers: implications for sociality and disease transmission. J. Anim. Ecol. *77*, 735-745.

Böhm, M., M. R. Hutchings, et al. (2009). Contact networks in a wildlife-livestock host community: identifying high-risk individuals in the transmission of bovine TB among badgers and cattle. PLoS One 4, e5016.

Borgatti, S., M. Everett, et al. (2002). Ucinet for Windows: Software for social network analysis. Harvard: Analytic Technologies. Soc. Networks 28, 165-178.

Börger, L., N. Franconi, G. D. Michele, A. Gantz, F. Meschi, A. Manica, s. Lovari and T. Coulson (2006). Effects of sampling regime on the mean and variance of home range size estimates. J. Anim. Ecol. *75*, 1393-1405.

Burt, W. (1943). Territoriality and home range concepts as applied to mammals. J. Mammal. *24*, 346-352.

Buston, P., C. Fauvelot, M. Wong and S. Planes (2009). Genetic relatedness in groups of the humbug damselfish *Dascyllus aruanus*: small, similar-sized individuals may be close kin. Mol. Ecol. *18*, 4707-4715.

Calenge, C. (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecol. Model. *197*, 516-519.

Caro, T. M. (1994). Cheetahs of the Serengeti Plains: group living in an asocial species (Chicago: University of Chicago Press).

Cattet, M., J. Boulanger, G. Stenhouse, R. A. Powell and M. J. Reynolds-Hogland (2008). An evaluation of long-term capture effects in ursids: implications for wildlife welfare and research. J. Mammal. *89*, 973-990.

Cauchemez, S., A. Bhattarai, T. L. Marchbanks, R. P. Fagan, S. Ostroff, N. M. Ferguson, D. Swerdlow and t. P. H. N. w. group (2011). Role of social networks in shaping disease transmission during a community outbreak of 2009 H1N1 pandemic influenza. PNAS *108*, 2825-2830.

Chamberlain, M. J. (2002). Spatio-temporal relationships among adult raccoons (*Procyon lotor*) in central Mississippi. Am. Midl. Nat. *148*, 297-308.

Chambers, J. L. and D. Garant (2010). Determinants of population genetic structure in eastern chipmunks (*Tamias striatus*): The role of landscape barriers and sex-biased dispersal. J. Hered. *101*, 413-422.

Cline, D. R., D. B. Siniff and A. W. Erickson (1969). Immobilizing and collecting blood from Antarctic seals. J. Wild. Manage. *33*, 138-144.

Clutton-Brock, T. (1989). Review lecture: mammalian mating systems. P. Roy. Soc. Lond. B. Bio. *236*, 339-372.

Clutton, R. and L. Duggan (1986). Saffan Anesthesia in the Raccoon: A Preliminary Report. J. Zoo. Anim. Med.*17*, 91-99.

Coltman, D. W., J. G. Pilkington and J. M. Pemberton (2003). Fine-scale genetic structure in a free-living ungulate population. Mol. Ecol. *12*, 733-742.

Côté, H., D. Garant, K. Robert, J. Mainguy and F. Pelletier (2012). Genetic structure and rabies spread potential in raccoons: the role of landscape barriers and sex-biased dispersal. Evol. Appl.

Côté, I. M. and R. Poulin (1995). Parasitism and group size in social animals: a meta-analysis. Behav. Ecol. *6*, 159-165.

Côté, S. D., M. Festa-Bianchet and F. Fournier (1998). Life-history effects of chemical immobilization and radiocollars on mountain goats. J. Wild. Manage. *62*, 745-752.

Craft, M. E., P. L. Hawthorne, C. Packer and A. P. Dobson (2008). Dynamics of a multihost pathogen in a carnivore community. J. Anim. Ecol. *77*, 1257-1264.

Creel, S. R. and N. M. Creel (1991). Energetics, reproductive suppression and obligate communal breeding in carnivores. Behav. Ecol. Sociobiol. *28*, 263-270.

Cullingham, C. I., C. J. Kyle and B. N. White (2006). Isolation, characterization and multiplex genotyping of raccoon tetranucleotide microsatellite loci. Mol. Ecol. Notes *6*, 1030-1032.

