



Utilisation de l'espace par le raton laveur et la moufette rayée, deux principaux hôtes d'un variant du virus de la rage

Thèse

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Résumé

Comprendre les mécanismes comportementaux qui régissent la transmission et la propagation de pathogènes est critique pour les programmes de contrôle et de prévention des maladies infectieuses. Ma thèse explore le lien entre l'hétérogénéité des paysages agroforestiers et la répartition spatio-temporelle du raton laveur (*Procyon lotor*) et de la mouffette rayée (*Mephitis mephitis*), deux principaux hôtes du variant de la rage du raton laveur. Pour cela, j'ai étudié les processus de sélection densité-dépendante de l'habitat à large et fine échelles spatiales, ainsi que les mécanismes de connectivité fonctionnelle chez ces deux espèces. Le chapitre 1 a révélé qu'à faibles abondances de congénères, les ratons laveurs sélectionnaient les secteurs avec une forte proportion de forêts, tandis que les mouffettes rayées préféraient les zones avec une large proportion de milieux anthropiques. À fortes abondances, cependant, les deux espèces sélectionnaient plutôt les secteurs composés d'une forte densité de bordures maïs-forêts et forte proportion de champs de maïs. Le chapitre 2 a montré que la sélection des champs de maïs par les ratons laveurs dépendait à la fois de la densité de congénères et de l'abondance des champs de maïs. Dans le chapitre 3, j'ai développé un modèle spatialement explicite basé sur l'individu pour évaluer comment des règles empiriques de déplacement font émerger des patrons de contacts chez des individus hôtes. Les simulations ont révélé trois patrons généraux dans les taux de contacts. Premièrement, une petite portion de ratons laveurs simulés était responsable de la majorité des contacts dans les paysages virtuels. Deuxièmement, les taux de contacts des ratons laveurs simulés augmentaient linéairement avec la densité de congénères plutôt qu'avec la proportion de congénères dans la plupart des paysages. Troisièmement, l'effet de la connectivité fonctionnelle sur les taux de contacts variait fortement en fonction des types de milieux et de leur disponibilité dans le paysage. Les modèles développés dans cette thèse procurent une base solide au développement de programmes de contrôle et de prévention des maladies infectieuses, en permettant d'identifier les zones à hautes densités d'individus et de taux de contacts entre eux, et donc où le risque de transmission de pathogènes est relativement élevé.

Abstract

Understanding behavioral mechanisms that determine the transmission and spread of pathogens is critical for control and prevention programs of infectious diseases. My thesis investigates the interplay between the heterogeneity of agriculturally fragmented landscapes and spatio-temporal distribution patterns of raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*), two main hosts of the raccoon rabies virus variant. To do this, I studied the processes of density-dependent habitat selection at large and fine spatial scales, together with the mechanisms determining functional connectivity for these two species. The first chapter revealed that at low conspecific abundances in the landscape, raccoons selected areas with a high proportion of forests, whereas striped skunks preferred areas with a large proportion of anthropogenic features. At high conspecific abundances, however, both species rather selected areas composed of a high density of corn-forest edges and a large proportion of corn fields. The second chapter showed that raccoons altered their selection of corn fields depending upon both conspecific density and abundance of corn fields. In the third chapter, I built a spatially explicit individual-based model to assess how empirical movement rules translate into spatial patterns of contact rates among individual hosts. The simulations revealed three general patterns in contact rates. First, a small number of simulated raccoons were responsible for the majority of contacts in virtual landscapes. Second, contact rates of simulated raccoons increased linearly with conspecific density rather than with the proportion of conspecifics in most of the virtual landscapes. Third, the influence of functional connectivity on contact rates varied strongly among land cover types and with their availability in the landscape. The models developed in this thesis provide a strong basis upon which to build control and prevention programs for infectious diseases, as they identify areas where animal density and contact rates should be relatively high and, hence, where the risk of pathogen transmission should also be high.

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Bonne lecture.

Avant-propos

Ce doctorat se présente sous la forme d'une thèse avec trois articles scientifiques. La thèse comporte une introduction et une conclusion générales qui lient l'ensemble des articles, bien que ces derniers puissent être lus séparément.

En tant que principal auteur des trois articles, j'ai élaboré les objectifs de recherche, j'ai effectué les analyses géospatiales, statistiques, la modélisation et j'ai rédigé les articles. Mon directeur de thèse, Daniel Fortin, a contribué aux étapes de planification de la recherche et à la rédaction des articles. Ma co-directrice de recherche, Fanie Pelletier, et les collaborateurs du projet, Ariane Massé et Julien Mainguy, ont participé à la révision des manuscrits.

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INTRODUCTION GÉNÉRALE

Les maladies infectieuses émergentes et réémergentes ont augmenté en fréquence dans les dernières décennies et constituent une menace majeure pour la santé humaine, partout dans le monde (Binder et al. 1999, Morens et al. 2004). Par exemple, d'après le rapport de l'Organisation Mondiale de la Santé pour l'année 2004, plus de 25% (environ 15 millions) des mortalités annuelles qui ont été recensées chez les humains dans le monde, résultaient directement des maladies infectieuses (Morens et al. 2004). La majorité des maladies infectieuses émergentes (60.3%) sont des zoonoses, c'est-à-dire des maladies dont les pathogènes sont surtout transmis par les animaux sauvages (71.8%) et qui peuvent infecter les vecteurs arthropodes, les animaux domestiques et les humains (Jones et al. 2008). Bien que les zoonoses jouent un rôle important dans les écosystèmes naturels en influençant la diversité génétique chez les espèces hôtes et les processus de coévolution hôtes-pathogènes (Altizer et al. 2003a), elles sont aussi devenues une préoccupation majeure dans la conservation de la biodiversité parce qu'elles peuvent déclencher le déclin des espèces animales qui prospéraient auparavant (par exemple, Roelke-Parker et al. 1996, Jensen et al. 2002) ou accélérer l'extinction des espèces qui étaient déjà en danger (par exemple, Thorne & Williams 1988, Alexander & Appel 1994, Ginsberg et al. 1995, Timm et al. 2009). En plus de constituer un danger substantiel pour les humains mais aussi pour la biodiversité, les zoonoses engendrent des coûts financiers considérables (Daszak et al. 2000). Par exemple, Karesh et al. (2012) ont rapporté que les zoonoses avaient causé des centaines de milliards de dollars de pertes économiques aux États-Unis depuis les 20 dernières années.

Plusieurs études ont reconnu que les facteurs qui conduisent à l'émergence ou la réémergence de maladies infectieuses sont dus à des changements qui sont liés soit à l'évolution des pathogènes ou à l'écologie des populations hôtes (Morse 1995, Schrag & Wiener 1995, Antia et al. 2003). Les facteurs liés à l'évolution concernent la résistance des pathogènes aux médicaments et leur capacité d'adaptation à de nouveaux hôtes, tandis que les facteurs écologiques font référence aux changements dans la démographie et le comportement des humains, aux changements environnementaux et climatiques, au commerce et les voyages

internationaux, à la technologie et l'industrie, et aux mesures de prévention inadéquates ou réduites (Morse 1995).

Dans ma thèse, je me suis plus particulièrement intéressée aux facteurs écologiques associés aux changements environnementaux. Dans les systèmes hôtes-pathogènes, étudier les réactions comportementales des individus hôtes face aux variations dans la densité de population et l'hétérogénéité du paysage s'avère essentiel pour anticiper le risque de transmission et de propagation d'agents pathogènes dans l'environnement. Dans cette perspective, ma thèse explore les changements dans la répartition spatio-temporelle des individus hôtes et les interactions intraspécifiques qui en résultent, compte-tenu des variations dans la densité de congénères et l'hétérogénéité du paysage.

1. Relation entre la densité de populations hôtes et la transmission d'agents pathogènes

Les pathogènes se dispersent d'un individu infecté à un individu sain selon différents modes de transmission. Ces modes impliquent soient des contacts directs tels que les contacts par morsure ou griffure ou lors de l'accouplement, ou des contacts indirects comme l'inhalation de particules d'air ou la consommation de carcasses contaminées, ou par l'intermédiaire de vecteurs arthropodes (Woolhouse et al. 2001). En général, la transmission de pathogènes dépend du taux de contact entre des individus infectés et sains, et de la probabilité que le contact soit infectieux (McCallum et al. 2001, Begon et al. 2002). D'après, les modèles mathématiques de dynamique hôtes-pathogènes, il existe deux relations de base entre le taux de contact *per capita* et la densité de population. Premièrement, le taux de contact *per capita* augmente linéairement avec la densité de population (Smith et al. 2009b). Dans ce cas, le taux de transmission dépend de la densité d'individus infectés (McCallum et al. 2001, Begon et al. 2002). La transmission densité-dépendante est généralement utilisée pour caractériser les maladies qui sont transmises à travers des contacts aléatoires parmi les individus ou par dissémination aérienne ou au sol (May & Anderson 1979, Anderson & May 1981). Deuxièmement, le taux de contact *per capita* reste constant quel que soit la densité de population (Smith et al. 2009b). Dans ce cas, le taux de transmission dépend de la proportion (ou fréquence) d'individus infectés (McCallum et al. 2001, Begon et al. 2002). La transmission

fréquence-dépendante est souvent utilisée pour caractériser les maladies qui sont transmises sexuellement ou par un vecteur arthropode (Thrall et al. 1993, Antonovics et al. 1995, Lockhart et al. 1996). Au final, la transmission densité-dépendante conduit à un seuil de densité de population en-dessous duquel le pathogène ne peut plus se propager dans une population d'individus sains tandis qu'un tel seuil n'existe pas si la transmission est fréquence-dépendante (Anderson et al. 1981, Anderson & May 1981, Getz & Pickering 1983). D'autres fonctions non-linéaires de transmission ont néanmoins été proposées pour capturer la complexité des systèmes hôtes-pathogènes réels (McCallum et al. 2001, Fenton et al. 2002, Ryder et al. 2007). Selon ces fonctions, les taux de contacts augmentent avec la densité de population mais tendent à se stabiliser à hautes densités, ce qui suggère que la transmission dans des systèmes complexes devrait s'appuyer sur les hypothèses extrêmes de transmission densité- et fréquence-dépendante (Smith et al. 2009b). Possiblement, les changements physiologiques et dans le comportement social des individus hôtes seraient responsables de cette non-linéarité (Wilson et al. 2001, Altizer et al. 2003b, Beldomenico & Begon 2010). Néanmoins, peu d'études ont considéré l'effet de l'hétérogénéité du paysage.

Étant donné le lien étroit qui existe entre la répartition spatio-temporelle des individus hôtes et la disponibilité ou l'accessibilité des ressources (Wright & Gompper 2005, Chapman et al. 2006, Tardy et al. 2014), l'hétérogénéité du paysage peut fortement influencer sur les processus de transmission et de propagation d'agents pathogènes (Figure 1). Dans ma thèse, j'ai donc évalué l'impact de l'hétérogénéité du paysage sur la répartition spatio-temporelle des individus hôtes et les taux de contacts entre des individus afin de mieux anticiper le risque de transmission et de propagation d'agents pathogènes dans l'environnement. L'impact des activités humaines est une des causes principales de l'hétérogénéité du paysage (Pickett & Cadenasso 1995, Chapin et al. 2012). Plusieurs études ont reconnu que les perturbations anthropiques qui sont causées par de multiples facteurs socio-économiques (par exemple, la densité de population humaine, les pratiques agricoles, les aménagements routiers et urbains, la surexploitation des forêts), étaient largement responsables de l'émergence et la réémergence des maladies infectieuses depuis ces dernières décennies (Daszak et al. 2001, Bradley & Altizer 2007, Aguirre & Tabor 2008, Jones et al. 2008).

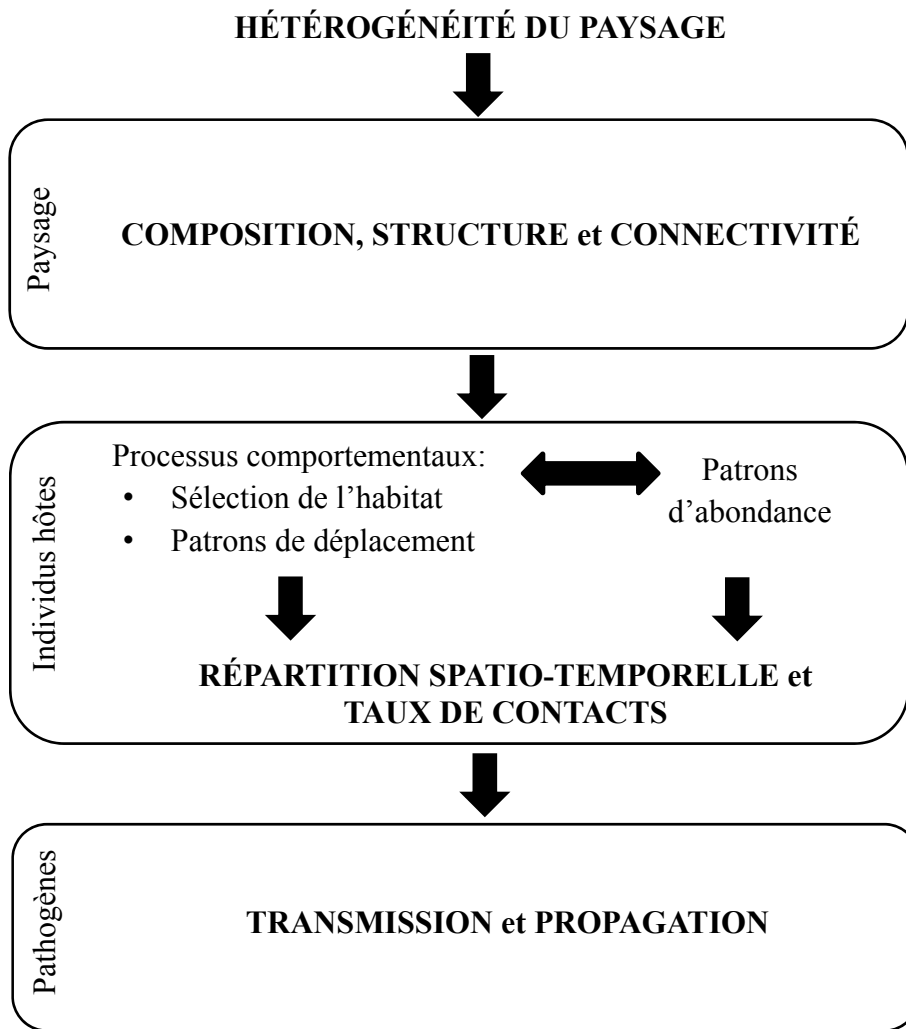


Figure 1. Effets potentiels de l'hétérogénéité du paysage sur la dynamique des maladies infectieuses

2. Impact des perturbations anthropiques sur la transmission et la propagation d'agents pathogènes

Les perturbations anthropiques sont souvent associées à l'urbanisation et la déforestation, ainsi qu'à une intensification de l'agriculture (Wilcox & Gubler 2005). Ces changements environnementaux altèrent l'habitat naturel des animaux sauvages, ce qui peut favoriser leur rapprochement avec les animaux domestiques et les humains (Jones et al. 2013). Par exemple, en Asie du Sud-Est, la perte des zones humides et leur reconversion en exploitations rizicoles ont augmenté les taux de contacts entre des oiseaux sauvages et des canards domestiques (*Anas platyrhynchos domesticus*) élevés en liberté, ce qui a favorisé l'apparition de foyers du virus influenza aviaire H5N1 (Gilbert et al. 2006, Gilbert et al. 2008). Les canards domestiques étaient amenés dans les rizières après les récoltes parce que les grains de riz restants dans les champs fournissent une source de nourriture peu coûteuse pour les éleveurs (Gilbert et al. 2007). Une étude dans l'Ouest de l'Ouganda en Afrique a montré que la déforestation avait favorisé la transmission bactérienne entre des primates, des humains et leur bétail (Goldberg et al. 2008). Notamment, les humains qui vivaient à proximité des parcelles de forêt fragmentées abritaient des bactéries *Escherichia coli* qui étaient 75% plus similaires génétiquement aux bactéries des primates vivant dans les forêts fragmentées que les bactéries des primates vivant dans les forêts non fragmentées (Goldberg et al. 2008). Des espèces de singes comme les cercopithèques à queue rouge (*Cercopithecus ascanius*) se nourrissent généralement de fruits et d'insectes dans les forêts non fragmentées (Struhsaker 1978) mais dans les forêts fragmentées, ils ne peuvent survivre qu'en volant leur nourriture dans les terres cultivées (Pienkowski et al. 1998).

Une autre conséquence importante induite par la réduction de l'habitat naturel est la diminution de la biodiversité qui peut affecter, notamment, les interactions entre des vecteurs arthropodes qui sont souvent porteurs d'agents pathogènes, et des populations hôtes (Pongsiri et al. 2009, Keesing et al. 2010). Par exemple, la réduction des forêts en Amérique du Sud a pu expliquer la réémergence de la maladie de Chagas au Brésil, en induisant une diminution de la biodiversité et en favorisant le maintien des espèces réservoirs (c'est-à-dire, qui sont capables de maintenir des pathogènes et transmettre l'infection à d'autres espèces) du parasite *Trypanosoma cruzi* comme l'Opossum commun du Brésil (*Didelphis aurita*) et l'Opossum aux

quatre yeux (*Philander frenatus*) (Vaz et al. 2007). En particulier, l'augmentation de l'abondance de ces espèces réservoirs fournit plus d'opportunités de nourriture (c'est-à-dire, des « repas de sang ») aux punaises hématophages qui sont les principaux vecteurs de cette maladie parasitaire (Gottdenker et al. 2012). Ces résultats supportent l'hypothèse d'un mécanisme de dilution qui peut s'opérer de différentes manières chez les maladies transmises par des vecteurs arthropodes (Ostfeld & Keesing 2000, Schmidt & Ostfeld 2001, Keesing et al. 2006). Entre autres, une haute diversité d'espèces hôtes peut réduire les taux de contacts entre les vecteurs et les hôtes réservoirs, et réguler l'abondance des hôtes réservoirs à travers la compétition interspécifique (Keesing et al. 2006). La disparition de populations de prédateurs peut également influencer sur la transmission de pathogènes (Pongsiri et al. 2009). Par exemple, la surpêche dans le lac Malawi en Afrique de l'Est a causé le déclin du *Trematocranus placodon*, un poisson mangeur de gastéropodes du genre *Bulinus* (Stauffer et al. 2006, Madsen & Stauffer 2011). En raison de ce déclin, l'augmentation de la densité d'escargots dans le lac a été responsable de la propagation de la schistosomiase (ou bilharziose), une maladie parasitaire provoquée par un ver plat du genre *Schistosoma* dont les larves sont libérées par les escargots (Stauffer et al. 1997, Evers et al. 2006). De plus, la perte de prédateurs dans les paysages fragmentés par l'agriculture pourrait avoir augmenté l'abondance d'espèces réservoirs généralistes comme les ratons laveurs (*Procyon lotor*) dans l'Indiana aux États-Unis, ce qui a eu pour conséquence une augmentation de la transmission féco-orale d'un ver parasite, l'ascaris du raton laveur (*Baylisascaris procyonis*), dont les larves causent la toxocarose chez les souris à pattes blanches (*Peromyscus leucopus*) qui sont des hôtes intermédiaires (Page et al. 2001).

D'une manière générale, une partie de l'impact des perturbations anthropiques sur la dynamique des maladies infectieuses peut être mesurée à travers l'analyse de la composition, de la structure et de la connectivité du paysage. Ces trois composantes définissent l'hétérogénéité du paysage (Figure 1).

3. Composition, structure, connectivité du paysage et relations hôtes-pathogènes

La composition, la structure et la connectivité du paysage jouent un rôle majeur dans la transmission et la propagation de pathogènes étant donné que ces trois composantes du paysage influencent fortement la répartition spatiale des espèces hôtes et les interactions entre des individus qui en résultent (Figure 1; McCallum & Dobson 2006, McCallum 2008).

3.1. Composition et structure du paysage

Les effets de la composition et de la structure du paysage sur la transmission et la propagation de maladies infectieuses sont souvent négligés dans l'étude des processus épidémiologiques (mais voir Langlois et al. 2001), et les mécanismes comportementaux qui régissent la répartition spatio-temporelle des individus hôtes en réponse à la composition et la structure du paysage sont généralement méconnus (Ostfeld et al. 2005). Concernant ce dernier point, j'y apporterai une attention particulière dans mes chapitres 1 et 2. Trop souvent, les cartes prédictives de risque qui sont construites à l'aide d'outils statistiques et de systèmes d'informations géographiques sont basées sur des données de présence-absence d'espèces hôtes (par exemple, Brownstein et al. 2003, Goodin et al. 2009). D'une manière générale, la composition du paysage définit la proportion relative de différents types de parcelles d'habitat (McGarigal 2006). Cette composante du paysage influence la transmission d'agents pathogènes à travers son impact sur l'abondance des individus hôtes et des vecteurs arthropodes (Ostfeld et al. 2005). Par exemple, Allan et al. (2003) ont trouvé qu'aux États-Unis, la densité de nymphes de tiques du genre *Ixodes scapularis* qui sont les principaux vecteurs de la maladie de Lyme, diminuait avec l'augmentation de la taille des parcelles de forêt. En fait, les petites parcelles de forêt abritent une plus forte abondance de souris à pattes blanches qui sont les principaux hôtes réservoirs de cette maladie bactérienne (Allan et al. 2003). Les prédateurs et les compétiteurs de cette espèce réservoir qui sont susceptibles de « diluer » la prévalence de la maladie de Lyme, tendent à être absents dans ce type de parcelle (LoGiudice et al. 2008).

La structure du paysage, quant à elle, représente la configuration ou l'arrangement spatial des parcelles d'habitat (Turner 1989). Cette composante du paysage influe sur la transmission et la propagation d'agents pathogènes en affectant l'abondance des individus

hôtes et leur capacité à se déplacer dans le paysage (McCallum 2008, Ward et al. 2009). Notamment, les structures aquatiques telles que les rivières et les lacs peuvent ralentir la propagation de pathogènes en empêchant le déplacement des individus hôtes (Real & Biek 2007, Arjo et al. 2008, Rees et al. 2011b). Par exemple, en simulant la propagation du variant du virus de la rage du raton laveur entre plusieurs municipalités du Connecticut (États-Unis) à partir d'un modèle probabiliste, Smith et al. (2002) ont montré que les grandes rivières pouvaient diminuer d'un facteur de 7 le taux de propagation de la rage entre les municipalités. Certains types de topographie comme des régions caractérisées par un relief très accidenté avec des pentes abruptes peuvent également restreindre les déplacements des individus hôtes et influencer la propagation d'agents pathogènes (Savill et al. 2006, Rees et al. 2011b). Par exemple, les chaînes de montagnes Allegheny et des Appalaches ont empêché, en 1977, l'expansion du variant de la rage du raton laveur vers l'ouest des États-Unis, ce qui a contribué à limiter la propagation de ce virus à l'est des États-Unis (Biek et al. 2007). De plus, les milieux alpins autour des chaînes de montagnes supportent généralement une faible densité de rats laveurs, et donc sont souvent associés à de faibles taux de transmission du variant de la rage du raton laveur (Rees et al. 2011b). L'interaction entre la structure du paysage et le comportement de déplacement des animaux détermine la capacité d'un animal à se déplacer entre des parcelles d'habitat (Goodwin & Fahrig 2002). La connectivité fonctionnelle du paysage est définie comme une propriété émergente qui résulte de cette interaction (Taylor et al. 2006) et, par conséquent, influence fortement la propagation d'agents pathogènes à travers le paysage.

3.2. Connectivité du paysage

L'augmentation de la fragmentation de l'habitat causée par les activités humaines et son impact sur la biodiversité (Fahrig 2003, Krauss et al. 2010) ont augmenté l'intérêt de considérer la connectivité du paysage dans les programmes de gestion et de conservation des espèces (Bennett 2003, Crooks & Sanjayan 2006). La fragmentation réduit la superficie des parcelles d'habitat et augmente les distances entre les parcelles, ce qui tend à diminuer la connectivité du paysage (Goodwin & Fahrig 2002, Fahrig 2003). La réduction de la superficie et l'isolement des parcelles d'habitat empêchent le déplacement des espèces animales entre les parcelles d'un paysage, ce qui, par conséquent, diminue le taux de recolonisation des parcelles

et augmente le taux d'extirpation locale des espèces (Fahrig 1997, Hanski 1997). Les discussions théoriques concernant l'impact de la fragmentation de l'habitat ont été largement basées sur la théorie des métapopulations.

3.2.1. Théorie des métapopulations

Une métapopulation est un ensemble de populations locales qui sont réparties sur un certain nombre de parcelles d'habitat de bonne qualité englobées dans une matrice de parcelles de moins bonne qualité et qui sont connectées entre elles par des immigrations occasionnelles (Levins 1969, Hanski & Gilpin 1991, Hanski 1998). La dynamique d'une métapopulation dépend donc à la fois des déplacements des individus entre des populations et à l'intérieur d'une population (Hess 1994). Beaucoup de modèles de métapopulation suggèrent que l'augmentation des déplacements entre les populations devrait réduire la probabilité d'extinction des espèces (Fahrig & Merriam 1985, Hanski 1985, 1989, Gonzalez et al. 1998). Néanmoins, la plupart de ces modèles ne prennent pas en compte les effets négatifs du rétablissement de la connectivité dans les paysages fragmentés, notamment, ceux concernant la propagation d'agents pathogènes (Hess 1994, 1996). En utilisant la structure d'un modèle épidémiologique de type « Sains-Infectés » [*Susceptible-Infected* (SI)], Hess (1996) a construit un modèle de métapopulation dans lequel les parcelles d'habitat contenaient soient des individus infectés par un pathogène, soient des individus sains, ou soit aucun individu. Le modèle a montré que l'augmentation du niveau de connectivité mesurée par la distance inter-parcelles induisait un plus grand nombre de parcelles infectées par le pathogène et, par conséquent, accélérât le taux d'extinction de l'espèce (Hess 1996). Cependant, le modèle de Hess (1996) comporte deux principales limites: 1) l'absence de rétablissement face à la maladie, c'est-à-dire une fois qu'une parcelle est infectée, elle demeure infectée jusqu'à l'extinction des individus hôtes et 2) le modèle ne fonctionne qu'avec une seule espèce (Gog et al. 2002, McCallum & Dobson 2002). Aussi, dans un modèle de métapopulation, McCallum & Dobson (2002) ont intégré des parcelles d'habitat résistantes à l'infection d'un pathogène et une seconde espèce qui agissait comme un hôte réservoir pour le pathogène. Contrairement à Hess (1996), McCallum & Dobson (2002) ont montré qu'une espèce hôte qui est hautement sensible à un pathogène peut persister avec une espèce hôte réservoir dans une métapopulation hautement connectée à condition que le taux de recolonisation par des individus sains soit

suffisamment élevé. Par contre, une métapopulation faiblement connectée a une plus forte probabilité d'extinction de l'espèce hôte sensible au pathogène (McCallum & Dobson 2002). Maintenir la connectivité du paysage apparaît donc être un objectif majeur pour la conservation des espèces même en présence d'agents pathogènes. Par définition, la connectivité du paysage peut être divisée en deux composantes: la connectivité structurelle et fonctionnelle.

3.2.2. Connectivité structurelle

La connectivité structurelle décrit la manière dont les parcelles d'habitat sont liées entre elles sans tenir compte de l'influence des caractéristiques du paysage sur le comportement de déplacement des animaux (Tischendorf & Fahrig 2000, Crooks & Sanjayan 2006). Elle est typiquement mesurée en analysant les éléments physiques du paysage tels que la présence, l'absence ou la configuration des corridors, des structures en « pas japonais » (*stepping-stones*), ou la distance entre les parcelles d'habitat (Kindlmann & Burel 2008). Comme ces éléments affectent les déplacements des animaux entre les parcelles d'habitat, la connectivité structurelle peut donc influencer sur la propagation de pathogènes dans le paysage (McCallum & Dobson 2006). Par exemple, des études ont montré que la taille et la connectivité entre des colonies de chiens de prairies à queue noire (*Cynomys ludovicianus*) dans les Grandes Plaines d'Amérique du Nord influençaient fortement la probabilité d'occurrence de cas de peste (*Yersinia pestis*), une maladie qui se transmet par morsure de puces infectées (Stapp et al. 2004, Johnson et al. 2011, Savage et al. 2011). Dans un paysage où les distances entre les colonies sont faibles (c'est-à-dire, avec une haute connectivité), une épidémie de peste peut décimer des colonies de chiens de prairies à queue noire réparties sur une large zone géographique (Collinge et al. 2005, Johnson et al. 2011). Par contre, dans un paysage qui est composé de hautes densités de routes et de structures aquatiques, et dans lequel les distances entre les colonies sont élevées (c'est-à-dire, avec une faible connectivité), seules les colonies concentrées sur une petite zone peuvent contenir des cas de peste (Collinge et al. 2005). Dans ce cas, les routes et les structures aquatiques agissent comme des barrières à la propagation de la peste (Collinge et al. 2005).

Dans les paysages fragmentés, une des solutions pour maintenir les populations et conserver la biodiversité est de créer ou de préserver des corridors de déplacement qui permettent de connecter les parcelles d'habitat isolées (Noss 1987, Hobbs 1992, Simberloff et

al. 1992, Hilty et al. 2006). Néanmoins, en augmentant les déplacements des animaux entre les parcelles, les corridors peuvent aussi favoriser la propagation d'agents pathogènes entre des populations et à l'intérieur d'une population dans le paysage (Hess 1994). Par exemple, des études ont montré que les chiens de prairies à queue noire utilisaient les rigoles d'irrigation et de drainage comme des corridors de déplacement dans les prairies au nord du Colorado aux États-Unis, et ont donc suggéré que ces rigoles étaient susceptibles de favoriser la propagation de la peste au sein des colonies (Roach et al. 2001, Antolin et al. 2006). Bien que l'effet de la connectivité sur la survie d'une métapopulation en présence d'un agent pathogène ait été établi (Hess 1996, Gog et al. 2002, McCallum & Dobson 2002), peu d'études ont évalué comment les changements dans la connectivité du paysage altéraient les taux de contacts et les déplacements des individus, probablement parce que les composantes fonctionnelles de la connectivité sont souvent omises (Meentemeyer et al. 2012). J'y apporterai donc une attention particulière dans mon chapitre 3.

3.2.3. Connectivité fonctionnelle

Contrairement à la connectivité structurelle, la connectivité fonctionnelle décrit la manière dont les caractéristiques du paysage facilitent ou empêchent le déplacement des animaux entre les parcelles d'habitat (Taylor et al. 1993, Bélisle 2005, Dancose et al. 2010). Par conséquent, la connectivité fonctionnelle peut directement altérer le déplacement des individus hôtes, et donc les taux de contacts entre des individus (Meentemeyer et al. 2012). Notamment, Remais et al. (2010) ont appliqué des mesures de connectivité fonctionnelle pour modéliser les trajets potentiels de propagation du parasite responsable de la schistosomiase, *Schistosoma japonicum*, et d'une espèce hôte d'escargots, *Oncomelania haupensis*, entre des paires de 32 villages situés dans l'Est et Sud-Est de l'Asie. Les auteurs de cette étude ont trouvé que l'identification des sites de transmission du parasite où le degré de connectivité fonctionnelle entre les villages est élevé, variait fortement entre l'utilisation d'une mesure de distance euclidienne en ligne droite et de distance géographique « efficace » [« *effective* » *geographical distance* (EGD)]. Les EGDs étaient estimées en utilisant une surface de coût de diffusion qui était paramétrée à partir de données comportementales chez le parasite et l'espèce d'escargots. La connectivité fonctionnelle entre les villages devenait apparente avec les mesures de EGDs, ce qui n'était pas le cas avec la distance euclidienne, suggérant que les

activités de contrôle des maladies infectieuses qui se basent sur la distance euclidienne peuvent ne pas être optimales (Remais et al. 2010). Bien que l'intérêt d'évaluer la connectivité fonctionnelle ait été largement reconnu dans le domaine de l'écologie (Bunn et al. 2000, McRae et al. 2008, Dancose et al. 2010, Galpern et al. 2011, Courbin et al. 2014), elle est souvent négligée dans l'étude des processus épidémiologiques, alors qu'elle peut fortement influencer le déplacement des animaux et les taux de contacts entre des individus hôtes dans le paysage (Meentemeyer et al. 2012). La connectivité fonctionnelle régit la répartition spatiale des animaux en influençant le choix de la prochaine parcelle d'habitat à visiter et les déplacements entre les parcelles (Dancose et al. 2010, Courbin et al. 2014).

4. Répartition spatio-temporelle des populations hôtes

La répartition spatio-temporelle des populations hôtes résulte du comportement des individus face aux changements environnementaux, et peut fortement influencer sur la transmission et la propagation d'agents pathogènes (Böhm et al. 2008, Houle et al. 2011, Silbernagel et al. 2011). La sélection de l'habitat et les déplacements sont des déterminants particulièrement importants de la répartition spatio-temporelle des populations dans les paysages hétérogènes (Figure 1; Lima & Zollner 1996, Fortin et al. 2005a, Fortin et al. 2008).

4.1. Sélection de l'habitat

La sélection de l'habitat est un processus hiérarchique qui est basé sur des décisions comportementales résultant de l'utilisation disproportionnée de certains types de milieux par rapport à leur disponibilité dans le paysage (Johnson 1980). Dans les environnements hétérogènes, les animaux devraient choisir les milieux leur conférant une plus haute aptitude phénotypique (Fretwell & Lucas 1969, Morris 2003b, McLoughlin et al. 2006, Morris 2006) sur la base d'un compromis entre les bénéfices associés à l'acquisition des ressources et les coûts liés à la compétition intra- et interspécifique, la prédation, aux déplacements et aux conditions météorologiques défavorables (Mysterud & Ims 1998, Kneitel & Chase 2004, Fortin et al. 2009, Hebblewhite & Merrill 2009). Pour atténuer les coûts associés à ces facteurs, les animaux peuvent soit éviter les types de milieux qui sont associés à ces contraintes, ou bien sélectionner les types de milieux qui leur permettent de les réduire (Dussault et al. 2005). Par exemple, le couvert végétal et topographique fournissent des abris contre les précipitations, les

températures extrêmes, le vent, le rayonnement solaire, les prédateurs, et atténuent les effets négatifs de la profondeur de la neige qui réduit les déplacements des individus et la disponibilité de la nourriture (Mysterud & Østbye 1999).

La disponibilité des ressources peut varier dans le temps et l'espace, ce qui amène les individus à s'ajuster à ces changements pour maximiser leur aptitude phénotypique. Johnson (1980) a proposé quatre niveaux hiérarchiques dans le processus de sélection de l'habitat: la sélection d'une aire de répartition (1^{er} ordre), la sélection d'un domaine vital ou groupe social à l'intérieur de l'aire de répartition (2^{ème} ordre), la sélection de sites d'alimentation au sein du domaine vital (3^{ème} ordre) et la sélection de ressources alimentaires à l'intérieur du site d'alimentation (4^{ème} ordre). Les animaux devraient adopter des stratégies comportementales de sélection à différentes échelles spatiales car l'importance relative des facteurs limitants peut varier avec celles-ci (Boyce et al. 2003, Mayor et al. 2009, Gaillard et al. 2010). Notamment, Rettie & Messier (2000) suggèrent que les facteurs les plus limitants qui affectent l'aptitude phénotypique des animaux devraient influencer leur sélection de l'habitat à larges échelles spatiales, alors que l'influence des facteurs moins limitants devrait être ressentie sur de fines échelles spatiales. Par exemple, plusieurs espèces d'ongulés vont préférentiellement utiliser les milieux offrant un couvert de protection contre les prédateurs à larges échelles spatiales (par exemple, à l'échelle du paysage), tandis que les milieux fournissant une plus grande disponibilité de nourriture vont davantage être sélectionnés à fines échelles spatiales (par exemple, à l'échelle du domaine vital) (Rettie & Messier 2000, Dussault et al. 2005). L'équilibre des compromis dans le processus de sélection de l'habitat chez les animaux peut néanmoins être affecté par les variations dans la densité de congénères et la disponibilité des ressources dans le paysage.

4.1.1. Sélection de l'habitat dépendante de la densité de congénères

Pour maximiser leur aptitude phénotypique, les animaux devraient choisir leur habitat en fonction de la densité de congénères étant donné que les ressources sont partagées entre plusieurs individus (Rosenzweig 1981, Morris 2003b). Par exemple, Mobæk et al. (2009) ont trouvé qu'à faibles densités de congénères dans le paysage, les moutons domestiques (*Ovis aries*) tendaient à s'agréger dans les milieux les plus productifs en végétation lorsqu'ils étaient actifs, alors qu'à hautes densités, ils sélectionnaient les milieux les moins productifs. Selon la

théorie de la distribution idéale libre [*Ideal free distribution* (IFD)], les individus devraient restreindre leur répartition spatiale aux habitats de plus haute qualité à faibles densités de congénères, mais comme l'aptitude phénotypique moyenne diminue avec l'augmentation de la densité, certains individus devraient être capables d'obtenir une aptitude phénotypique égale en occupant les habitats de plus faible qualité à hautes densités de congénères (Figure 2; Fretwell & Lucas 1969, Morris 1988) . L'IFD a été mise en évidence chez plusieurs espèces, notamment chez le chevreuil (*Capreolus capreolus*) en Suède (Walhström & Kjellander 1995), le bécasseau maubèche (*Calibris canutus*) dans des sites d'hivernage aux Pays-Bas, au Royaume-Uni et en France (Quaintenne et al. 2011), et le brochet (*Esox lucius*) grâce à l'utilisation de 40 années de données de capture-marquage-recapture récoltées dans le lac Windermere en Angleterre (Haugen et al. 2006). Récemment, Haché et al. (2012) ont aussi fourni un support empirique d'une IFD chez une espèce d'oiseaux territoriaux du Nouveau Brunswick au Canada, la paruline couronnée (*Seiurus aurocapilla*). En supposant que les individus sont libres de choisir leurs parcelles d'habitat, les animaux qui vivent dans une mosaïque de parcelles devraient tous acquérir la même aptitude phénotypique moyenne à travers leur décision de déplacement entre les différentes parcelles. Basée sur ce principe, la théorie de l'isodar permet d'évaluer les conséquences de stratégies de maximisation de l'aptitude phénotypique à différents niveaux de densités d'individus sur la répartition spatiale des animaux dans le paysage (Morris 1988). Une isodar d'habitat est la droite de régression entre la densité d'individus dans un habitat et la densité dans un second habitat à chaque point duquel l'aptitude phénotypique est égale dans les deux habitats (Figure 2; Morris 1987, 1992, Knight & Morris 1996). L'ordonnée à l'origine d'une isodar révèle des différences entre les deux habitats en termes d'aptitude phénotypique maximale que des individus peuvent atteindre à faibles densités de congénères (Morris 1988). Si l'ordonnée à l'origine est différente de 0, des individus devraient sélectionner plus fortement un habitat par rapport à l'autre à faibles densités de congénères dans le paysage. La pente représente des différences entre les deux habitats par rapport au taux par lequel l'aptitude phénotypique diminue lorsque la densité de congénères augmente dans chaque habitat (Morris 1988). Si la pente est différente de 1, des individus devraient sélectionner plus fortement un habitat par rapport à l'autre à fortes densités de congénères dans le paysage. La théorie de l'isodar peut également être appliquée dans des situations où le choix de l'habitat est restreint par des comportements territoriaux (Morris

1994, 2003b). Ce principe est la base de la théorie de la distribution idéale despotique (*Ideal despotic distribution*), selon laquelle les individus dominants vont monopoliser les ressources dans les habitats de plus haute qualité et, par conséquent, vont forcer les individus subordonnés à occuper les habitats de moins bonne qualité (Fretwell 1972). Dans ce cas, l'isodar d'habitat sera simplement curvilinéaire (Morris 1994, 2003b).