Dalerum, F., S. Creel and S. Hall (2006). Behavioral and endocrine correlates of reproductive failure in social aggregations of captive wolverines (*Gulo gulo*). J. Zool. *269*, 527-536.

76

Dematteis, A., A. Menzano, G. Canavese, P. Meneguz and L. Rossi (2009). Anaesthesia of free-ranging Northern chamois (*Rupicapra rupicapra*) with xylazine/ketamine and reversal with atipamezole. Eur. J. Wild. Res. *55*, 567-573.

Dexter, N. (2003). Stochastic models of foot and mouth disease in feral pigs in the Australian semi-arid rangelands. J. Appl. Ecol. *40*, 293-306.

Diekmann, O., M. C. M. D. Jong, A. A. D. Koeijer and P. Reijnders (1995). The force of infection in populations of varying size: A modelling problem. J. Biol. Syst. *3*, 519-529.

Doncaster, C. P. (1990). Non-parametric estimates of interaction from radio-tracking data. J. Theor. Biol. *143*, 431-443.

Dunbar, R. I. M. (1988). Primate social systems (Princeton: Princeton University Press).

Dzialak, M. R., T. L. Serfass and T. L. Blankenship (2001). Reversible chemical restraint of fishers with medetomidine-ketamine and atipamezole. J. Wild. Manage. *65*, 157-163.

Ebensperger, L. A. (2001). A review of the evolutionary causes of rodent group-living. Acta Theriol. *46*, 115-144.

Ebensperger, L. A., M. J. Hurtado, M. Soto-Gamboa, E. A. Lacey and A. T. Chang (2004). Communal nesting and kinship in degus (*Octodon degus*). Naturwissenschaften *91*, 391-395.

Eberhard, M. J. W. (1975). The Evolution of Social Behavior by Kin Selection. Q. Rev. Biol. *50*, 1-33.

Eberle, M. and P. M. Kappeler (2006). Family insurance: kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*). Behav. Ecol. Sociobiol. *60*, 582-588.

Edelman, A. J. and J. L. Koprowski (2007). Communal nesting in asocial Abert's squirrels: The role of social thermoregulation and breeding strategy. Ethology *113*, 147-154.

Environnement Canada (2011). "Magog climate summaries". Retrived 7 december 2011, from http://www.climat.meteo.gc.ca/climateData.

Evans, R. (2002). Raccoons and relatives (Carnivora, Procyonidae). In Zoological restraint and anesthesia, D. Heard, ed. (New York: International Veterinary Information Service), pp. 1-8.

Farley, S. D. and C. T. Robbins (1995). Lactation, hibernation, and mass dynamics of American black bears and grizzly bears. Can. J. Zool.*73*, 2216-2222.

Fassoulaki, A., R. Farinotti, J. Mantz and J. Desmonts (1994). Does tolerance develop to the anaesthetic effects of propofol in rats? Brit. J. Anaesth. *72*, 127-128.

Festa-Bianchet, M. (1991). The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. Anim. Behav.*42*, 71-82.

Fieberg, J. and C. O. Kochanny (2005). Quantifying home-range overlap: the importance of the utilization distribution. J. Wild. Manage. *69*, 1346-1359.

Field, I. C., C. McMahon, H. Burton, C. Bradshaw and J. Harrinigton (2002). Effects of age, size and condition of elephant seals (*Mirounga leonina*) on their intravenous anaesthesia with tiletamine and zolazepam. Vet. Rec. *151*, 235-240.

Fike, J. A., A. M. Drauch, J. C. Beasley, G. Dharmarahan and O. E. R. Jr (2007). Development of 14 multiplexed microsatellite loci for raccoons *Procyon lotor*. Mol. Ecol. 7, 525-527.

Fisher, D., S. Nuske, S. Green, J. Seddon and B. McDonald (2011). The evolution of sociality in small, carnivorous marsupials: the lek hypothesis revisited. Behav. Ecol. Sociobiol. *65*, 593-605.

Fletcher, Q. E. and R. Boonstra (2006). Impact of live trapping on the stress response of the meadow vole (*Microtus pennsylvanicus*). J. Zool. *270*, 473-478.