La théorie de l'isodar a été appliquée avec succès chez de nombreuses espèces, en particulier chez les petits mammifères (Knight & Morris 1996, Abramsky et al. 1997, Shenbrot 2004, Hodson et al. 2010, Ale et al. 2011, Morris et al. 2012), mais aussi les oiseaux (Fernandez-Juricic 2001, Shochat et al. 2002, Shochat et al. 2005), les poissons (Rodríguez 1995), les insectes (Krasnov et al. 2003), quelques grands mammifères (Ramp & Coulson 2002, van Beest et al. 2014) et, récemment, chez des algues unicellulaires (Moses et al. 2013). Les isodars peuvent être aussi particulièrement utiles pour évaluer les conséquences, en termes d'aptitude phénotypique, des perturbations naturelles ou anthropiques de l'habitat pour la faune sauvage (Morris 1990, Shochat et al. 2005, Hodson et al. 2010). Par exemple, Hodson et al. (2010) ont montré que lorsque l'abondance de congénères était faible dans le paysage, les lièvres d'Amérique (*Lepus americanus*) sélectionnaient les forêts non coupées, mais à fortes abondances, les forêts coupées étaient préférées, en particulier lorsque la différence de pourcentage de couvert forestier entre les forêts non coupées et coupées était faible. Malgré l'utilisation croissante de la théorie de l'isodar pour caractériser la sélection densité-dépendante de l'habitat chez les animaux, son application reste largement limitée à des zones composées de deux habitats adjacents qui sont définis *a priori*. Or, la plupart des programmes de gestion et de surveillance de la faune sauvage ne sont pas basés sur un tel plan d'échantillonnage. Une méthode qui permettrait de construire des isodars d'habitat dans des paysages hétérogènes sans avoir à prédéfinir des types de milieux serait donc particulièrement utile dans beaucoup de domaines tels que l'écologie appliquée incluant la gestion et la conservation des espèces animales et, également, en épidémiologie. J'ai donc développé une telle méthode dans le chapitre 1.

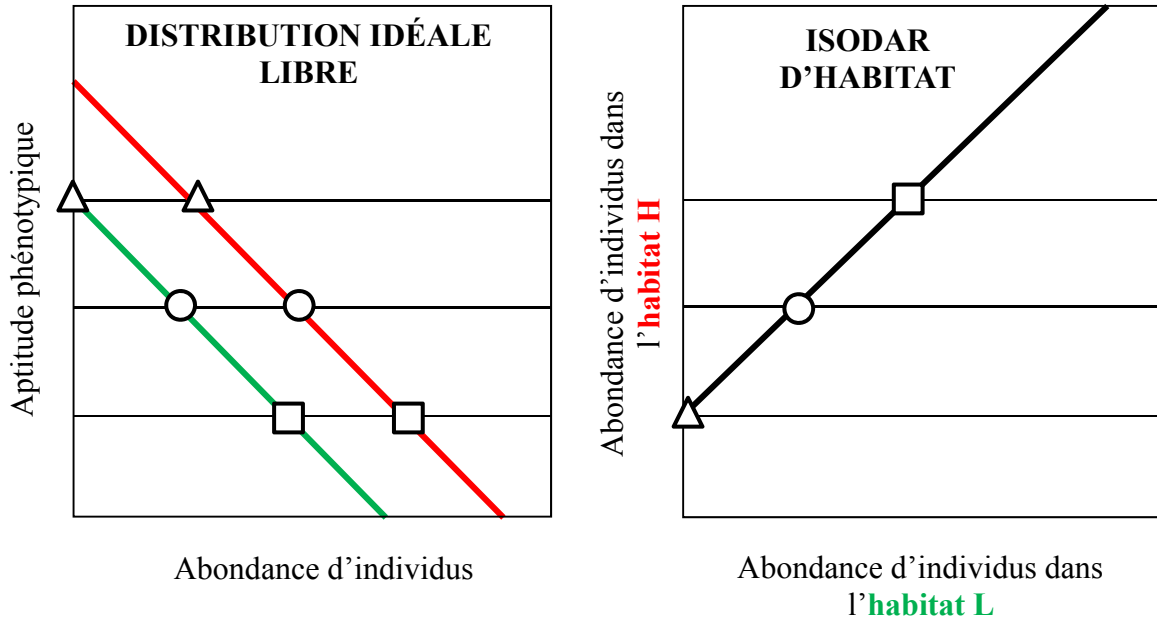


Figure 2. Exemple de répartition spatiale d'individus entre deux habitats H et L de différente qualité selon la théorie de la distribution idéale libre et la théorie de l'isodar qui en résulte. L'habitat H qui est représenté en rouge est de meilleure qualité que l'habitat L qui est représenté en vert. Les symboles situés à l'intersection des lignes horizontales représentent les valeurs d'abondance d'individus où l'aptitude phénotypique est égale dans les deux habitats.

4.1.2. Sélection de l'habitat dépendante des ressources

La sélection d'un type de milieu par les animaux peut aussi changer en fonction de sa disponibilité dans le paysage ou en fonction de la disponibilité d'autres types de milieux (Osko et al. 2004, Fortin et al. 2008, Courbin et al. 2009). Ces changements réfèrent à une réponse fonctionnelle dans la sélection de l'habitat (Mysterud & Ims 1998) qui apparaît généralement quand la disponibilité des ressources les plus limitantes varie spatialement. Par exemple, au Royaume-Uni, les écureuils gris (*Sciurus carolinensis*) sélectionnaient davantage les milieux ouverts riches en nourriture quand ces derniers étaient peu présents dans le paysage, alors que la sélection pour ces milieux diminuait avec l'augmentation de leur disponibilité (Mysterud & Ims 1998).

Les réponses fonctionnelles peuvent changer durant les heures de la journée ou entre les saisons, étant donné que les besoins alimentaires ou physiologiques des animaux peuvent varier au cours de la journée, ou que la quantité et la qualité des ressources peuvent différer entre les saisons (Godvik et al. 2009). Il est donc attendu que les animaux modifient leur stratégie de sélection de l'habitat pour combler leurs besoins lorsque la disponibilité des ressources varie au cours du temps. Par exemple, Godvik et al. (2009) ont montré que les cerfs élaphe (*Cervus elaphus*) en Norvège sélectionnaient plus fortement les prés dans leur domaine vital lorsque ces derniers étaient composés d'une faible proportion de prés, et cette sélection était plus élevée au printemps et à l'automne comparativement à l'été et à l'hiver. Ces réponses fonctionnelles suggèrent que les cerfs élaphe utilisent préférentiellement les prés pour leurs besoins alimentaires puisque ce type de milieu offre une source de nourriture abondante et de haute qualité, tandis qu'en été et en hiver, les milieux forestiers deviennent plus prisés car, contrairement aux prés, les forêts fournissent un couvert de protection contre les facteurs climatiques et les prédateurs (Godvik et al. 2009).

La réaction comportementale des animaux face à l'hétérogénéité du paysage peut différer parmi les individus d'une population ou d'un groupe social, ou entre des populations ou groupes sociaux (Osko et al. 2004, Hebblewhite & Merrill 2008, Hansen et al. 2009). Grâce à l'intégration d'effets aléatoires dans des fonctions de sélection de ressources [*Resource selection function* (RSF); Manly et al. 2002] (Gillies et al. 2006, Hebblewhite & Merrill 2008, Matthiopoulos et al. 2010), il est possible de modéliser des réponses fonctionnelles qui tiennent

compte de cette variabilité dans la réaction comportementale (Aarts et al. 2008, Houle et al. 2010, McLoughlin et al. 2010, Moreau et al. 2012). En utilisant de tels modèles, Moreau et al. (2012) ont notamment démontré que les réponses fonctionnelles dans la sélection de l'habitat pouvaient se produire simultanément à deux niveaux hiérarchiques imbriqués: à l'intérieur des domaines vitaux (intra-DV) et entre les domaines vitaux des animaux (inter-DV). Par exemple, les auteurs ont trouvé que durant l'été, au Canada, la sélection pour les forêts denses et matures de conifères dans les zones des domaines vitaux qui étaient composées d'une forte proportion de coupes forestières récentes (intra-DV) était plus élevée chez les caribous (*Rangifer tarandus*) qui avaient une forte proportion de coupes forestières dans l'ensemble de leur domaine vital (inter-DV). Au contraire, durant la mise-bas, la sélection pour les forêts de conifères dans les zones des domaines vitaux qui contenaient une forte proportion de coupes était plus faible chez les caribous qui avaient une forte proportion de coupes dans l'ensemble de leur domaine vital (Moreau et al. 2012).

Les réponses fonctionnelles sont de plus en plus utilisées dans les études de sélection de l'habitat car la considération de celles-ci peut fournir une description plus précise de la répartition des animaux dans le paysage (Hebblewhite & Merrill 2008, Godvik et al. 2009, Houle et al. 2010, Moreau et al. 2012). Par exemple, les réponses fonctionnelles ont été étudiées chez l'ours blanc (*Ursus maritimus*) dans l'Archipel de Svalbard et la mer de Barents au nord de la Norvège (Mauritzen et al. 2003), l'ours brun (*Ursus arctos*) dans les montagnes rocheuses de l'Alberta au Canada (Gillies et al. 2006), le loup gris dans le parc national de Banff en Alberta au Canada (Hebblewhite & Merrill 2008), l'orignal dans l'Archipel de Vega en Norvège (Herfindal et al. 2009), le batara rayé (*Thamnophilus doliatus*) et le troglodyte à nuque rousse (*Campylorhynchus rufinucha*) au Costa Rica en Amérique centrale (Gillies & St. Clair 2010) et l'éléphant de savane d'Afrique (*Loxodonta africana*) (Roever et al. 2012). Malgré ces nombreuses études, aucune n'a évalué la possibilité que les réponses fonctionnelles puissent varier avec la densité de congénères. La présence de densité-dépendance dans les réponses fonctionnelles peut être testée en intégrant un terme d'interaction entre les effets de la densité de congénères et de la disponibilité des ressources dans une RSF. Une telle approche de modélisation permettrait de mieux prédire la répartition spatio-temporelle des animaux étant donné la plasticité observée dans la sélection de l'habitat et, donc, serait particulièrement utile

dans beaucoup de domaines de l'écologie et, également, en épidémiologie. J'ai utilisé cette approche de modélisation dans le chapitre 2.

4.2. Déplacements entre des parcelles d'habitat

La capacité d'un animal à se déplacer entre des parcelles d'habitat dépend des propriétés intrinsèques des parcelles mais aussi de la matrice environnante, et de l'accessibilité des parcelles, c'est-à-dire de leur degré de connectivité dans le paysage (Dancose et al. 2010, Hodgson et al. 2011). Généralement, les RSFs sont utilisées pour évaluer la sélection des attributs intrinsèques des parcelles d'habitat sur plusieurs échelles spatiales (Boyce 2006, McLoughlin et al. 2010), mais ne permettent pas de caractériser l'accessibilité des parcelles (Chetkiewicz et al. 2006). Comprendre les processus de déplacement des animaux est crucial pour évaluer si les parcelles leur sont accessibles pour survivre et se reproduire, et ainsi améliorer les programmes de gestion et de conservation de la faune sauvage (Nathan et al. 2008, Morales et al. 2010). Cependant, les déplacements sont des comportements qui peuvent être difficiles à quantifier.

Il existe plusieurs méthodes quantitatives pour mieux comprendre les réponses comportementales de déplacement des animaux face à l'hétérogénéité spatiale, comme les fonctions de sélection de pas (Fortin et al. 2005a, Forester et al. 2009), les marches aléatoires corrélées et biaisées (Turchin 1998, Fortin et al. 2005b), les modèles mécanistes de domaines vitaux (Moorcroft et al. 1999, Moorcroft et al. 2006) et la méthode des chemins de moindre coût [*Least-cost path* (LCP); Adriaensen et al. 2003]. Notamment, cette dernière méthode peut être utilisée pour tenir compte de l'effet des caractéristiques de la matrice séparant les parcelles d'habitat de haute qualité sur le comportement de déplacement des animaux (Dancose et al. 2010). En particulier, les LCPs évaluent les routes potentielles de déplacement des animaux à travers le paysage en se basant sur une surface de coûts (Theobald 2006). L'utilisation d'une telle surface fournit une estimation quantitative sur la manière dont l'hétérogénéité du paysage affecte les déplacements des animaux, étant donné que les surfaces de coûts se basent sur les coûts hypothétiques que les types de milieux imposent sur les déplacements (Zeller et al. 2012). Typiquement, un faible coût dénote la facilité pour un animal de se déplacer à travers un type de milieu donné, tandis qu'un coût élevé représente souvent une barrière aux déplacements (Zeller et al. 2012). Les surfaces de coûts peuvent être générées

en inversant les indices de sélection de l'habitat qui sont calculés à partir d'une RSF (O'Brien et al. 2006). L'utilisation combinée de RSFs et LCPs fournit un cadre conceptuel utile pour examiner la connectivité fonctionnelle du paysage et pour trouver des corridors potentiels de dispersion (Chetkiewicz et al. 2006, Chetkiewicz & Boyce 2009, Hebblewhite et al. 2011). Par exemple, en combinant des RSFs et LCPs, Chetkiewicz & Boyce (2009) ont identifié des corridors de conservation chez deux grands carnivores, l'ours brun et le cougar (*Puma concolor*) dans les montagnes rocheuses de l'Alberta au Canada.

Comprendre comment la répartition spatio-temporelle des populations hôtes agit sur la dynamique d'une maladie infectieuse est primordial pour mieux anticiper une potentielle épizootie (c'est-à-dire, une maladie qui touche un grand nombre d'espèces animales). Une telle compréhension est désormais possible grâce au développement continu de modèles mathématiques de plus en plus sophistiqués qui permettent de modéliser la transmission et la propagation d'agents pathogènes.

5. Modélisation de la transmission et de la propagation d'agents pathogènes

Les modèles compartimentaux (Anderson & May 1979, 1991, Hethcote 2000) et les modèles de réseaux sociaux (Klovdahl 1985, Keeling & Eames 2005, Craft 2015) ont amplement contribué à la compréhension actuelle des systèmes hôtes-pathogènes. Néanmoins, ces modèles ont leur limite. Notamment, les modèles compartimentaux ignorent la variabilité dans les attributs de l'individu et assument que tous les individus d'une population interagissent entre eux [hypothèse dite de « *homogeneous-mixing* » (Anderson & May 1979, 1991)]. Bien que les réseaux sociaux puissent prendre en compte les variations dans les taux de contacts entre les sexes, les âges et les saisons (Hamede et al. 2008, Hirsch et al. 2013, Reynolds et al. 2015), la plupart d'entre eux ne considèrent pas l'effet de l'hétérogénéité spatiale du paysage. Plus récemment, les modèles spatialement explicites basés sur l'individu [*Individual based model* (IBM)] sont devenus des stratégies prometteuses pour modéliser les interactions entre les individus et leur environnement.

Les IBMs spatialement explicites permettent de simuler des systèmes dynamiques complexes dans lesquels des phénomènes émergents peuvent être observés (Railsback 2001,

Bousquet & Le Page 2004, Matthews et al. 2007). Dans ces IBMs, les individus sont définis par des entités mobiles qui interagissent avec leur environnement et d'autres individus (Grimm & Railsback 2005). Chaque individu est caractérisé par un ensemble de variables d'états qui permettent de modéliser des processus de prises de décision et les comportements associés en réaction à l'environnement (Russell & Norvig 1995, Tang & Bennett 2010). Ces variables d'états peuvent être de nature physiologique comme la masse, la taille et l'âge, ou psychologique comme la mémoire, l'apprentissage et la perception (Shettleworth 2001, Nathan et al. 2008). La plupart des IBMs spatialement explicites utilisent une grille à deux dimensions pour représenter l'environnement. Plus spécifiquement, la zone d'étude est divisée en un ensemble de cellules interconnectées de forme carrée ou hexagonale qui sont associées à des variables environnementales et qui peuvent être occupées par un individu (Macal & North 2010, Tang & Bennett 2010). L'avantage des IBMs spatialement explicites est qu'ils permettent d'étudier des processus stochastiques et spatialement dépendants au niveau de l'individu qui sont difficiles à quantifier de manière empirique (DeAngelis & Mooij 2005). Ils peuvent également inclure la variabilité dans le comportement des individus. Notamment, les IBMs spatialement explicites sont des outils particulièrement utiles pour modéliser les patrons de déplacement des animaux dans le paysage (Tang & Bennett 2010). Plusieurs études ont d'ailleurs utilisé des IBMs spatialement explicites pour simuler le déplacement chez de nombreuses espèces, incluant les oiseaux (Bélisle & Desrochers 2002, Levey et al. 2005, St-Louis et al. 2014), les poissons (Railsback et al. 1999, Hölker & Breckling 2005), les insectes (Arrignon et al. 2007, Linard et al. 2009), les grands carnivores et herbivores (Ahearn et al. 2001, Morales et al. 2005, Latombe et al. 2014), les primates (Sellers et al. 2007), ainsi que chez des assemblages d'espèces (Filotas et al. 2008, 2010). Ils permettent également de modéliser les décisions collectives de déplacement chez des espèces vivant en groupe (Couzin et al. 2002, Couzin et al. 2005).

L'utilisation d'un tel cadre de modélisation est donc pertinente pour étudier les processus de transmission et de propagation d'agents pathogènes, ce qui explique que les IBMs spatialement explicites soient de plus en plus utilisés en épidémiologie (Rushton et al. 2000, Bonnell et al. 2010, Ramsey & Efford 2010, Dion et al. 2011, Rees et al. 2013). Par exemple, Bonnell et al. (2010) ont simulé, à l'aide d'un IBM spatialement explicite, les comportements de déplacement et de recherche de nourriture d'une population de singes colobes rouges

(*Piliocolobus rufomitratatus*) infectée par un microparasite dans un paysage de ressources qui était estimé à partir d'une carte forestière du parc national de Kibale dans l'Ouganda en Afrique de l'Est. Leur IBM a permis de mieux comprendre comment la répartition des ressources dans un paysage perturbé par les activités humaines affecte la dynamique des maladies infectieuses. De plus, Dion et al. (2011) ont simulé dans un IBM spatialement explicite des taux de contacts entre des buffles d'Amérique (*Syncerus caffer*) et des troupeaux de bovins à la bordure du parc national Kruger en Afrique du Sud pour identifier les attributs du paysage qui influencent le risque de transmission de la fièvre aphteuse. Dans cette perspective, les IBMs spatialement explicites seraient un outil idéal pour intégrer les mécanismes de connectivité fonctionnelle afin d'évaluer comment les changements dans la connectivité du paysage altèrent le risque de transmission et de propagation de pathogènes. Ce sera l'objet de mon chapitre 3.

6. Objectif et organisation de la thèse

Afin d'évaluer le risque de transmission et de propagation d'agents pathogènes dans un paysage, l'objectif de ma thèse est d'explorer les changements dans la répartition spatio-temporelle de populations hôtes et les interactions intraspécifiques qui en résultent, compte tenu des variations dans la densité de congénères et l'hétérogénéité du paysage. Pour répondre à cet objectif, j'ai étudié la densité-dépendance dans les processus de sélection de l'habitat à large et fine échelles spatiales (Chapitres 1 et 2), ainsi que les mécanismes de connectivité fonctionnelle (Chapitre 3) chez deux principaux hôtes du variant de la rage du raton laveur en Amérique du Nord: les ratons laveurs et les mouffettes rayées (*Mephitis mephitis*). La répartition spatio-temporelle de ces deux espèces a été évaluée à partir du suivi télémétrique à l'aide de colliers GPS (*Global positioning system*) de 54 ratons laveurs de 2009 à 2011 et de 12 mouffettes rayées en 2009 dans des paysages agroforestiers des régions de la Montérégie et de l'Estrie au sud du Québec (Canada) où une épidémie de rage a sévit chez ces espèces entre 2006 et 2009 (Rees et al. 2011a, Côté et al. 2012).

Chapitre 1

Dans ce chapitre, j'ai développé une méthode de ré-échantillonnage basée sur des simulations qui utilise des données de recensement de la faune sauvage pour appliquer la

théorie de l'isodar dans des paysages hétérogènes sans avoir à prédéfinir des types de milieux. Grâce à cette méthode, il est possible d'étudier la sélection densité-dépendante de l'habitat sur de larges étendues géographiques et pour une grande variété d'espèces, en particulier les méso- et grands mammifères à haute mobilité. J'ai appliqué cette méthode aux données d'abondance de rats laveurs et de mouffettes rayées qui ont été récoltées dans les régions de la Montérégie et de l'Estrie au Québec, Canada.

Chapitre 2

Dans ce chapitre, j'ai vérifié si les réponses fonctionnelles pouvaient dépendre de la densité de population en évaluant, à l'aide de RSFs, les effets simultanés de la densité de congénères et de la disponibilité des ressources sur la sélection de l'habitat. Plus spécifiquement, j'ai testé si les rats laveurs et les mouffettes rayées altéraient leur sélection des champs de maïs en fonction de la densité de congénères et de la disponibilité ou de la structure des champs de maïs dans les paysages agroforestiers des régions de la Montérégie et de l'Estrie au Québec, Canada.

Chapitre 3

Dans ce chapitre, j'ai évalué comment les changements dans la densité de congénères, la composition du paysage et la connectivité fonctionnelle altèrent les taux de contacts entre des individus hôtes. Pour cela, j'ai intégré dans un IBM spatialement explicite les composantes d'utilisation de l'espace de rats laveurs porteurs de colliers GPS et simulé les déplacements de rats laveurs dans différents paysages agroforestiers virtuels qui différaient dans la proportion de forêts et l'arrangement spatial de corridors agricoles.

7. Modèles d'étude: le raton laveur et la mouffette rayée

Les rats laveurs et les mouffettes rayées sont des espèces généralistes non-territoriales qui peuvent s'acclimater aux changements de l'environnement (Gehrt 2003, Rosatte & Larivière 2003) et, par conséquent, qui sont capables d'exploiter une variété de paysages (Wade-Smith & Verts 1982, Larivière 2004), en particulier les paysages agroforestiers (Beasley et al. 2007b, Beasley & Rhodes 2010, Houle et al. 2011). Ces espèces sympatriques partagent souvent les mêmes besoins en habitat (Heske et al. 1999, Frey & Conover 2006).

Lorsqu'il est disponible, le maïs (*Zea mays*) est la principale source de nourriture des rats laveurs (Rivest & Bergeron 1981) et est également consommé par les mouffettes rayées (Rosatte & Larivière 2003).

Les populations de rats laveurs sont des réservoirs majeurs du variant du virus de la rage du raton laveur étant donné qu'ils ont été responsables de plus de 85% des cas de rage rapportés chez des animaux sauvages aux États-Unis en 2000 (Dobson 2000). Le nombre de cas de rage chez les mouffettes rayées tend aussi à augmenter avec la progression de cas de rage chez les rats laveurs (Guerra et al. 2003). Par exemple, le nombre de cas de rage rapporté chez les mouffettes rayées en 2011 a augmenté de 12.4% par rapport à l'année 2010 aux États-Unis (Blanton et al. 2012). La rage est une maladie virale qui est mortelle chez toutes les espèces de mammifères, dont l'homme, et qui touche plusieurs pays du monde (Warrell & Warrell 2004). Elle se transmet chez un animal ou chez l'homme par inoculation transcutanée ou par les muqueuses, en général par morsure ou griffure d'un animal rabique (Rupprecht et al. 2002). Les symptômes apparaissent quelques semaines voire plusieurs mois après la contamination et une fois que les signes d'encéphalite rabique apparaissent, la mort est inévitable (Baer 1991, Rupprecht et al. 2002).

La souche du virus de la rage du raton laveur a été identifiée pour la première fois en Floride (États-Unis) 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). À la suite du transport de rats laveurs infectés dans les États de la Virginie et de la Caroline du Nord par des trappeurs en 1997, le virus s'est ensuite propagé lentement pendant plusieurs années depuis le Sud-Est des États-Unis vers le Canada où les premiers cas ont été recensés en 1999 en Ontario (Rupprecht et al. 1995, Childs et al. 2000, Zeveloff 2002). En particulier, 89 cas de rage ont été rapportés chez des rats laveurs au Québec entre 2006 et 2009 dans la région de la Montérégie (Rees et al. 2011a, Côté et al. 2012). Un raton laveur rabique a récemment été trouvé en 2015 dans la partie québécoise de la réserve Akwesasne qui est située à la frontière du Québec, de l'Ontario et de New York [source: <http://rageduratonlaveur.gouv.qc.ca/index.asp> (site identifié au nom du gouvernement du Québec)]. La propagation du virus a été en grande partie contrôlée par l'utilisation accrue de mesures de prévention et de contrôle telles que la réduction des populations, les opérations « trapper-vacciner-relâcher » (TVR) et les épandages d'appâts

vaccinaux oraux (Rosatte et al. 1992a, Rosatte et al. 2001, Rees et al. 2011a). Néanmoins, l'apparition de nouveaux foyers de rage du raton laveur reste toujours possible, notamment par la présence de cas positifs dans les États américains limitrophes au Québec. Malgré le fait que les mortalités humaines causées par la rage du raton laveur soient assez rares, cette maladie engendre des coûts très importants qui sont associés à sa détection, sa prévention et son contrôle [par exemple, entre 230 millions et 1 milliard de dollars par an aux États-Unis (Rupprecht et al. 1995)]. L'acquisition de connaissances sur la répartition spatio-temporelle des ratons laveurs et des mouffettes rayées est donc indispensable pour accroître l'efficacité des interventions de contrôle qui visent à limiter la propagation de la rage du raton laveur au Québec et ailleurs en Amérique du Nord. En particulier, les approches de modélisation que j'ai développées dans les trois chapitres peuvent être utilisées pour délimiter les zones à fortes densités de population et de taux de contacts où le risque de transmission et de propagation d'agents pathogènes est élevé.

CHAPITRE 1

Resampling method for applying density-dependent habitat selection theory to wildlife surveys

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Résumé

La théorie de l'isodar peut être utilisée pour évaluer les conséquences, en termes d'aptitude phénotypique, de la sélection densité-dépendante de l'habitat par les animaux. Une isodar d'habitat est une droite de régression représentant des densités d'individus dans deux habitats adjacents lorsque l'aptitude phénotypique des individus est égale. Malgré l'augmentation de l'utilisation des isodars d'habitat, leur application reste essentiellement limitée aux paysages composés de deux habitats définis *a priori*. Nous avons développé une méthode de ré-échantillonnage qui utilise des données de recensement de la faune pour construire des isodars dans des paysages hétérogènes sans avoir à prédéfinir des types de milieux. La méthode consiste à placer aléatoirement des blocs à travers la zone recensée et à diviser ces blocs en deux sous-blocs adjacents de même taille. L'abondance animale est alors estimée dans les deux sous-blocs. Ce processus est répété 100 fois. Différentes formes fonctionnelles d'isodars peuvent être examinées en liant l'abondance animale et les différences dans les caractéristiques de l'habitat entre les sous-blocs. Nous avons appliqué cette méthode aux données d'abondance de rats laveurs et de mouffettes rayées, deux des principaux hôtes du virus de la rage en Amérique du Nord. La sélection de l'habitat par les rats laveurs et les mouffettes rayées dépendait à la fois de l'abondance de congénères et des différences dans la composition et la structure du paysage entre les sous-blocs. Lorsque peu de congénères étaient présents, les rats laveurs et les mouffettes rayées sélectionnaient préférentiellement les zones avec une forte proportion de forêts et de caractéristiques anthropiques, respectivement. Cependant, à fortes abondances de congénères, les deux espèces préféraient les zones avec une forte densité de bordures maïs-forêts et une large proportion de champs de maïs. Basée sur les techniques de ré-échantillonnage aléatoire, nous fournissons une méthode robuste qui est applicable pour une grande variété d'espèces, en particulier les espèces de taille moyenne et large qui sont hautement mobiles. La méthode est suffisamment flexible pour incorporer plusieurs covariables environnementales qui peuvent refléter les besoins des espèces focales. Ainsi, notre étude illustre comment la théorie de l'isodar peut être utilisée avec des données de recensement faunique pour évaluer la sélection densité-dépendante de l'habitat sur de grandes étendues géographiques.

Abstract

Isodar theory can be used to evaluate fitness consequences of density-dependent habitat selection by animals. A typical habitat isodar is a regression curve plotting competitor densities in two adjacent habitats when individual fitness is equal. Despite the increasing use of habitat isodars, their application remains largely limited to areas composed of pairs of adjacent habitats that are defined *a priori*. We developed a resampling method that uses data from wildlife surveys to build isodars in heterogeneous landscapes without having to predefine habitat types. The method consists in randomly placing blocks over the survey area and dividing those blocks in two adjacent sub-blocks of the same size. Animal abundance is then estimated within the two sub-blocks. This process is done 100 times. Different functional forms of isodars can be investigated by relating animal abundance and differences in habitat features between sub-blocks. We applied this method to abundance data of raccoons and striped skunks, two of the main hosts of rabies virus in North America. Habitat selection by raccoons and striped skunks depended on both conspecific abundance and the difference in landscape composition and structure between sub-blocks. When conspecific abundance was low, raccoons and striped skunks favored areas with relatively high proportions of forests and anthropogenic features, respectively. Under high conspecific abundance, however, both species preferred areas with rather large corn-forest edge densities and corn field proportions. Based on random sampling techniques, we provide a robust method that is applicable to a broad range of species, including medium- to large-sized mammals with high mobility. The method is sufficiently flexible to incorporate multiple environmental covariates that can reflect key requirements of the focal species. We thus illustrate how isodar theory can be used with wildlife surveys to assess density-dependent habitat selection over large geographic extents.

1. Introduction

Density-dependent habitat selection theories hold a central position in evolutionary ecology research, as they can explain spatial distribution patterns of animals and fitness consequences of intra- and interspecific interactions (Rosenzweig 1981, Morris 2011). The ideal free distribution (IFD) and the ideal despotic distribution (IDD) are two such theories. According to IFD, individuals should restrict their distribution to habitats of the highest quality at low densities of conspecifics, but as mean fitness declines with increasing conspecific density in higher-quality habitats, some individuals should be able to obtain equal fitness by moving to lower-quality habitats with relatively few conspecifics (Fretwell & Lucas 1969, Morris 1988). Assuming that individuals are free to choose among habitat patches, individuals living in a mosaic of habitat patches should all end up with the same mean fitness in the landscape through adaptive inter-patch movement decisions. Based on these principles, isodar theory has been designed as a dynamic solution to assess density- and frequency-dependent evolutionary strategies (Morris 2011).

The fitness consequences of density-dependent habitat selection strategies on spatial distribution of animals can be revealed by using habitat isodars. A habitat isodar is a regression curve that plots individual density in one habitat type against density in a second habitat type at each point where fitness is equal among individuals within and across both habitat types (*e.g.*, Morris 1987, 2003b). The intercept of an isodar reveals differences between two habitats in terms of maximal fitness that individuals can attain at a low density of conspecifics (Morris 1988). An isodar may have a negative, a positive, or a null intercept. An isodar with an intercept of 0 indicates that there is no selection between the two habitats at a low conspecific density and, therefore, individuals could achieve maximal fitness by being uniformly distributed between habitat types. In contrast, an intercept that is > 0 indicates that maximal fitness in habitat y (*i.e.*, associated with the Y-axis) exceeds that in habitat x (X-axis) and individuals should more strongly select habitat y than habitat x at a low density of conspecifics. A positive intercept can be due, for example, to higher resource availability in habitat y than in habitat x (Morris 1988). The slope represents differences between two habitats in the rate at which fitness decreases as conspecific density increases in each habitat (Morris 1988).

The slope of a habitat isodar provides insights into density-dependent habitat selection. For example, an isodar with a slope of 1 indicates that individuals do not change their selection between the two habitats as conspecific density increases. According to IFD, fitness should therefore decrease at an equal rate in the two habitats (Morris 1988). A slope steeper than 1 indicates that individuals increase their relative use of habitat *y* as population size increases (see Morris 1988 for a representation of habitat isodars with various intercept and slope estimates). According to IFD, fitness should in this case decline more slowly in habitat *y* with increasing conspecific density. This may reflect disparities in resource quality or habitat structure between habitats that affect resource acquisition, consumption, and conversion into descendants more strongly in habitat *x* than in habitat *y* as conspecific density increases (Morris 1990). Isodar theory can also be applied in situations where the habitat choice is restricted by territorial behaviors. This principle is the basis of IDD, in which dominant individuals monopolize resources in higher-quality habitats and force subordinate individuals to occupy lower-quality habitats (Fretwell 1972). Subordinates select habitats in a way that equalizes “perceived” fitness in each habitat, but mean fitness differs between habitats (Morris 1994, 2003b).

Isodar theory has been successfully applied to numerous taxa, in particular small mammals (Abramsky et al. 1997, Hodson et al. 2010, Ale et al. 2011, Morris et al. 2012), but also birds (Fernandez-Juricic 2001), fishes (Rodríguez 1995), insects (Krasnov et al. 2003), some large-sized mammals (Ramp & Coulson 2002, van Beest et al. 2014), and recently, unicellular algae (Moses et al. 2013). These isodar studies typically contrast conspecific densities in two adjacent habitats that are defined *a priori*. Many wildlife surveys, such as those employed in most wildlife monitoring programs, are not based on this design. Shenbrot and Krasnov (2000) developed a “paraisodar” method that allows density-dependent habitat selection to be assessed along an environmental gradient. In contrast to habitat isodars that use abundance patterns in two habitat types at different times, paraisodars contrast individual densities that are sampled in several habitat types at two different times (*i.e.*, at low and high densities). However, paraisodars have only been applied over small spatial extents and require several successive surveys.

Here, we propose a resampling procedure that extracts data from wildlife surveys with a design that is suitable for constructing isodars in heterogeneous landscapes without having to predefine habitat types. We then apply this method to evaluating density-dependent habitat selection by two hosts of the raccoon rabies virus variant: raccoon (*Procyon lotor* L.) and striped skunk (*Mephitis mephitis* L.). Raccoon populations act as a major wildlife reservoir of rabies virus in North America, whereas the number of rabid striped skunks tends to increase as the number of rabies cases in raccoons increases (Blanton et al. 2012). Identification and characterization of areas at high densities of raccoons and striped skunks should increase the efficiency of prevention and control programs (Houle et al. 2011, Rees et al. 2011a).

2. Materials and Methods

2.1. Random resampling across the survey area

To apply isodar theory to observations from wildlife surveys, independent sampling units need to be randomly placed over the survey area. This process involves two steps: 1) randomly placing blocks over the survey area, and 2) dividing those blocks into two adjacent sub-blocks of the same size where animal abundance will be estimated based on the survey data. A broad range of field methods can be used to estimate animal abundance (*e.g.*, capture, sightings, and census) (Krebs 1999). Given these two steps, however, our resampling method would be particularly effective when wildlife surveys are intensive and the allocation of sampling effort is uniform over the study area. With intensive surveys, mark-recapture techniques [as, *e.g.*, in the oral rabies vaccination programs in the U.S. and North America (Rosatte et al. 2007, Ramey et al. 2008, Beasley et al. 2015) and in Merkle & Fortin 2014] could be used to estimate animal abundance in each sub-block, thereby providing particularly reliable estimates of local abundance. With a uniform allocation of sampling effort, the random blocks are more likely to consistently contain the minimum sampling effort needed to obtain reliable estimates of local animal abundances (the creation of valid sub-blocks [see Step 2 below] would then be relatively simple because each area of the survey region would be sampled with the same intensity). Our approach, however, can be used in more complex settings. Here, we considered a case study where sampling effort varied over the survey area, with live traps being strategically distributed to maximize the number of captures (near streams and roads, at the base of trees) (Houle et al. 2011) (see section “Survey areas and captures of

raccoons and striped skunks” for further details about the capture procedure). The case study thus demonstrates how our method can be applied to non-uniform sampling schemes. We now describe Steps 1 and 2 in detail.