Frère, C. H., M. Krützen, J. Mann, J. J. Watson-Capps, Y. J. Tsai, E. M. Patterson, R. Connor, L. Bejder and W. B. Sherwin (2010). Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. Anim. Behav. *80*, 481-486.

Frey, S. N. and M. R. Conover (2007). Influence of population reduction on predator home range size and spatial overlap. J. Wild. Manage. *71*, 303-309.

Fritzell, E. K. (1978). Aspects of raccoon (*Procyon lotor*) social organization. Canadian J. Zool. *56*, 260-271.

Fromont, E., D. Pontier and M. Langlais (1998). Dynamics of a feline retrovirus (FeLV) in host populations with variable spatial structure. P. Roy. Soc. Lond. B. Bio. *265*, 1097-1104.

Fromont, E., D. Pontier and M. Langlais (2003). Disease propagation in connected host populations with density-dependent dynamics: the case of the Feline Leukemia Virus. J. Theor. Biol. *223*, 465-475.

Fu, Z. F. (1997). Rabies and rabies research: past, present and future. Vaccine *15*, S20-S24.

Gannon, W. and R. Sikes (2007). The Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J. Mammal. *88*, 809–823.

Gehrt, S. D. (2003). Raccoon (*Procyon lotor*) and allies. In Wild mammals of North America, G. A. Feldhamer, B. C. Thompson and J. A. Chapman, eds. (Baltimore: The johns hopkins university press), pp. 611-635.

Gehrt, S. D. and E. K. Fritzell (1997). Sexal differences in home ranges of raccoons. J. Mammal. *78*, 921-931.

Gehrt, S. D. and E. K. Fritzell (1998a). Duration of familial bonds and dispersal patterns for raccoons in south texas. J. Mammal. *79*, 859-872.

Gehrt, S. D. and E. K. Fritzell (1998b). Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. Anim. Behav. *55*, 1211-1227.

Gehrt, S. D. and E. K. Fritzell (1999). Behavioural aspects of the raccoon mating system: determinants of consortship success. Anim. Behav. *57*, 593-601.

Genstat (2005). GenStat Release 8 Reference Manual. VSN International. Oxford, United Kingdom.

Giraldeau, L. A. and T. Caraco (2000). Social foraging theory (Princeton: Princeton University Press).

Gompper, M. E., J. L. Gittleman and R. K. Wayne (1997). Genetic relatedness, coalitions and social behaviour of white-nosed coatis, *Nasua narica*. Anim. Behav. *53*, 781-797.

Goodman, E. (2007). Quantifying interactions in a high-density badger (*Meles meles*) population. P.h.D. thesis, University of York, York.

Goudet, J. (2002). FSTAT, a program to estimate and test gene diversities and fixation indices (version 2.9. 3.2). Lausanne: University of Lausanne, Department of Ecology and Evolution.

Grear, D. A., M. D. Samuel, K. T. Scribner, B. V. Weckworth and J. A. Langenberg (2010). Influence of genetic relatedness and spatial proximity on chronic wasting disease infection among female white-tailed deer. J. Appl. Ecol. *47*, 532-540.

Gregg, D. and L. Olson (1975). The use of ketamine hydrochloride as an anesthetic for raccoons. J. Wild. Dis. *11*, 335-337.

Grenfell, B. T. and A. P. Dobson (1995). Ecology of infectious diseases in natural populations (New York: Cambridge University press).

Gudelj, I. and K. A. J. White (2004). Spatial heterogeneity, social structure and disease dynamics of animal populations. Theor. Popul. Biol. *66*, 139-149.

Habib, T. J., E. H. Merrill, M. J. Pybus and D. W. Coltman (2011). Modelling landscape effects on density-contact rate relationships of deer in eastern Alberta: Implications for chronic wasting disease. Ecol. Model. *222*, 2722-2732.

Halloran, M. E. and M. Bekoff (1994). Nesting behaviour of Abert squirrels (*Sciurus aberti*). Ethology *97*, 236-248.

Hamilton, W. (1964). The genetical evolution of social behaviour. I. I. J. Theor. Biol. *7*, 1-16.

Hamilton, W. D. (1971). Geometry for the selfish herd. J. Theor. Biol. *31*, 295-311.

Hardy, O. J. and X. Vekemans (2002). SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. Mol. Ecol. Notes *2*, 618-620.

Hardy, O. J. (2003). Estimation of pairwise relatedness between individuals and characterization of isolation-by-distance processes using dominant genetic markers. Mol. Ecol. *12*, 1577-1588.

Harper, J. M. and S. N. Austad (2001). Effect of Capture and Season on Fecal Glucocorticoid Levels in Deer Mice (*Peromyscus maniculatus*) and Red-Backed Voles (*Clethrionomys gapperi*). Gen. Comp. Endocr. *123*, 337-344.

Haydon, D., M. Chase-Topping, D. Shaw, L. Matthews, J. Friar, J. Wilesmith and M. Woolhouse (2003). The construction and analysis of epidemic trees with reference to the 2001 UK foot-and-mouth outbreak. P. Roy. Soc. Lond. B. Bio. *270*, 121-127.

Hays, W. S. T. and S. Conant (2003). Male social activity in the small Indian mongoose *Herpestes javanicus*. Acta Theriol. *48*, 485-494.

Hedenqvist, P., J. Roughan and P. Flecknell (2000). Effects of repeated anaesthesia with ketamine/medetomidine and of pre-anaesthetic administration of buprenorphine in rats. Lab. Anim. *34*, 207-211.

Hinde, R. (1976). Interactions, relationships and social structure. Man *11*, 1-17.

Hirth, D. H. (1977). Social behavior of white-tailed deer in relation to habitat. Wild. monogr. *53*, 3-55.

Hoilien, J. and D. Oates (1981). Tranquilizer use in wildlife damage control. In Great Plains Wild. Damage Control Workshop Proceedings. University of Nebraska, Lincoln, Nebraska.

Hwang, Y. T., S. Larivière and F. Messier (2007). Energetic consequences and ecological significance of heterothermy and social thermoregulation in striped skunks (*Mephitis mephitis*). Physiol. Biochem. Zool. *80*, 138-145.

Jalanka, H. and B. Roeken (1990). The use of medetomidine, medetomidine-ketamine combinations, and atipamezole in nondomestic mammals: a review. J. Zoo Wild. Med. *21*, 259-282.

Jarman, P. J. and Kruuk, H. (1996). Phylogeny and social organization in mammals. In Comparaison of marsupial and placental behavior, D. B. Croft, U. Ganslober, eds. (Fürth: Filander), pp. 80-101.

Johnson, A. S. (1970). Johnson 1970. Biology of the raccoon (*Procyon lotor varius* Nelson and Goldman) in Alabama. Agricultural experiment station, Auburn university, Bulletin 402.

Jorgenson, J., J. Samson and M. Festa-Bianchet (1990). Field immobilization of bighorn sheep with xylazine hydrochloride and antagonism with idazoxan. J. Wild. Dis. *26*, 522-527.

Kalinowski, S. T., M. L. Taper and T. C. Marshall (2007). Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol. Ecol. *16*, 1099-1106.

Kaufmann, J. (1982). Raccoons and allies. (Baltimore: Johns Hopkins University Press).

Kenward, R. E. and K. H. Hodder (1998). Red squirrels (*Sciurus vulgaris*) released in conifer woodland: the effects of source habitat, predation and interactions with grey squirrels (*Sciurus carolinensis*). J. Zool. *244*, 23-32.

Kerth, G. (2008). Causes and consequences of sociality in bats. BioScience *58*, 737-746.

King, R., R. Lapid, A. Epstein, T. Bdolah-Abram and Y. Shilo (2008). Field anesthesia of golden jackals (*Canis aureus*) with the use of medetomidine-ketamine or medetomidine-midazolam with atipamezole reversal. J. Zoo Wild. Med. *39*, 576-581.

Klaassen, R. H. G., B. A. Nolet and D. Bankert (2006). The influence of social interactions on the foraging path of Bewick's Swans *Cygnus columbianus bewickii*. Ardea *94*, 477-484.

Krause, J. and G. D. Ruxton (2002). Living in groups (New York: Oxford University Press).

Krause, J., D. Lusseau, et al. (2009). Animal social networks: an introduction. Behav. Ecol. Sociobiol. *63*, 967-973.