Step 1: creating random blocks

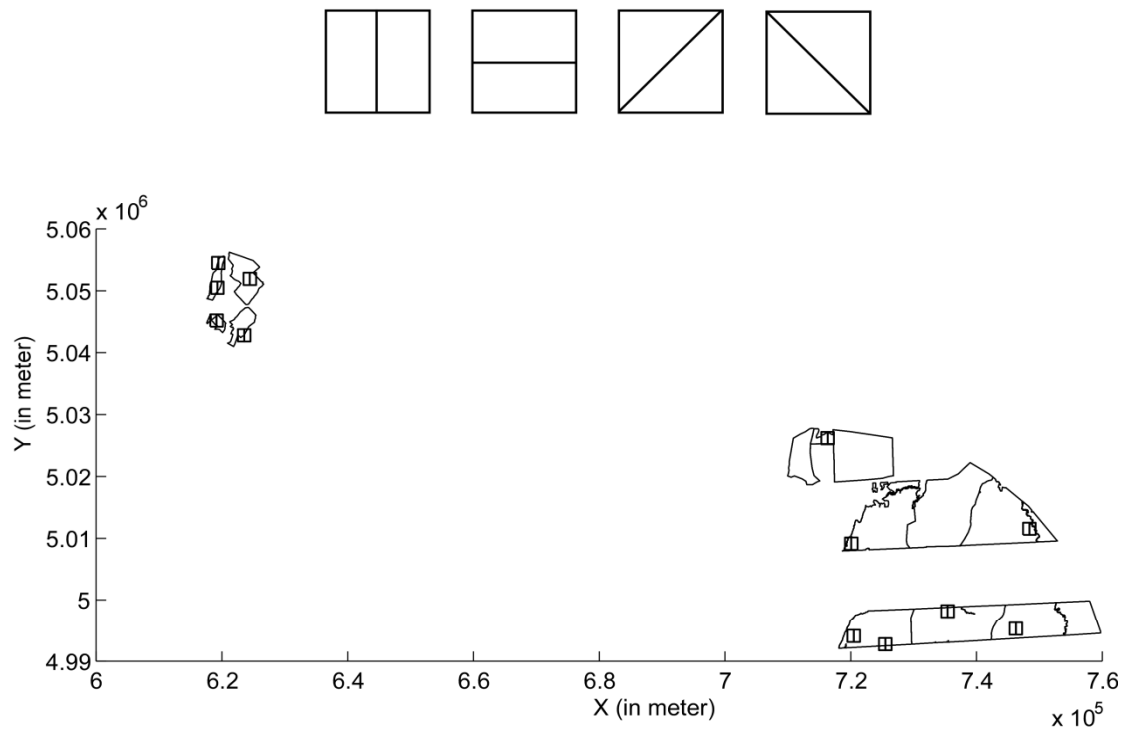
The centroids of square blocks are randomly placed across the survey area (Figure 1A). The X and Y coordinates of each centroid are randomly generated from a list containing all possible coordinates that encompass the survey area. As suggested by Tyler & Hargrove (1997), the spatial extent over which IFD is applied should correspond to maximum daily movements of animals. Block size can thus be defined from mean home range size of the focal species. The distance between blocks must be determined in such a way that no individual is captured in more than one block. Each block (*i.e.*, a pair of sub-blocks, see below) should thus be sufficiently spaced apart at a distance that would ensure their independence. This distance should exceed the typical dispersal distance of the species. Further, all blocks should have the same size to avoid a potential correlation between block size and animal abundance.

Step 2: creating pairs of adjacent sub-blocks

Each block is divided into two adjacent sub-blocks of the same area in four different configurations (Figure 1A). This approach should reduce the potential risk of biases that are due, for example, to anisotropic patterns in habitat features across the survey area and, hence, in animal abundance.

The number of independent blocks that should be placed across the survey area can be determined by visually examining a plot of the number of spatially independent blocks that can be randomly distributed over the survey area against the minimum number of sampling units (*e.g.*, live traps, sampling plots) that are contained in each paired sub-block (Figure 2). To determine the number of blocks that should be used in the analysis, we randomly place blocks across the survey area according to the protocol defined in the section “Step 1: creating random blocks” and count the number of blocks that satisfies a predefined minimum number of sampling units in each paired sub-block. While the number of blocks has to be sufficiently large to provide a reasonable sample size for regression analysis, the number of sampling units

(A)



(B)

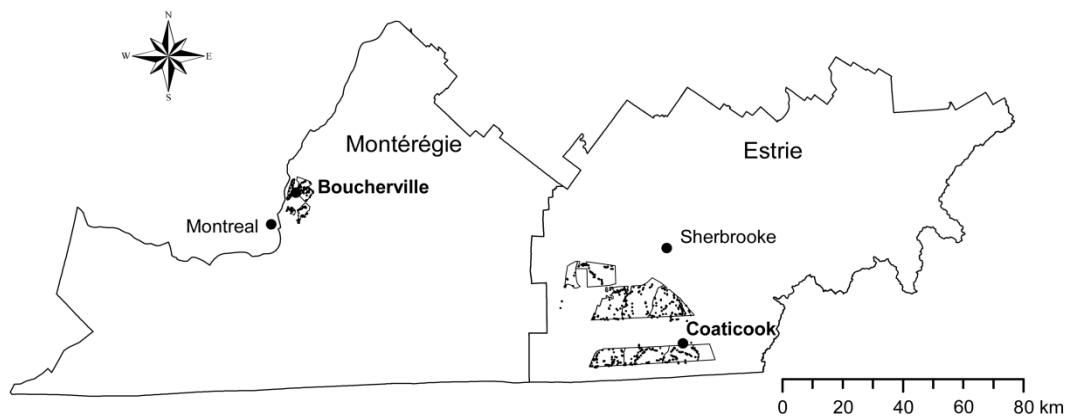


Figure 1. (A) Representation of four designs of sub-blocks, *i.e.*, with horizontal, vertical, and diagonal (right and left) dividing line of sub-blocks. We illustrate below an example of vertical pairs of sub-blocks randomly placed over the survey areas. (B) Map of two survey areas situated in the Montérégie and Estrie regions, Québec, Canada. Trapping sites and live traps (black points) are represented.

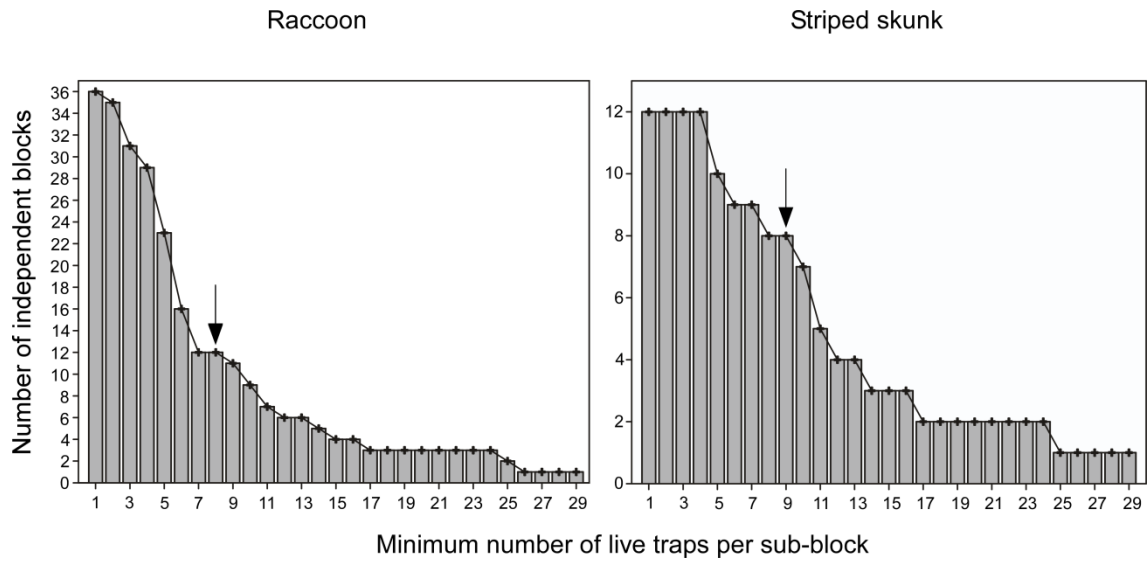


Figure 2. Frequency histogram for raccoons (left-hand side) and striped skunks (right-hand side) summarizing the number of independent blocks that can be placed in the survey areas for a predefined minimum number of live traps contained in each paired sub-block in the Montérégie and Estrie regions, Québec, Canada. The point under the arrow represents the favored trade-off that was used to determine the number of blocks to place across the survey areas.

also has to be large enough to estimate the relative animal abundance adequately within the sub-blocks of each pair. An adequate trade-off between these two variables could be found by the inflection point in the relationship between the number of spatially independent blocks as a function of the minimum number of sampling units that are contained in each sub-block. In this way, the entire survey area should be sampled with sufficient intensity to build isodar models.

2.2. Replication

The random placing of blocks and associated sub-blocks (Steps 1 and 2) is performed 100 times for each design of paired sub-blocks (Figure 1A). This level of replication provides the basis for quantifying the variability in animal abundance between the sub-blocks, and consequently, improves statistical inference relative to methods without replication (Dennis et al. 2010). At each replication, randomly generated blocks that do not respect conditions relative to the minimum number of sampling units in each paired sub-block, and distance between blocks, are removed and substituted by a new block that is randomly placed in the survey area. Blocks without any animals are also removed because they provide no information on density-dependent habitat selection. In this case, the block is substituted by a new one.

2.3. Isodar theory

Morris & Kingston (2002) and Hodson et al. (2010) demonstrated how to incorporate continuous habitat covariables into density-dependent fitness equations, and subsequently, into isodars. As proposed by Hodson et al. (2010), we calculate differences in habitat features (*e.g.*, measures of habitat disturbance intensity, differences in resource availability and in habitat structure) between pairs of adjacent sub-blocks, and we integrate the related covariates into isodars. If we consider two adjacent sub-blocks named H and L that vary in terms of their habitat features, the isodar then takes this general structure:

$$N_{H_{Cov\ i}} = \beta_0 + \beta_{N_{L_{Cov\ i}}} \times N_{L_{Cov\ i}} + \beta_{\Delta_{Cov\ i}} \times \Delta_{Cov\ i} + \beta_{N_{L_{Cov\ i}} \times \Delta_{Cov\ i}} \times N_{L_{Cov\ i}} \times \Delta_{Cov\ i} \quad (1)$$

where sub-block H is the pair member with the highest value for the focal habitat feature *i* (Cov *i*), so that the difference in habitat features between sub-blocks H and L ($\Delta_{Cov\ i}$) is

necessarily ≥ 0 . $N_{H_{Cov\ i}}$ then corresponds to conspecific abundance in sub-blocks H for which the value of the focal habitat feature i (Cov i) is the highest and $N_{L_{Cov\ i}}$ is conspecific abundance in sub-blocks L for which the value of the focal habitat feature i (Cov i) is the lowest. From eqn 1, several functional forms of density-dependence in habitat selection can be tested because they would be represented by different isodars that vary according to their intercept (equal to $\beta_0 + \beta_{\Delta_{Cov\ i}} \times \Delta_{Cov\ i}$) and slope (equal to $\beta_{N_{L_{Cov\ i}}} + \beta_{N_{L_{Cov\ i}} \times \Delta_{Cov\ i}} \times \Delta_{Cov\ i}$). In particular, the signs of β_0 and $\beta_{N_{L_{Cov\ i}}}$ inform on the selection for a sub-block type (*i.e.*, H or L) at low and high conspecific densities in the landscape, respectively. However, the signs of $\beta_{\Delta_{Cov\ i}}$ and $\beta_{N_{L_{Cov\ i}} \times \Delta_{Cov\ i}}$ indicate how the selection for a given sub-block type varies with increasing differences in habitat features between the two types of sub-blocks ($\Delta_{Cov\ i}$) at low and high conspecific densities, respectively. For example, if $\beta_0 \geq 0$, $\beta_{N_{L_{Cov\ i}}} = 1$, $\beta_{\Delta_{Cov\ i}} > 0$, and $\beta_{N_{L_{Cov\ i}} \times \Delta_{Cov\ i}} = 0$ in eqn 1, individuals should more strongly select sub-blocks H than sub-blocks L at a low density of conspecifics within the landscape, and the selection for sub-blocks H should increase with increasing differences in habitat features between the two types of sub-blocks. If $\beta_0 = 0$, $\beta_{N_{L_{Cov\ i}}} > 0$, $\beta_{\Delta_{Cov\ i}} = 0$, and $\beta_{N_{L_{Cov\ i}} \times \Delta_{Cov\ i}} > 0$ in eqn 1, individuals should more strongly select sub-blocks H than sub-blocks L at a high density of conspecifics within the landscape, and the selection for sub-blocks H should increase with increasing differences in habitat features between the two types of sub-blocks. If $\beta_0 \geq 0$, $\beta_{N_{L_{Cov\ i}}} > 0$, $\beta_{\Delta_{Cov\ i}} > 0$, and $\beta_{N_{L_{Cov\ i}} \times \Delta_{Cov\ i}} > 0$ in eqn 1, individuals should more strongly select sub-blocks H than sub-blocks L at both high and low densities of conspecifics within the landscape, and the selection for sub-blocks H should increase with increasing differences in habitat features between the two types of sub-blocks. Other forms of isodars are also shown in Hodson et al. (2010).

With our method, isodars can be constructed using linear mixed-effects models (LMMs) that consider hierarchical structure in the data (factor “replication” is nested within factor “design of paired sub-blocks”). In eqn 1, $N_{H_{Cov\ i}}$ corresponds to conspecific abundance in the sub-block with the highest value for a habitat feature i (Cov i), and $N_{H_{Cov\ i}}$ is systematically assigned to the Y-axis in isodars. Therefore, animal abundance in a given sub-block may be associated with the dependent variable ($N_{H_{Cov\ i}}$) of the isodar for a particular

habitat feature and with the independent variable ($N_{L_{Cov i}}$) for another feature. This possibility has some implications for the statistical comparison of candidate isodars. Indeed, an information-theoretic approach (Burnham & Anderson 2002) can only be used to compare different functional forms of isodars involving a given habitat covariate ($\Delta_{Cov i}$) because, in this case, the response variable ($N_{H_{Cov i}}$) does not differ among nested models. However, information theory cannot be used to contrast models involving different habitat covariates (Nakagawa & Schielzeth 2013). In this case, we can compare models with the same number of parameters based on goodness-of-fit statistics. Marginal and conditional R^2 , as calculated by Nakagawa & Schielzeth (2013), appear particularly suitable because they assess the proportion of variance that is explained by the fixed effects and the entire model (*i.e.*, both the fixed and random effects), respectively. We illustrate the replication-based random resampling method in the following case study.

2.4. Case study

2.4.1. Ethics Statement

All observations and surveys were conducted by personnel of the Ministère des Ressources Naturelles et de la Faune du Québec (MRNF) and its partners in a rabies management program. The study was carried out in accordance with the recommendations outlined in the Guide to the Care and Use of Experimental Animals (Olfert et al. 1993). Animal capture and handling procedures complied with the Agreement on International Humane Trapping Standards (Government of Canada, 1998) and were approved by the Animal Care Committee of the MRNF. All manipulations were performed by qualified wildlife professionals, and all efforts were made to minimize suffering and stress in the animals.

2.4.2. Survey areas and captures of raccoons and striped skunks

The study was conducted in the Montérégie region (45°23'23''N, 73°06'05''W), where 104 cases of the raccoon rabies virus variant were reported between 2006 and 2009 (Rees et al. 2011a), and the Estrie region (45°28'54''N, 71°40'05''W) of Québec, Canada. The two regions are characterized by forest patches, agricultural fields, urban and residential zones, and numerous water bodies.

From 27 September to 20 October 2008, raccoons and striped skunks were captured in four trapping sites in the Montérégie region and in eight trapping sites in the Estrie region (Figure 1B) over ten consecutive nights. The live traps (Tomahawk Live Trap, Tomahawk, Wisconsin, USA; Havahart, Woodstream, Lititz, Pennsylvania, USA) were baited with sardines, marshmallows, and an olfactory lure (ProCoon, Leurres Forget, Mauricie, Québec, Canada). A total of 1164 live traps were placed across the two survey areas (334 traps in the Montérégie region and 830 in the Estrie region). Each live trap was inspected daily. Captured animals were immobilized with an injection of ketamine and medetomidine that was administered intramuscularly (Robert et al. 2012a). Animals were then sexed and marked with ear tags before being released. A handheld Global Positioning System (GPS) location was noted at each installation and removal of a live trap, and at each capture site, to determine trapping effort and number of captures per trap according to its location. Trapping effort was defined as the total number of trap nights deployed minus the number of trap nights where individuals were recaptured and, non-target species were captured. A total of 610 raccoons and 121 striped skunks were captured in October 2008 across the two survey areas.

2.4.3. Resampling procedure

We drew blocks of 2 km × 2 km that were spaced at least 2 km apart, given that mean home range size is 2.58 km² for raccoons and 2.32 km² for striped skunks (based on GPS location data, data not shown). No raccoon and striped skunk was recaptured > 2 km from the position of its first capture. From the frequency histogram showing the number of spatially independent blocks that can be placed in the survey areas for a predefined minimum number of live traps contained in each paired sub-block (Figure 2), we noted that when we placed a single block over the two survey areas, it generally fell in an area where both of its sub-blocks had as many as 29 traps. Conversely, when we randomly placed 36 blocks (while respecting the 2-km spacing), some of the sub-blocks had no more than one trap, which is insufficient to obtain a valid estimate of relative animal abundance. For raccoons, we found that by placing 12 blocks, we were able to maintain a minimum of eight live traps per sub-block. For striped skunks, we identified that each of two sub-blocks could encompass at least nine live traps by randomly placing eight blocks over the survey areas (Figure 2). Consequently, we chose to randomly place 12 blocks for raccoons and eight blocks for striped skunks containing at least eight live

traps for raccoons and nine live traps for striped skunks across the two survey areas. We calculated relative abundance of raccoons and striped skunks in each paired sub-block as the total number of unique individuals per species captured per 100 trap nights, corrected for trapping effort. In total, 4800 blocks (*i.e.*, 9600 sub-blocks = 2 sub-blocks/block \times 12 blocks \times 100 replications \times 4 designs of sub-blocks) for raccoons and 3200 blocks (*i.e.*, 6400 sub-blocks = 2 sub-blocks/block \times 8 blocks \times 100 replications \times 4 designs of sub-blocks) for striped skunks were randomly generated and placed across the Montérégie and Estrie regions using MATLAB software (MathWorks 2011). The relative abundance of raccoons in the 9600 sub-blocks varied from 1 to 52.4 raccoons per 100 trap nights (mean = 14.1), whereas the relative abundance of striped skunks in the 6400 sub-blocks varied from 0.4 to 45.2 striped skunks per 100 trap nights (mean = 8.1).

2.4.4. Measures of landscape composition and structure

Landscape composition and structure were measured in each pair of sub-blocks according to land cover types that were delineated on 1:15,000 scale aerial photographs that had been taken in 1999 by the MRNF and information that was obtained from the Financière Agricole du Québec about the different crops that had been cultivated in the agricultural fields. We calculated the proportion of forests, corn fields, wetlands and anthropogenic areas, and quantified the density (km/km²) of forest edges bordering corn fields in each paired sub-block (Table S1) by using ArcGIS (version 10.0; Environmental Systems Research Institute, Redlands, California, USA) and Geospatial Modelling Environment (version 0.7.1.0; Beyer 2012). We retained these environmental covariables because they influence the spatial distribution and abundance of raccoons and striped skunks (Pedlar et al. 1997, Larivière & Messier 2000, Houle et al. 2011). Given that habitat covariates were spatially auto-correlated in the landscape, we used principal component analysis (PCA) to reduce the dimensionality of the multivariate data to independent components that characterize environmental gradients. We determined the number of significant PCA axes by using the broken-stick method (Legendre & Legendre 2012). The significant PCA axes are those for which the percentage of explained variance is larger than the percentage calculated by the broken-stick distribution (Legendre & Legendre 2012). For raccoons, the first principal component (PC1) and the second principal

component (PC2) were significant, whereas only PC1 was significant for striped skunks. Accordingly, we used significant PCA axes to characterize each sub-block, for each species.

2.4.5. Statistical analysis

To construct isodars, we need to identify the sub-block of each pair with the highest PC1 or PC2 score. We refer to sub-block H of a pair as the one with the highest PC1 or PC2 score (*i.e.*, sub-block H can be different when identified with PC1 versus PC2 score). Following Hodson et al. (2010), we introduced landscape features into the isodars by estimating the difference in landscape composition and structure between sub-blocks H and L along an environmental gradient that was represented by PC1 or PC2 scores:

$\Delta_{PCi} = (\text{PCi score of sub-block H}) - (\text{PCi score of sub-block L})$. By definition, PCi ($i = 1$ or 2) scores for sub-blocks H were larger than or equal to scores for sub-blocks L and $\Delta_{PCi} \geq 0$. The isodars had the following general structure:

$$N_{H_{PCi}} = \beta_0 + \beta_{N_{L_{PCi}}} \times N_{L_{PCi}} + \beta_{\Delta_{PCi}} \times \Delta_{PCi} + \beta_{N_{L_{PCi}} \times \Delta_{PCi}} \times N_{L_{PCi}} \times \Delta_{PCi} + \gamma_i \times Z_i + \gamma_{ij} \times Z_{ij}$$

where $N_{H_{PCi}}$ corresponds to conspecific abundance in sub-blocks H that have the highest PCA scores (PCi), and $N_{L_{PCi}}$ is conspecific abundance in sub-blocks L that have the lowest PCA scores. Z_i represents the random effect for a disposition i of sub-blocks and Z_{ij} corresponds to the random effect for a replication j within a disposition i of sub-blocks. The γ are the coefficients associated with each random effect.

For each species and its significant principal component (PC1 or PC2), we tested four candidate isodar models according to eqn 1 (Table S2). We used linear mixed-effects models, assuming a Gaussian distribution for the response variable. Because the data structure was hierarchical (factor “replication” is nested within factor “design of paired sub-blocks”), the mixed models included a random intercept for each design of sub-blocks (four different designs) to accommodate non-independence of blocks between the different designs and within each design of paired sub-blocks. Also, we considered an exchangeable (or compound symmetry) correlation structure that takes into account the correlation between observations of the same replication within a given design of paired sub-blocks (Pinheiro & Bates 2000).

Adding a correlation structure increased model fit (likelihood ratio [LR] = 54.28, $P < 0.0001$ for raccoon PC1 model; LR = 7.92, $P = 0.005$ for raccoon PC2 model; LR = 38.36, $P < 0.0001$ for striped skunk PC1 model). Further, we included a variance structure to stabilize residual heteroscedasticity by allowing for variance increases or decreases with predicted values (Pineiro & Bates 2000). Adding a variance structure also increased model fit (LR = 672.58, $P < 0.0001$ for raccoon PC1 model; LR = 364.41, $P < 0.0001$ for raccoon PC2 model; LR = 717.23, $P < 0.0001$ for striped skunk PC1 model).

Normality of random effects and residuals, together with variance homogeneity, were respected for each PCA model. Rather low multicollinearity (variance inflation factor of each covariate < 10) contributed to making reliable statistical inferences (Dormann et al. 2013). The isodar estimations were computed with the package *nlme* of R statistical software (R Development Core Team 2012). We compared the four candidate models for each principal component (PC1 or PC2) by using the AIC (Akaike's Information Criterion) and AIC weights (Burnham & Anderson 2002). When several nested models received similar empirical support ($\Delta_{AIC} < 2$), we applied the principle of parsimony by retaining the model with fewer parameters (Burnham & Anderson 2002). We then contrasted the goodness-of-fit of the top-ranking models for each principal component (PC1 or PC2) by calculating the marginal and conditional R^2 (Nakagawa & Schielzeth 2013).

We used a randomization method (Manly 2006) to insure that the observed relationships from best isodar models for raccoons and striped skunks would not be expected by random chance alone; rather, they would instead have resulted from density-dependent habitat selection. To develop a null model for raccoons, we randomized the 12 pairs of adjacent sub-blocks so that "non-adjacent" sub-blocks were associated in the regression analyses. This process was performed for the 400 times that 12 pairs of adjacent sub-blocks were drawn over the survey areas in the original isodar analyses (*i.e.*, for each of the 100 replicates performed for each of the four sub-block dispositions). We then followed the same procedure as described in the section "Isodar theory" by identifying the sub-blocks H and L, and by estimating the relationship between the paired sub-blocks (non-adjacent in this case). This entire process was done 200 times, and the results were used to determine the 95% confidence intervals that would be expected by random chance alone. The same method was applied to striped skunk

abundance data, with the only difference that individual isodars were based on eight rather than 12 pairs of sub-blocks.

3. Results

For raccoons, the first two PCA axes explained respectively 53% and 31% of the variation in landscape attributes within pairs of adjacent sub-blocks. The PC1 axis represented a gradient from corn fields to forests, whereas PC2 reflected a gradient from anthropogenic areas to forests (Table 1). For striped skunks, PC1 (only significant PCA axis) explained 65% of the variation in landscape attributes and defined a gradient from corn fields to anthropogenic areas (Table 1).

The isodar models including the effect of the corn field – forest gradient (PC1) and the effect of the anthropogenic area – forest gradient (PC2) explained a high proportion of variation in the spatial distribution of raccoons (marginal $R^2 = 0.93$ and conditional $R^2 = 0.99$ for PC1 model, and marginal $R^2 = 0.95$ and conditional $R^2 = 0.96$ for PC2 model, in Table S3). Because the marginal and conditional R^2 remain consistently high for the PC1 model, and because PC1 explained more spatial variation in landscape attributes than PC2, we considered the PC1 model as the top-ranking isodar for raccoons. Striped skunk distribution was related to the corn field – anthropogenic area gradient (marginal $R^2 = 0.93$ and conditional $R^2 = 0.96$, in Table S3). Comparison of candidate isodar models based on AIC revealed that raccoon abundance in sub-blocks H ($N_{H_{PC1}}$) along a corn field – forest gradient (PC1) and striped skunk abundance in sub-blocks H ($N_{H_{PC1}}$) along a corn field – anthropogenic area gradient (PC1) depended upon conspecific abundance in sub-blocks L ($N_{L_{PC1}}$), the difference in landscape composition and structure between sub-blocks H and L (Δ_{PC1}), and the interaction between $N_{L_{PC1}}$ and Δ_{PC1} (Model 4 in Table S3). All other candidate isodar models that were based on PC1 received no empirical support ($\omega_i < 0.03$, in Table S3). The randomization procedure demonstrates that the spatial distribution of raccoons and striped skunks between adjacent sub-blocks could not be expected due to random chance alone (Figures S1 & S2).

For raccoons and striped skunks, the isodar intercept (equal to $\beta_0 + \beta_{\Delta_{PC1}} \times \Delta_{PC1}$) was positive within the range of observed values of Δ_{PC1} (Table 2 and Figure 3), indicating that

Table 1. Factor loadings for the first two axes resulting from principal component analysis (PCA) that was conducted on proportions of land cover types and density (km/km²) of corn-forest edges characterizing pairs of adjacent sub-blocks in the Montérégie and Estrie regions, Québec, Canada

Land cover type	Raccoon		Striped skunk
	PC1: Corn field to forest gradient	PC2: Anthropogenic area to forest gradient	PC1: Corn field to anthropogenic area gradient
Proportion of forests	0.559	0.739	-0.170
Proportion of corn fields	-0.922	-0.058	-0.668
Proportion of anthropogenic areas	0.252	-0.856	0.760
Proportion of wetlands	-0.071	0.102	0.036
Density of corn-forest edges	-0.738	0.331	-0.798

Table 2. Parameter estimates (β) and 95% confidence intervals (CI) for the best isodar model predicting raccoon abundance (a) and striped skunk abundance (b) in sub-blocks H ($N_{H_{PC1}}$) as a function of conspecific abundance in sub-blocks L ($N_{L_{PC1}}$) and the difference in landscape characteristics between sub-blocks H and L (Δ_{PC1})

Fixed effect	Estimate	95% CI
a. Raccoon		
Corn field to forest gradient (PC1)		
β_0	7.089	[5.841; 8.337]
$\beta_{N_{L_{PC1}}}$	0.512	[0.475; 0.548]
$\beta_{\Delta_{PC1}}$	0.735	[0.370; 1.100]
$\beta_{N_{L_{PC1}} \times \Delta_{PC1}}$	-0.154	[-0.187; -0.122]
Random effect		
$\sigma_{\text{inter-disposition}}^2$	1.175	[0.430; 3.208]
$\sigma_{\text{intra-disposition}}^2$	0.502	[0.416; 0.606]
$\rho_{\text{replication}}$	-0.034	[-0.041; -0.025]
b. Striped skunk		
Corn field to anthropogenic area gradient (PC1)		
β_0	2.924	[2.087; 3.760]
$\beta_{N_{L_{PC1}}}$	0.738	[0.684; 0.793]
$\beta_{\Delta_{PC1}}$	1.459	[1.189; 1.729]
$\beta_{N_{L_{PC1}} \times \Delta_{PC1}}$	-0.191	[-0.237; -0.144]
Random effect		
$\sigma_{\text{inter-disposition}}^2$	0.771	[0.201; 2.952]
$\sigma_{\text{intra-disposition}}^2$	0.849	[0.748; 0.964]
$\rho_{\text{replication}}$	-0.046	[-0.059; -0.031]

Δ_{PC1} is estimated as the difference in PC1 scores between sub-blocks H and L. Sub-block H represents the area with a relatively high proportion of forests (raccoon model) or anthropogenic features (striped skunk model). Sub-block L corresponds to the area with a rather high density of corn-forest edges and a large proportion of corn fields (raccoon and striped skunk models). Variances of random effects

between the four designs of sub-blocks ($\sigma_{\text{inter-disposition}}^2$) and within each design of sub-blocks ($\sigma_{\text{intra-disposition}}^2$), correlation between observations of a same replication within a given design of sub-blocks ($\rho_{\text{replication}}$) are shown.

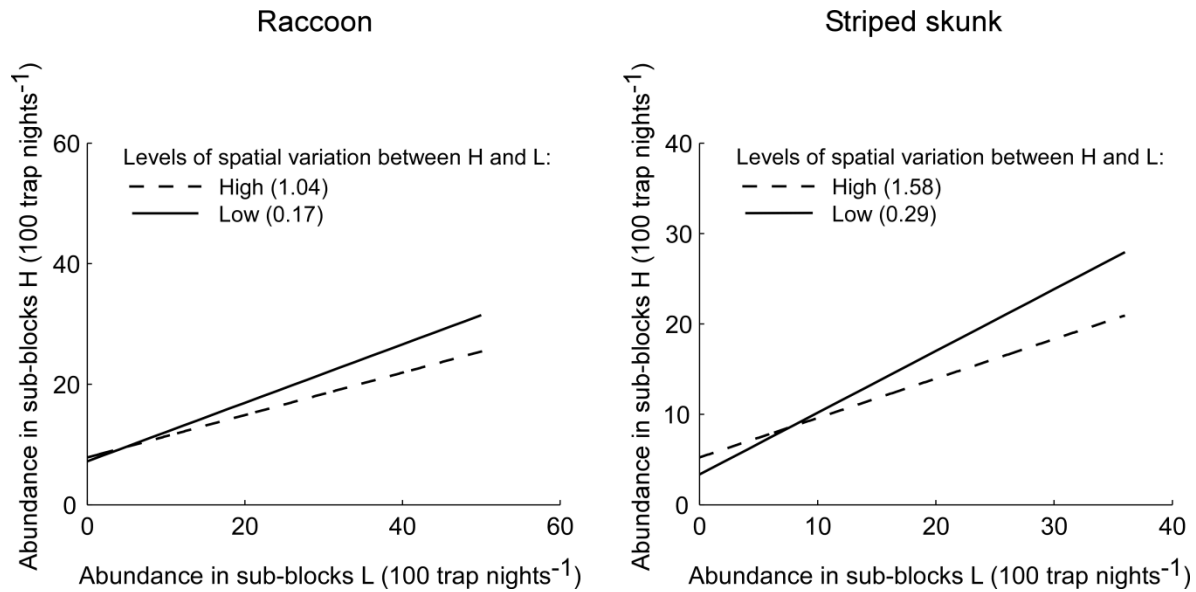


Figure 3. Estimated isodars for raccoons (left-hand side) and striped skunks (right-hand side) at different levels of variation in landscape composition and structure between sub-blocks H and L along a corn field – forest gradient for raccoons and along a corn field – anthropogenic area gradient for striped skunks. In the raccoon isodar, sub-blocks H correspond to areas with relatively high proportions of forests, whereas sub-blocks L represent areas with rather high densities of corn-forest edges and large proportions of corn fields. In the striped skunk isodar, sub-blocks H define areas with rather high proportions of anthropogenic features, whereas sub-blocks L correspond to areas with relatively high densities of corn-forest edges and large proportions of corn fields. The levels of spatial variation “Low” and “High” represent the values at the 25th and 75th percentiles in the distribution of differences in PC1 scores between sub-blocks H and L (Δ_{PC1}). The percentile values are indicated within parentheses in the figure.

when conspecific abundance was low in the landscape, raccoons and striped skunks selected areas with relatively high proportions of forests and anthropogenic features, respectively. This selection for these areas increased when the difference in landscape composition and structure between pairs of adjacent sub-blocks was high ($\beta_{\Delta_{PC1}} > 0$ in Figure 3).

The isodar slope for raccoons and striped skunks (equal to $\beta_{N_{L_{PC1}}} + \beta_{N_{L_{PC1}} \times \Delta_{PC1}} \times \Delta_{PC1}$) was positive within the range of observed values of Δ_{PC1} (Table 2 and Figure 3). The slope was less than 1 (Table 2), indicating that at high abundance of conspecifics in the landscape, raccoons and striped skunks favored areas with rather high densities of corn-forest edges and high proportions of corn fields, particularly when the difference in landscape characteristics between pairs of adjacent sub-blocks was high ($\beta_{N_{L_{PC1}} \times \Delta_{PC1}} < 0$ in Figure 3).

4. Discussion

In this study, we developed a resampling procedure that allows isodar theory to be applied over large geographic extents, by contrasting animal densities between pairs of adjacent sub-blocks that are randomly placed within surveyed areas. Using this method, we illustrate how isodar theory can be used with typical wildlife surveys to identify density-dependent habitat selection strategies without having to predefine habitat features. We provide a robust approach for applying isodar theory for a wide range of species, including medium- to large-sized mammals with high mobility. The proposed approach thus has the advantage of being applicable to existing wildlife surveys to reveal the adaptive nature of density-dependent habitat selection for a broad range of wildlife species. In our case study, we used the procedure to identify fitness-rewarding land cover types for raccoons and striped skunks. By revealing behavioral strategies of the main hosts of the raccoon rabies virus variant, the method can delineate areas that are most likely to be occupied by high densities of individuals and, consequently, those that are susceptible to promote rabies virus transmission.

4.1. Resampling procedure to apply isodar theory to wildlife surveys

Generally, studies using classical habitat isodars assess animal densities in multiple sampling plots that are replicated in space along symmetrical line or belt transects over two adjacent habitat types [*e.g.*, forest versus agricultural field (Morris 2009)]; see Figure 4 in

Knight & Morris 1996] for an illustration of one sampling transect). Accordingly, a pair of adjacent sub-blocks is the experimental unit of the resampling method that we propose to contrast animal densities in areas (sub-blocks) that can be composed of multiple habitat types. In our case, however, the method involves the use of computer modeling to randomly place blocks over the survey area while respecting certain constraints (*e.g.*, inter-block distance and block size) set by the user. Then, the blocks are divided in two adjacent sub-blocks of the same size, and relative animal abundance is estimated in each sub-block based on the wildlife survey data. Each time blocks (*e.g.*, 12 blocks for raccoons and eight blocks for striped skunks) are randomly placed over the landscape, we sample only a small portion of the entire survey area because of the constraints that we set, such as maintaining minimum distance between blocks to insure their statistical independence. Nevertheless, because the blocks are replicated several times over the landscape, we end up considering individuals captured over the entire survey area, and we are therefore able to make general inferences about density-dependent habitat selection. Our method is sufficiently flexible to incorporate a broad-range of environmental covariates. Covariates that are considered in developing candidate isodars should still be carefully selected based on the ecology of the focal species, and the resulting isodars should be vetted by ecologists that are familiar with the focal species and the survey area.

The proposed method can be applied over large geographic extents, and provides a helpful framework for wildlife management programs that are based on the broad-scale monitoring of population abundances. Whenever possible, mark-recapture or other types of analysis (*e.g.*, distance sampling analysis) that incorporate uncertain detection (Anderson 2001, Beasley et al. 2012) should be used to build isodars. In fact, this point has been recognized in early isodar studies (Morris 1987). Most isodar studies, however, do not use mark-recapture data (but see Haugen et al. 2006); instead, they rely upon various estimates of relative abundance. For example, relative animal abundance is often defined as the number of different individuals that are captured (minimum number known to be alive, MNA) during a sampling period (Morris 1988, 1992, Knight & Morris 1996, Hodson et al. 2010, Morris & Dupuch 2012), or as the fecal pellet deposition rate (Ramp & Coulson 2002, Hodson et al. 2010). In our case, we could not estimate animal abundance from capture-mark-recapture analysis because the number of recaptures was relatively low in each trapping site (raccoons: range = 0-11 and mean = 2.67; striped skunks: range = 0-10 and mean = 2.25), which implies that a large

number of sub-blocks contained very few or no recaptures. We thus used the most common approach for building isodars and considered MNA as an index of conspecific abundance.