Kreeger, T., J. Arnemo and J. Raath (2002). Handbook of wildlife chemical immobilization. (Fort Collins: Wild. Pharmaceuticals, Inc.).

Lacey, E. A. and J. R. Wieczorek (2004). Kinship in colonial tuco-tucos: evidence from group composition and population structure. Behav. Ecol. *15*, 988-996.

Leuthold, B. (1979). Social organization and behaviour of giraffe in Tsavo East National Park. Afr. J. Ecol *17*, 19–34.

Lewandowski, A. H., C. J. Bonar and S. E. Evans (2002). Tiletamine-Zolazepam, Ketamine, and Xylazine Anesthesia of Captive Cheetah (*Acinonyx jubatus*). J. Zoo Wild. Med. *33*, 332-336.

Lichstein, J. W. (2007). Multiple regression on distance matrices: a multivariate spatial analysis tool. Plant Ecol. *188*, 117-131.

Lloyd-Smith, J. O., P. C. Cross, C. J. Briggs, M. Daugherty, W. M. Getz, J. Latto, M. S. Sanchez, A. B. Smith and A. Swei (2005). Should we expect population thresholds for wildlife disease? Trends Ecol. Evol. *20*, 511-519.

Lott, D. F. (1984). Intraspecific variation in the social systems of wild vertebrates. Behaviour *88*, 266-325.

Lott, D. F. (1991). Intraspecific variation in the social systems of wild vertebrates (Cambridge: Cambridge University Press).

Loveridge, A. and D. Macdonald (2001). Seasonality in spatial organization and dispersal of sympatric jackals (*Canis mesomelas* and *C. adustus*): implications for rabies management. J. Zool. *253*, 101-111.

Lynn, S. E. and A. J. Porter (2008). Trapping initiates stress response in breeding and non-breeding house sparrows *Passer domesticus*: Implications for using unmonitored traps in field studies. J. Avian Biol. *39*, 87-94.

Madden, J. R., J. A. Drewe, G. P. Pearce and T. H. Clutton-Brock (2009). The social network structure of a wild meerkat population: 2. Intragroup interactions. Behav. Ecol. Sociobiol. *64*, 81-95.

Maher, C. and D. Lott (2000). A review of ecological determinants of territoriality within vertebrate species. Am. Midl. Nat. *143*, 1-29.

McCallum, H., N. Barlow and J. Hone (2001). How should pathogen transmission be modelled? Trends Ecol. Evol. *16*, 295-300.

McEachern, M. B., J. M. Eadie and D. H. V. Vuren (2007). Local genetic structure and relatedness in a solitary mammal, *Neotoma fuscipes*. Behav. Ecol. Sociobiol. *61*, 1459-1469.

McGuire, B. and L. L. Getz (1998). The nature and frequency of social interactions among free-living prairie voles (*Microtus ochrogaster*). Behav. Ecol. Sociobiol. *43*, 271-279.

McLean, R. G. (1975). Raccoon rabies. In The Natural History of rabies., M. G. Baer, ed. (New York: Academic Press, Inc), pp. 53-77.

McNab, B. K. (2002). The physiological ecology of vertebrates: a view from energetic (Ithaca: Comstock/Cornell University Press).

Mech, L. D., D. M. Barnes and J. R. Tester (1968). Seasonal weight changes, mortality, and population structure of raccoons in Minnesota. J. Mammal. *49*, 63-73.

Mech, L. D. and F. J. Turkowski (1966). Twenty-three raccoons in one winter den. J. Mammal. *47*, 529-530.

Merritt, J. F. and D. A. Zegers (2002). Maximizing survivorship in cold: Thermogenic profiles of non-hibernating mammals. Acta Theriol. *47*, 221-234.

Millspaugh, J. J., G. C. Brundige, R. A. Gitzen and K. J. Raedeke (2000). Elk and Hunter Space-Use Sharing in South Dakota. J. Wild. Manage. *64*, 994-1003.

Ministère des Ressources Naturelles et de la Faune (2009). "Rage du raton laveur." from http://www.rageduratonlaveur.gouv.qc.ca/index.asp.

Nams, V. (2006). Locate III User's Guide. Pacer Computer Software, Tatamagouche, Nova Scotia, Canada.

National Climatic Data Center (2012). "Illinois climate summaries." Retrieved 5 January 2012, from http://www.noaa.gov/climate.

Nituch, L. A., J. A. Schaefer and C. D. Maxwell (2008). Fine-scale spatial organization reflects genetic structure in sheep. Ethology *114*, 711-717.

Nixon, C. M., L. P. Hansen, P. A. Brewer and J. E. Chelsvig (1992). Stability of white-tailed doe parturition ranges on a refuge in east-central Illinois. Can. J. Zool. *70*, 968-973.

Norment, J., C. Elliott and P. Costello (1994). Another look at chemical immobilization of raccoons (Procyon lotor) with ketamine hydrochloride. J. Wild. Dis. *30*, 541-544.

Oosthuizen, W. C., P. C. Cross, J. A. Bowers, C. Hay, M. R. Ebinger, P. Buss, M. Hofmeyr and E. Z. Cameron (2009). Effects of chemical immobilization on survival of African buffalo in the Kruger National Park. J. Wild. Manage. *73*, 149-153.

Packer, C., D. Gilbert, A. Pusey and S. O'Brien (1991). A molecular genetic analysis of kinship and cooperation in African lions. Nature *351*, 562-565.

Palla, G., A.-L. Barabási and T. Vicsek (2007). Quantifying social group evolution. Nature *446*, 664-667.

Pelletier, F., J. T. Hogg and M. Festa-Bianchet (2004). Effect of chemical immobilization on social status of bighorn rams. Anim. Behav. *67*, 1163-1165.

Pitt, J., S. Larivière and F. Messier (2006). Efficacy of Zoletil® for field immobilization of raccoons. Wild. Soc. B. *34*, 1045-1048.

Pitt, J. A., S. Larivière and F. Messier (2008a). Social organisation and group formation of raccoons at the edge of their distribution. J. Mammal. *89*, 646-653.

Pitt, J. A., S. Larivière and F. Messier (2008b). Survival and Body Condition of Raccoons at the Edge of the Range. The J. Wild. Manage. *72*, 389-395.

Pomeroy, P., J. Wilmer, W. Amos and S. Twiss (2001). Reproductive performance links to fine-scale spatial patterns of female grey seal relatedness. P. Roy. Soc. Lond. B. Bio. *268*, 711-171

Poole, K. G., G. Mowat and B. G. Slough (1993). Chemical immobilization of lynx. Wild. Soc. B. *21*, 136-140.

Prange, S., S. D. Gehrt and S. Hauver (2011). Frequency and duration of contacts between free-ranging raccoons: uncovering a hidden social system. J. Mammal. *92*, 1331-1342.

Prange, S., T. Jordan, C. Hunter and S. D. Gehrt (2006). New radiocollars for the detection of proximity among individuals. Wild. Soc. B. *34*, 1333-1344.

R, Development Core Team (2009). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria.

Ratnayeke, S., G. A. Tuskan and M. R. Pelton (2002). Genetic relatedness and female spatial organization in a solitary carnivore, the raccoon, *Procyon lotor*. Mol. Ecol. *11*, 1115-1124.

Ratnayeke, S. M. (1997). Female philopatry and spatial organization in the raccoon (*Procyon lotor*). P.h.D. thesis, University of Tennessee, Tennessee.

Raymond, M. and F. Rousset (1995). GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. J. Hered. *86*, 248-249.

Rice, W. R. (1989). Analyzing tables of statistical tests. Evolution *43*, 223-225.

Robert, K., D. Garant and F. Pelletier (2012). Chemical immobilization of raccoons (*Procyon lotor*) with ketamine-medetomidine mixture and reversal with atipamezole. J. Wild. Dis. *48*, 122-130.

Rosatte, R. (2000). Management of raccoons (*Procyon lotor*) in Ontario, Canada: Do human intervention and disease have significant impact on raccoon populations? Mammalia *64*, 369-390.

Rosatte, R., K. Sobey, D. Donovan, M. Allan, L. Bruce, T. Buchanan and C. Davies (2007). Raccoon density and movements after population reduction to control rabies. J. Wild. Manage. *71*, 2373-2378.