4.2. Response of raccoons and striped skunks to environmental gradients: implications for rabies virus transmission

In the context of infectious disease dynamics, areas with high host densities must be delineated to increase the efficiency of control and prevention programs (Houle et al. 2011, Tardy et al. 2014). To characterize these areas, most studies examine the relationship between environmental covariates and host abundance patterns (*e.g.*, Rogers & Randolph 1991, Houle et al. 2011), without considering the fitness consequences that are associated with abundance patterns at low and high densities of conspecifics. However, the understanding of adaptive habitat selection can be critical for resolving various problems of wildlife management and conservation (Morris 2003a, Hodson et al. 2010). Our method that is based on isodar theory can help identify areas at risk for infectious disease transmission, while permitting the explanation of observed spatial patterns in host densities and their consequences on fitness. To minimize the costs that are associated with vaccination against rabies, densities of oral vaccine baits should be provided in proportion to local host densities (Boyer et al. 2011). In our study, isodar models suggested that at low abundance of conspecifics in the landscape, raccoons and striped skunks selected areas with rather high proportions of forests and anthropogenic features, respectively. This selection for these areas increased with increasing differences in landscape composition and structure between pairs of adjacent sub-blocks. Both species should achieve maximal potential fitness in areas with high proportions of forests and anthropogenic features, given that these habitats offer larger quantities of resources, such as den sites (*e.g.*, tree holes for raccoons and burrows under buildings for striped skunks) and occasional food items (*e.g.*, small mammals, birds, insects, human food, or garbage) (Larivière & Messier 1998, Henner et al. 2004). However, in landscapes with relatively high local population sizes, raccoons and striped skunks favored areas with rather high densities of corn-forest edges and high proportions of corn fields, particularly when differences in landscape characteristics between pairs of adjacent sub-blocks were great. Our models predict a lower reduction of potential fitness in these areas when conspecific abundance increases in the landscape. Areas with high densities of corn-forest edges provide raccoons and striped skunks with abundant and

highly nutritional food sources from the corn fields and safe cover within the forests (Larivière & Messier 2000, Houle et al. 2011). The inter-species transmission risk of rabies virus thus would be highest in the areas with rather high densities of corn-forest edges and high proportions of corn fields, since they support a larger raccoon and striped skunk population. Distribution of oral vaccine baits should be mainly concentrated in these areas, as they are more likely to generate rabies outbreaks due to more frequent contacts among raccoons and striped skunks.

Isodar theory can help to identify ecological traps if fitness components are measured as along with animal densities in two habitats (Shochat et al. 2005). An ecological trap is an area that animals preferentially select and in which they have lower fitness compared to other available areas (Robertson et al. 2013). In most cases, ecological traps occur in landscapes that have been degraded by human activities, which alter formerly reliable environmental cues and induce maladaptive habitat choices (Schlaepfer et al. 2002). To demonstrate the existence of an ecological trap, individuals must show a preference for a trap habitat over other habitats, and must have lower fitness in the habitat trap than in other available habitats (Robertson & Hutto 2006, Robertson et al. 2013). In the case of a disease outbreak, there might be a mismatch between animal density and fitness because disease transmission is often a positive density-dependent process. Pathogenic and parasitic infections can decrease fitness due to their effects on survival and fecundity (McCallum & Dobson 1995). In this context, our analysis indicates that areas with high densities of corn-forest edges and high proportions of corn fields could become ecological traps. Indeed, our isodars revealed that when many conspecifics were present in the landscape, raccoons and striped skunks preferred areas with high densities of corn-forest edges and high proportions of corn fields relative to areas with high proportions of forests and anthropogenic features, respectively. Because there is no difference in movement behavior and home range size between rabid and nonrabid individuals (Greenwood et al. 1997, Rosatte et al. 2006, Talbot et al. 2013), habitat selection strategies among nonrabid hosts should be representative of those of rabid hosts. Accordingly, mean fitness should be lower for the two species in areas with high densities of corn-forest edges and high proportions of corn fields during an epidemic, because individuals would be more likely to be infected by the rabies virus in these areas due to high densities of conspecifics. By studying density-dependent habitat selection of the main hosts of the raccoon rabies virus variant, our study illustrates how

isodar theory can be used to delineate areas of high animal densities where the risk of disease transmission is the greatest.

5. Supplemental material

Table S1. Range of land cover type proportions and density of corn-forest edges (km/km²) characterizing pairs of adjacent sub-blocks for raccoons and striped skunks in the Montérégie and Estrie regions, Québec, Canada

	Raccoon	Striped skunk
Proportion of forests	0-1	0-0.77
Proportion of corn fields	0-0.61	0-0.62
Proportion of anthropogenic areas	0-0.99	0-0.87
Proportion of wetlands	0-0.46	0-0.48
Density of corn-forest edges	0-2.3	0-1.62

Table S2. Hypotheses and associated isodar models for raccoons and striped skunks predicting conspecific abundance in sub-blocks H ($N_{H_{PCi}}$) as a function of conspecific abundance in sub-blocks L ($N_{L_{PCi}}$) and the difference in landscape composition and structure between sub-blocks H and L (Δ_{PCi}). Δ_{PCi} is measured as the difference in scores obtained from principal component analysis (PCA) between sub-blocks H and L in the Montérégie and Estrie regions, Québec, Canada

No.	Hypothesis	Model
	Effect of environmental gradient (PCi) on density-dependent habitat selection	
1	No effect	$N_{H_{PCi}} = \beta_0 + \beta_{N_{L_{PCi}}} \times N_{L_{PCi}}$
2	Effect at low densities of conspecifics	$N_{H_{PCi}} = \beta_0 + \beta_{N_{L_{PCi}}} \times N_{L_{PCi}} + \beta_{\Delta_{PCi}} \times \Delta_{PCi}$
3	Effect at high densities of conspecifics	$N_{H_{PCi}} = \beta_{N_{L_{PCi}}} \times N_{L_{PCi}} + \beta_{N_{L_{PCi}} \times \Delta_{PCi}} \times N_{L_{PCi}} \times \Delta_{PCi}$
4	Effect at low and high densities of conspecifics	$N_{H_{PCi}} = \beta_0 + \beta_{N_{L_{PCi}}} \times N_{L_{PCi}} + \beta_{\Delta_{PCi}} \times \Delta_{PCi} + \beta_{N_{L_{PCi}} \times \Delta_{PCi}} \times N_{L_{PCi}} \times \Delta_{PCi}$

Table S3. List of isodar models predicting raccoon abundance (a) and striped skunk abundance (b) in sub-blocks H ($N_{H_{PCi}}$) as a function of conspecific abundance in sub-blocks L ($N_{L_{PCi}}$) and the difference in landscape characteristics between sub-blocks H and L (Δ_{PCi}). Δ_{PCi} is estimated as the difference in scores obtained from principal component analysis (PCA) between sub-blocks H and L. Sub-block H defines either the area with a relatively high proportion of forests (raccoon PC1 and PC2 models) or the area with a rather large proportion of anthropogenic features (striped skunk PC1 model). Sub-block L corresponds to either the area with a relatively high density of corn-forest edges and a large proportion of corn fields (raccoon PC1 model and striped skunk PC1 model) or the area with a rather high proportion of anthropogenic features (raccoon PC2 model). Number of parameters (K), Akaike's Information Criterion (AIC), delta-AIC values (Δ_{AIC}), and AIC weights (ω) are presented. The selected models are identified in bold with their values of marginal and conditional R^2 (R_M^2 : marginal R^2 and R_C^2 : conditional R^2).

No.	Model	K	AIC	Δ_{AIC}	ω	R_M^2	R_C^2
a. Raccoon							
Effect of corn field – forest gradient (PC1)							
4	$N_{H_{PC1}} = \beta_0 + \beta_{N_{L_{PC1}}} \times N_{L_{PC1}} + \beta_{\Delta_{PC1}} \times \Delta_{PC1} + \beta_{N_{L_{PC1}} \times \Delta_{PC1}} \times N_{L_{PC1}} \times \Delta_{PC1}$	8	18869.4	0.00	1	0.93	0.99
3	$N_{H_{PC1}} = \beta_{N_{L_{PC1}}} \times N_{L_{PC1}} + \beta_{N_{L_{PC1}} \times \Delta_{PC1}} \times N_{L_{PC1}} \times \Delta_{PC1}$	7	18972.2	102.86	0	0.92	0.98
2	$N_{H_{PC1}} = \beta_0 + \beta_{N_{L_{PC1}}} \times N_{L_{PC1}} + \beta_{\Delta_{PC1}} \times \Delta_{PC1}$	7	19076.7	207.32	0	0.91	0.98
1	$N_{H_{PC1}} = \beta_0 + \beta_{N_{L_{PC1}}} \times N_{L_{PC1}}$	6	19088.6	219.19	0	0.92	0.98
Effect of anthropogenic area – forest gradient (PC2)							
4	$N_{H_{PC2}} = \beta_0 + \beta_{N_{L_{PC2}}} \times N_{L_{PC2}} + \beta_{\Delta_{PC2}} \times \Delta_{PC2} + \beta_{N_{L_{PC2}} \times \Delta_{PC2}} \times N_{L_{PC2}} \times \Delta_{PC2}$	8	31261.7	0.00	0.972	0.95	0.96

2	$N_{HPC2} = \beta_0 + \beta_{N_{LPC2}} \times N_{LPC2} + \beta_{\Delta PC2} \times \Delta PC2$	7	31269.2	7.50	0.023	0.95	0.96
3	$N_{HPC2} = \beta_{N_{LPC2}} \times N_{LPC2} + \beta_{N_{LPC2} \times \Delta PC2} \times N_{LPC2} \times \Delta PC2$	7	31272.4	10.65	0.005	0.95	0.96
1	$N_{HPC2} = \beta_0 + \beta_{N_{LPC2}} \times N_{LPC2}$	6	31413.6	151.92	0.000	0.92	0.93

b. Striped skunk

Effect of corn field – anthropogenic area gradient (PC1)

4	$N_{HPC1} = \beta_0 + \beta_{N_{LPC1}} \times N_{LPC1} + \beta_{\Delta PC1} \times \Delta PC1 + \beta_{N_{LPC1} \times \Delta PC1} \times N_{LPC1} \times \Delta PC1$	8	18869.4	0.00	1	0.93	0.96
2	$N_{HPC1} = \beta_0 + \beta_{N_{LPC1}} \times N_{LPC1} + \beta_{\Delta PC1} \times \Delta PC1$	7	18972.2	102.86	0	0.92	0.95
3	$N_{HPC1} = \beta_{N_{LPC1}} \times N_{LPC1} + \beta_{N_{LPC1} \times \Delta PC1} \times N_{LPC1} \times \Delta PC1$	7	19076.7	207.32	0	0.86	0.94
1	$N_{HPC1} = \beta_0 + \beta_{N_{LPC1}} \times N_{LPC1}$	6	19088.6	219.19	0	0.86	0.94

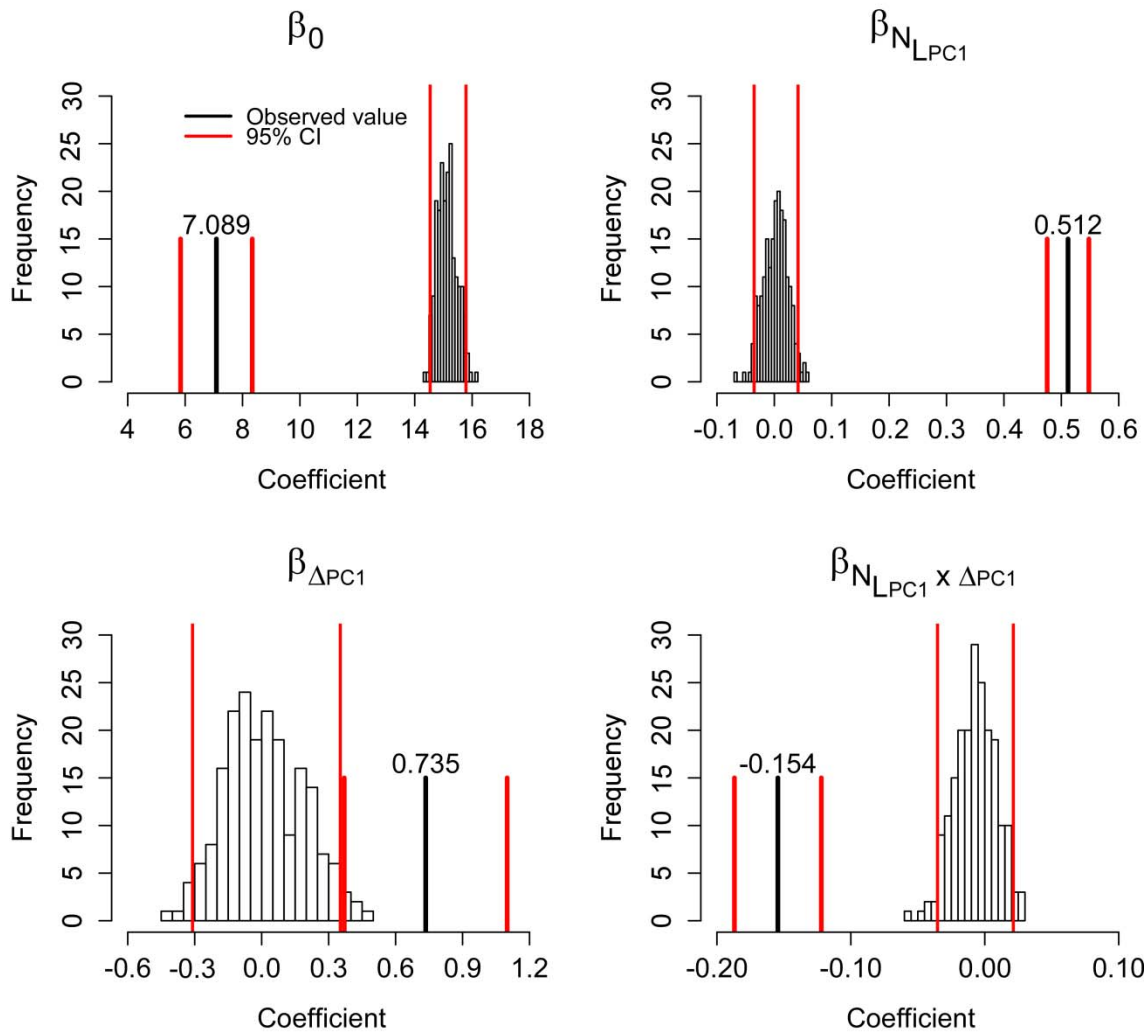


Figure S1. Randomization distributions of parameter estimates of the best isodar model for raccoons and their observed values (black vertical line). The 95% confidence intervals (CI) are represented by a red vertical line. For randomization distributions, the measure of 95% CIs is based on the values at the 2.5th and 97.5th percentiles in the randomization distribution.

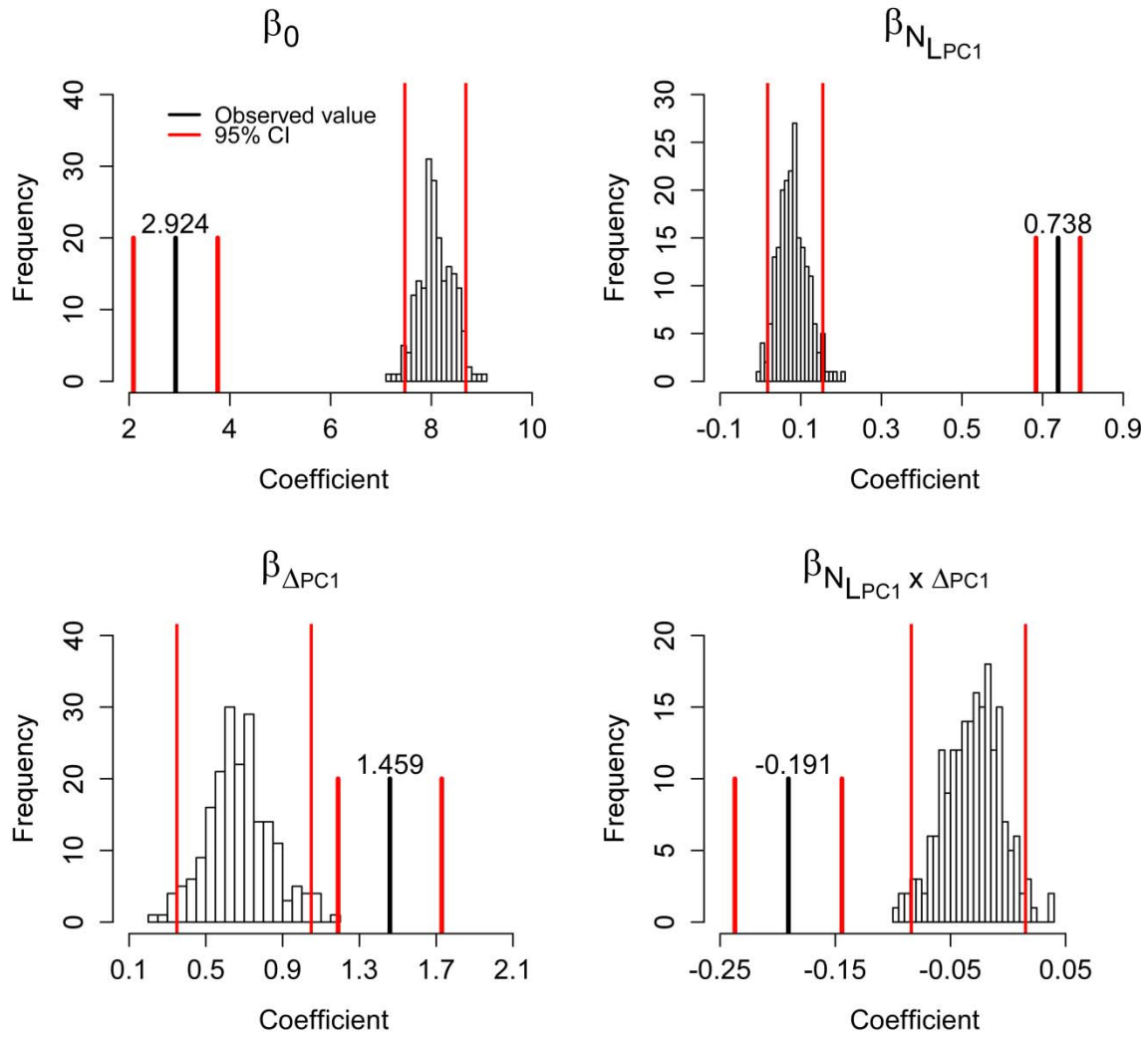


Figure S2. Randomization distributions of parameter estimates of the best isodar model for striped skunks and their observed values (black vertical line). The 95% confidence intervals (CI) are represented by a red vertical line. For randomization distributions, the measure of 95% CIs is based on the values at the 2.5th and 97.5th percentiles in the randomization distribution.