Rosatte, R., K. Sobey, D. Donovan, L. Bruce, M. Allan, A. Silver, K. Bennett, M. Gibson, H. Simpson and C. Davies (2006). Behavior, movements, and demographics of rabid raccoons in Ontario, Canada: management implications. J. Wild. Dis. *42*, 589-605.

Roscoe, D. E. (1993). Epizootiology of canine distemper in New Jersey raccoons. J. Wild. Dis. *29*, 390-395.

Roughton, R. (1975). Xylazine as an immobilizing agent for captive white-tailed deer. J. Am. Vet. Med. Assoc. *167*, 574.-576.

Rowell, T. and C. Rowell (1993). The Social Organization of Feral *Ovis aries* Ram Groups in the Prerut Period. Ethology *95*, 213-213.

Rubin, R. H., L. Sullivan, R. Summers, M. B. Gregg and R. K. Sikes (1970). A case of human rabies in Kansas: epidemiologic, clinical and laboratory considerations. J. Infect. Dis. *122*, 318-322.

Rupprecht, C. E., J. S. Smith, M. Fekadu and J. E. Childs (1995). The ascension of wildlife rabies: a cause for public health concern or intervention? Emerg. Infect. Dis. *1*, 107-114.

Samelius, G., S. Lariviere and R. T. Alisauskas (2003). Immobilization of arctic foxes with tiletamine hydrochloride and zolazepam hydrochloride (Zoletil®). Wild. Soc. B. *31*, 192-196.

Saraux, C., C. Le Bohec, J. M. Durant, V. A. Viblanc, M. Gauthier-Clerc, D. Beaune, Y.-H. Park, N. G. Yoccoz, N. C. Stenseth and Y. Le Maho (2011). Reliability of flipper-banded penguins as indicators of climate change. Nature *469*, 203-206.

Schauber, E. M., D. J. Storm and C. K. Nielsen (2007). Effects of Joint Space Use and Group Membership on Contact Rates Among White-Tailed Deer. J. Wild. Manage. *71*, 155-163.

Schenk, A., M. E. Obbard and K. M. Kovacs (1998). Genetic relatedness and home-range overlap among female black bears (*Ursus americanus*) in northern Ontario, Canada. Can. J. Zool. *76*, 1511-1519.

Seidel, K. D. (1992). Statistical properties and applications of a new measure of joint space use for wildlife. Master thesis, University of Washington, Seattle.

Shilo, Y., R. Lapid, R. King, T. Bdolah-Abram and A. Epstein (2010). Immobilization of red fox (*Vulpes vulpes*) with medetomidine-ketamine or medetomidine-midazolam and antagonism with atipamezole. J. Zoo Wild. Med. *41*, 28-34.

Silk, J. B. (2007). The adaptive value of sociality in mammalian groups. Philos. T. Roy. Soc. B. *362*, 539-559.

Siripunkaw, C., C. Kongrit, K. M. Faries, R. J. Monello, M. E. Gompper and L. S. Eggert (2008). Isolation and characterization of polymorphic microsatellite loci in the raccoon (*Procyon lotor*). Mol. Ecol. *8*, 199-201.

Spong, G., J. Stone, S. Creel and M. Bjorklund (2002). Genetic structure of lions (*Panthera leo L.*) in the Selous Game Reserve: implications for the evolution of sociality. J. Evolution. Biol. *15*, 945-953.

Sterling, E. and A. Richard (1995). Social organization in the aye-aye (*Daubentonia madagascariensis*) and the perceived distinctiveness of nocturnal primates. In Creatures of the dark: the nocturnal prosimians, L. Alterman, G. A. Doyle, M. K. Izard, eds. (New York: Plenum Press), pp. 439-451.

Støen, O., E. Bellemain, S. Sæbø and J. Swenson (2005). Kin-related spatial structure in brown bears *Ursus arctos*. Behav. Ecol. Sociobiol. *59*, 191-197.

Storms, T. N., J. Schumacher, N. Zagaya, D. A. Osborn, K. V. Miller and E. C. Ramsay (2005). Determination and evaluation of an optimal dosage of carfentanil and xylazine for the immobilization of white-tailed deer (*Odocoileus virginianus*). J. Wild. Dis. *41*, 559-568.

Schwarz, M. P., Richards, M. H. & Danforth, B. N. (2007). Changing paradigms in insect social evolution: insights from halictine and allodapine bees. Annu. Rev. Entomol. *52*, 127-150.

Thil, M. A. and R. Groscolas (2002). Field immobilization of King Penguins with tiletamine-zolazepam. J. Field Ornithol. *73*, 308-317.

Thorington, K. K. and P. D. Weigl (2011). Persistence of southern flying squirrel winter aggregations: roles of kinship, familiarity, and intruder squirrels. J. Mammal. *92*, 1005-1012.

Travaini, A., P. Ferreras, M. Delibes and J. J. Aldama (1992). Xylazine hydrochloride-ketamine hydrochloride immobilization of free-living red foxes (*Vulpes vulpes*) in Spain. J. Wild. Dis. *28*, 507-509.

Van Winkle, W. (1975). Comparison of several probabilistic home-range models. J. Wild. Manage. *39*, 118-123.

Vander Wal, E., H. Yip and P. McLoughlin (2012). Sex-based differences in density-dependant sociality an experiment with a gregarious ungulate. Ecology *21*, 1271-1282.

Viblanc, V. A., C. M. Arnaud, F. S. Dobson and J. O. Murie (2010). Kin selection in Columbian ground squirrels (Urocitellus columbianus): littermate kin provide individual fitness benefits. P. Roy. Soc. Lond. B. Bio. *277*, 989-994.

Walrath, R., T. R. Van Deelen and K. C. Vercauteren (2011). Efficacy of proximity loggers for detection of contacts between maternal pairs of white tailed deer. Wild. Soc. B. *35*, 452-460.

Wang, J. (2002). An estimator for pairwise relatedness using molecular markers. Genetics *160*, 1203-1215.

Waser, P. M. and W. T. Jones (1983). Natal philopatry among solitary mammals. Q. Rev. Biol. *58*, 355-390.

West, G., D. J. Heard and N. Caulkett (2007). Zoo animal and wildlife immobilization and anesthesia. (Ames: Wiley-Blackwell).

Wheatley, K. E., C. J. A. Bradshaw, R. G. Harcourt, L. S. Davis and M. A. Hindell (2006). Chemical immobilization of adult female Weddell seals with tiletamine and zolazepam: Effects of age, condition and stage of lactation. BMC Vet. Res. *2*, 1-8.

White, G. and R. Garrott (1990). Analysis of wildlife radio-tracking data (San Diego: Academic Press).

White, P., K. Ralls and R. A. Garrott (1994). Coyote-kit fox interactions as revealed by telemetry. Can. J. Zool. *72*, 1831-1836.

White, P. C. L. and S. Harris (1994). Encounters between red foxes (*Vulpes vulpes*): implications for territory maintenance, social cohesion and dispersal. J. Anim. Ecol. *63*, 315-327.

White, P. C. L. and S. Harris (1995). Bovine tuberculosis in badger (*Meles meles*) populations in southwest England: the use of a spatial stochastic simulation model to understand the dynamics of the disease. Philos. T. Roy. Soc. B. *349*, 391-413.

Whitney, L. F. (1952). The raccoon. (Orange : Practical Science Publication Co.).

Willis, C. and R. Brigham (2007). Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. Behav. Ecol. Sociobiol. *62*, 97-108.

Willis, C. K. R. and R. M. Brigham (2007). Social thermoregulation exerts more influence than microclimate on forest roost preferences by a cavity-dwelling bat. Behav. Ecol. Sociobiol. *62*, 97-108.

Wolf, J. and F. Trillmich (2007). Beyond habitat requirements: individual fine-scale site fidelity in a colony of the Galapagos sea lion (*Zalophus wollebaeki*) creates conditions for social structuring. Oecologia *152*, 553-567.

Worton, B. (1989). Kernel methods for estimating the utilization distribution in home-range studies. Ecology *70*, 164-168.

Zeveloff, S. I. (2002). Raccoons: a natural history. (Washington, D.C.: Smithsonian Institution).