CHAPITRE 2

Density-dependent functional responses in habitat selection by two hosts of the raccoon rabies virus variant

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Résumé

Les variations spatio-temporelles dans la densité de congénères et la disponibilité des ressources sont deux des principaux facteurs responsables de la plasticité dans la sélection de l'habitat. Bien que les modèles de sélection de l'habitat doivent pouvoir prévoir au mieux la répartition des animaux malgré cette plasticité dans le processus de sélection, aucune étude n'a évalué si les réponses fonctionnelles pouvaient varier en fonction de la densité de congénères. Nous avons examiné les effets simultanés de la densité de congénères et de la disponibilité des ressources sur la sélection de l'habitat chez les ratons laveurs (*Procyon lotor*) et les mouffettes rayées (*Mephitis mephitis*), deux des principaux hôtes du virus de la rage en Amérique du Nord. Nous avons suivi 54 ratons laveurs et 12 mouffettes rayées par télémétrie GPS dans un paysage agroforestier. Nous avons ensuite construit des fonctions de sélection de ressources pour tester si la sélection des champs de maïs variait en fonction de la densité de congénères et de la disponibilité des champs de maïs dans des polygones convexes minimum à 100%. Notre étude montre que les réponses fonctionnelles peuvent effectivement changer en fonction de la densité de congénères. Dans les zones avec une faible densité de bordures maïs-forêts et une faible proportion de champs de maïs, les ratons laveurs montraient une plus forte sélection pour les champs de maïs par rapport aux forêts quand peu de congénères étaient présents. À hautes densités de congénères, la sélection des champs de maïs était la plus élevée dans les zones avec une forte densité de bordures maïs-forêts et une faible proportion de champs de maïs. Pour les mouffettes rayées, nous n'avons pas détecté de réponses fonctionnelles qui dépendent de la densité de congénères. Cependant, la probabilité de rencontre entre des mouffettes rayées était plus élevée dans les corridors agricoles. Dans un contexte de dynamique de maladies infectieuses, nos modèles permettent de mieux prévoir les variations spatio-temporelles dans la répartition des espèces hôtes et donc, d'identifier avec plus d'exactitude les zones à hautes densités animales où le risque de transmission est élevé. Par exemple, l'omission de la densité-dépendance dans les réponses fonctionnelles sous-estimait la probabilité relative d'occurrence de ratons laveurs dans les champs de maïs, et surestimait celle dans les zones anthropiques et les zones humides. Notre étude met en avant le besoin d'analyser la sélection de l'habitat chez tous les hôtes d'une zoonose. Les programmes de contrôle et de prévention qui sont utilisés pour limiter la propagation de maladies devraient tenir compte des réponses fonctionnelles densité-dépendantes dans des systèmes multi-hôtes.

Abstract

Spatio-temporal variations in conspecific density and resource availability are two of the main factors responsible for plasticity in habitat selection. Despite the need for habitat selection models that can accurately predict animal distribution given the plasticity in the selection process, no study has assessed the synergistic effects of these factors on habitat selection. We investigated density-dependent functional responses by raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*), two of the main hosts of the rabies virus in North America. We monitored 54 raccoons and 12 striped skunks with Global-Positioning-System collars in a landscape dominated by corn fields and forest patches. We built resource selection functions to evaluate if the selection of corn fields varied with conspecific density and corn field availability within 100% minimum convex polygons. Raccoons altered their selection of corn fields depending on both conspecific density and corn-forest edge density or corn field proportion. In areas of low corn-forest edge densities and a low corn field proportion, raccoons showed stronger selection for corn fields when few conspecifics were present. At high conspecific densities, the selection of corn fields was stronger in areas with high corn-forest edge densities and a low corn field proportion. For striped skunks, we did not detect any synergistic effect of density-dependence and functional responses. Unlike raccoons, striped skunks displayed a selection that was strongest for agricultural corridors. We show that functional responses in habitat selection can be density-dependent. In a context of infectious disease dynamics, modeling density-dependence in functional responses increases the ability to predict spatio-temporal variations in the distribution of reservoir species and thus, to delineate areas at high animal densities where the risk of disease outbreaks is relatively high. For example, the omission of density-dependence in functional responses underestimated the relative probability of raccoon occurrence in corn fields, while overestimating the relative probability of occurrence in anthropogenic areas and wetlands. Our study underscores the relevance of considering the complexity of habitat selection by all hosts of a zoonosis. Cost-effective control and prevention programs used to limit disease spread can benefit from accounting for density-dependent functional responses of a multi-host disease system.

1. Introduction

From zoonosis management to wildlife conservation, managers from many fields of applied ecology face the challenge of having to anticipate the distributional dynamics of animals in different spatial contexts. A main difficulty arises from the plasticity of habitat selection that is commonly observed within and among animal populations (Rettie & Messier 2000, Osko et al. 2004). The assumption that habitat selection is a fixed rather than a plastic process can often result in misguided management and conservation practices (Osko et al. 2004). A solution to this problem is to develop more comprehensive models integrating factors that are linked to the spatio-temporal changes in habitat selection (Fortin et al. 2008, Godvik et al. 2009). Spatio-temporal variations in conspecific density and in habitat patch availability have emerged as two factors that commonly induce plasticity in habitat selection (Morris 2006, Moreau et al. 2012).

To achieve maximum fitness, animals should choose their habitats according to local conspecific densities (Rosenzweig 1981, Morris 2003b). Density-dependence in ecological processes, such as in competition and predation, implies that the strength of selection for a particular habitat type may vary with population density (Morris et al. 2000a, Morris 2005). This principle is the basis of ideal free distribution (Fretwell & Lucas 1969) and isodar theory (Morris 1988), which have received extensive empirical support (*e.g.*, Haugen et al. 2006, Haché et al. 2012).

The selection of habitat features by animals may also change as a function of the availability of those features in the landscape (Osko et al. 2004). These changes are referred to as a functional response in habitat selection (*sensu* Mysterud & Ims 1998), which generally occurs when the availability of the most limiting resources vary spatially. For example, many animals require daily access to water (McHugh 1958). If water-holes are broadly available over the landscape, spatial patterns in the availability of this resource should not have a strong influence on animal distribution. If, however, the resource is limited over space, animal distribution will be closely tied to water availability. The consideration of functional responses in habitat selection can thus provide a more accurate description of animal distributions, and as such, they are increasingly used in habitat selection studies (Mauritzen et al. 2003, Hebblewhite & Merrill 2008, Godvik et al. 2009, Houle et al. 2010, Moreau et al. 2012).

To maximize fitness, animals should be spatially distributed as a function of resource abundance. For example, animals may be more abundant in areas comprised of a high proportion of food-rich patches. At a finer scale in those areas, food may not be the most limiting factor (*e.g.*, water-holes, resting sites, or refuges against predators may become more limiting), and the selection for food-rich patches may not be as strong as in areas poor in food resources (Rettie & Messier 2000). Different spatial patterns of individual abundance can thus emerge from variations in resource availability and can affect habitat selection of other individuals through both direct competition for limiting resources and predator attraction due to high prey densities (Morris et al. 2000b, Morris 2005, Gaillard et al. 2010). Because habitat selection is a scale-dependent process (Johnson 1980), animal density can display spatial patterns that are driven by both density-dependent habitat selection and functional responses in habitat selection. Further, habitat selection theories are often based on the assumption that animals respond to changes in habitat quality with consequences on their abundance patterns in the landscape (Fretwell & Lucas 1969, Morris 1988). For example, the resource quality and quantity determine maximal fitness that can be achieved in different habitats at low conspecific densities (Morris 1988). The habitat structure can also influence the efficiency with which animals extract, consume, and convert resources into descendants, and determine the relative decline rate of fitness when conspecific density increases in the landscape (Morris 1990). Consequently, functional responses can appear under density-dependent habitat selection. Given the rapid increase in empirical tests of functional responses in habitat selection (Herfindal et al. 2009, Gillies & St. Clair 2010, Bjørneraas et al. 2012, Mabile et al. 2012, Roever et al. 2012) and the long-lasting interest in density-dependent habitat selection (Morris 1987, Møbæk et al. 2009, Hodson et al. 2010, Morris & MacEachern 2010, van Beest et al. 2014), it is surprising that to our knowledge, no study has investigated the possibility of density-dependence in functional responses.

Such a more holistic modeling approach should improve our ability to predict distributional dynamics of animals given spatio-temporal patterns of habitat selection, and accordingly, it would be valuable in ecological fields such as epidemiology. Indeed, the transmission of zoonotic diseases requires direct contacts between susceptible and infectious hosts, which depend on local population density (Anderson & May 1979). The integration of both density-dependence and functional responses in habitat selection models of disease hosts

should provide a useful analytical framework, which would better delineate areas of high animal concentration that are susceptible to promote disease transmission.

Here, we examined the synergistic effects of density-dependence and functional responses in habitat selection by two mesocarnivores that maintain and transmit rabies virus: raccoons (*Procyon lotor* L.) and striped skunks (*Mephitis mephitis* L.). We used resource selection functions (Manly et al. 2002) to assess how habitat selection varied among individuals as a function of changes in both conspecific density and local habitat characteristics. Raccoon populations act as major reservoirs of the raccoon rabies virus variant in North America, whereas the number of rabies cases in striped skunks attributable to this variant only tends to increase with rabies cases in the main host (Blanton et al. 2012). Although human deaths due to rabies are rare, the costs that are associated with the detection, prevention and control programs against this disease ranged between US \$230 million and US \$1000 million per year in the United States alone (Rupprecht et al. 1995). The development of cost-effective strategies to limit rabies epizootics (*e.g.*, population reduction, trap-vaccinate-release, and oral vaccination) requires the identification of areas where the probability of intra- and inter-specific contacts is the highest (Rosatte et al. 2010, Houle et al. 2011). Raccoons and striped skunks can exploit a wide range of landscapes. In agriculturally fragmented landscapes, corn (*Zea mays* L.) is the main food source of raccoons when it is available (Rivest & Bergeron 1981), and it is also consumed by striped skunks (Rosatte & Larivière 2003). We thus analyzed the synergistic effects of density-dependence and functional responses in the selection of corn fields.

2. Materials and Methods

2.1. Study areas

The study was conducted in two areas of southern Québec, Canada. Data were collected in the first area, located in the Montérégie region (45°23'23''N, 73°06'05''W), in 2009 and 2010, and in the second area, which was located in the Estrie region (45°28'54''N, 71°40'05''W), in 2011. Between 2006 and 2009, 104 rabies cases (4 raccoons in 2006; 59 raccoons, 6 striped skunks, and 1 red fox (*Vulpes vulpes*) in 2007; 26 raccoons and 6 striped skunks in 2008; 2 striped skunks in 2009) have been reported in the Montérégie study area

(Rees et al. 2011a, Côté et al. 2012). The two regions are characterized by heterogeneous landscapes that are composed of forest patches of different sizes which are embedded within an agricultural matrix. The primary types of forest patches are maples (genus *Acer* L.), birches (genus *Betula* L.), and poplars (genus *Populus* L.). The agricultural fields are dominated by corn and soybean (*Glycine max* L.) fields. Oat (*Avena sativa* L.), wheat (*Triticum aestivum* L.), hay (genus *Fenum* L.), and barley (*Hordeum vulgare* L.) are also cultivated in these regions. Urban and residential areas, water bodies, and drainage systems are also sparsely distributed in these agriculturally fragmented landscapes.

2.2. Monitoring of habitat selection by raccoons and striped skunks

Raccoons and striped skunks were live trapped over the two regions (see “Materials and methods: Relative abundance of raccoons and striped skunks” for details on trapping sites). Captured individuals were immobilized with an injection of ketamine and medetomidine administered intramuscularly (Robert et al. 2012a). Animals were sexed, aged by a tooth-wear technique (Grau et al. 1970), and marked with ear tags before being released. Adults (≥ 1 -year-old) were fitted, each with a Quantum 4000 Enhanced Global Positioning System (GPS) collar (model 925-0022-00 “Small Collar” for raccoons and model 925-0020-00 “Mini Collar” for striped skunks; Telemetry Solutions, Concord, California, USA). Animals were captured and handled following a protocol approved by the Ministère des Ressources Naturelles et de la Faune. We monitored 54 raccoons and 12 striped skunks with GPS collars: 10 raccoons (5 males, M; 5 females, F) and 12 striped skunks (5 M and 7 F) in 2009, 20 raccoons (11 M and 9 F) in 2010, and 24 raccoons (12 M and 12 F) in 2011. Raccoons and striped skunks were followed from June/July to September/October between 2009 and 2011, with a recording duration of 10-116 days (median = 63) per raccoon and 29-95 days (median = 66) per striped skunk. Variations in the length of the monitoring period are attributable to collar malfunctioning in most cases, or to the death of the monitored individual. In 2009, GPS collars were programmed to record a location every 2 h from 00:00 hours for raccoons and every 4 h from 00:00 hours for striped skunks. This schedule was applied from Sunday to Friday, whereas on Saturday, a location was recorded for each hour for both species. In 2010 and 2011, GPS collars were fitted to raccoons only and recorded a location every hour all week long. We considered only GPS locations obtained with a high number of satellites ($n \geq 3$) resulting in a

precision of 3-30 m in 93% of cases and 50 m in the remaining cases. A total of 38 555 locations were obtained for raccoons, with an average of 714 locations per individual (range = 42-1584; median = 775.5). A total of 2044 locations were obtained for striped skunks, with an average of 171 locations per individual (range = 57-352; median = 163.5).

2.3. Relative abundance of raccoons and striped skunks

Local abundance of raccoons and striped skunks was evaluated by live trapping (Tomahawk Live Trap Co., Tomahawk, Wisconsin, USA; Havahart, Woodstream Corporation, Lititz, Pennsylvania, USA) conducted over about seven consecutive days in June 2009 and in July 2010-2011. Over the years 2009 and 2010, animals were captured in nine trapping sites in the Montérégie region and two trapping sites in the Estrie region in 2011. The size of the trapping sites varied from 10 to 185 km² (mean = 58 km²). The live traps were baited with sardines, marshmallows, and an olfactory lure (Procoon®, Leurres Forget, Mauricie, Québec, Canada). Each live trap was inspected daily. Over the three years of the study, on average 170 live traps (range = 56-298) were distributed across all trapping sites (see Houle et al. 2011 for further details). For each trapping site, we calculated relative raccoon and striped skunk abundance as the number of unique individuals per species captured per 100 trap nights. The number of trap nights was defined as the total number of trap nights deployed minus the number of sprung traps, and minus the number of traps where a non-target species was captured, and those where an individual was recaptured (Houle et al. 2011, Mainguy et al. 2012). A total of 243 raccoons were captured across 2009, 2010 and 2011, and 34 striped skunks were captured in 2009. The number of unique individuals was not correlated (Spearman rank correlation) to the size of the trapping site (raccoon: $r_s = -0.35$, $P = 0.29$; striped skunk: $r_s = -0.04$, $P = 0.91$).

2.4. Habitat characteristics

Land cover types were delineated from 1:15000 scale aerial photographs that had been taken in 1999 by the Ministère des Ressources Naturelles et de la Faune, while information about different crops that had been cultivated in the agricultural fields in the areas of interest was obtained from the Financière Agricole du Québec. The landscape was then split into nine

classes: forests (covering 35% of all of the study areas), corn fields (12%), crops (13%), open-uncultivated areas (17%), water bodies (4%, including lakes, rivers, and streams), wetlands (2%, including riparian areas), anthropogenic areas (9%), agricultural corridors (7%), and others (1%) (see Table S1). Riparian areas were delimited by a 20-m buffer around water bodies (Houle et al. 2011), whereas agricultural corridors were delimited by a 10-m buffer around agricultural fields (corn and other crop fields) (Beasley et al. 2007a).

2.5. Resource selection functions

Following several recent studies that modeled functional responses in habitat selection (Hebblewhite & Merrill 2008, Gillies & St. Clair 2010, Moreau et al. 2012, Roever et al. 2012), we used resource selection functions (RSFs) to model the synergistic effects of density-dependence and functional responses in the selection of corn fields when corn became available (01 August – 15 October). RSFs were developed by comparing habitat characteristics of observed (coded 1) locations with habitat characteristics of an equal number of random (coded 0) locations (Manly et al. 2002) that were drawn within the 100% minimum convex polygon (MCP) of each collared individual. In this study, our objective was not to evaluate variations in home range size, but rather to delineate areas that were available to individuals as it was done in several studies (Gillies et al. 2006, Hebblewhite & Merrill 2009, Herfindal et al. 2009, Moreau et al. 2012). Given that 100% MCP generally exceeds home range size (Burgman & Fox 2003), we investigated habitat selection between Johnson's (1980) second- and third-order of selection. All of the locations (observed vs. random) were assigned to a land cover type among nine land cover classes. With Geospatial Modelling Environment (version 0.7.1.0, Beyer 2012) and ArcGIS (version 10.0, Environmental Systems Research Institute 2010, Redlands, California, USA), we also calculated the density (km/km²) of forest edges bordering corn fields and the proportion of corn fields in the 100% MCP of each animal that was monitored. The density of conspecifics (individuals/100 trap nights/km²) was estimated in the 100% MCP of each radio-collared individual. This density corresponded to relative abundance of the two species obtained within trapping sites which overlapped the 100% MCPs of individuals. Preliminary results showed that raccoon and striped skunk abundance did not change spatially and temporally between June-July and August-October with respect to corn-forest edge density and corn field proportion.

Several studies emphasized the use of mixed-effects models to estimate population-level and animal-specific responses to habitat availability (Gillies et al. 2006, Hebblewhite & Merrill 2008, Moreau et al. 2012). We thus modeled RSFs using a logistic generalized linear mixed-effects model (logit link). RSFs for raccoons included a random intercept for “individual” nested within “year” to account for the unbalanced sampling design and changes in the GPS schedule among years, and to accommodate for non-independence of observations for a given raccoon (Gillies et al. 2006). Mixed-effects RSFs took the general structure:

$$w(\mathbf{x}) = \exp(\beta_{\text{Land cover}} x_{\text{Land cover } ijt} + \beta_{\text{Corn} \times \text{Density}} x_{\text{Corn } ijt} x_{\text{Density } jt} + \beta_{\text{Corn} \times \text{Covar}} x_{\text{Corn } ijt} x_{\text{Covar } jt} + \beta_{\text{Corn} \times \text{Density} \times \text{Covar}} x_{\text{Corn } ijt} x_{\text{Density } jt} x_{\text{Covar } jt} + \gamma_{0jt}) \quad (1)$$

where $w(\mathbf{x})$ represents the RSF scores, β are selection coefficients for covariates x , and γ_{0jt} is the random intercept associated with animal j nested in year t . RSFs for striped skunks included only a random intercept for each individual because individuals were monitored over a single year. The nine land cover types were coded as dichotomous covariates, with forest being the reference category. Thus, $x_{\text{Land cover } ijt}$ corresponds to a dichotomous covariate specific to a given land cover type and takes the value of 1 if the location i of animal j in year t is in that land cover type, and 0 otherwise. The term $x_{\text{Corn } ijt}$ represents a binary covariate taking the value of 1 if the location i of animal j in year t is in a corn field, and 0 otherwise. The term $x_{\text{Density } jt}$ is the relative abundance of raccoons or striped skunks within the 100% MCP of animal j in year t . The term $x_{\text{Covar } jt}$ is either the density of corn-forest edges or the proportion of corn fields within the 100% MCP of animal j in year t . The interaction $x_{\text{Corn } ijt} x_{\text{Density } jt}$ tests for density-dependence in the selection of corn fields within the 100% MCP (McLoughlin et al. 2010). The interaction $x_{\text{Corn } ijt} x_{\text{Covar } jt}$ assesses whether or not there were functional responses in the selection of corn fields within the 100% MCP. The interaction $x_{\text{Corn } ijt} x_{\text{Density } jt} x_{\text{Covar } jt}$ tests for synergistic effects of density-dependence and functional responses in the selection of corn fields within the 100% MCP.

We built separate RSFs for day and night because raccoons and striped skunks tend to rest during the day and be active at night (Gehrt 2003, Rosatte & Larivière 2003). The night period extended from the beginning of dusk (sunset - 1h) until the end of dawn (sunrise + 1h), whereas the day period occurs from the end of dawn until the beginning of dusk (data obtained from National Research Council Canada and available at <http://www.nrc-cnrc.gc.ca/eng/services/sunrise/>). RSFs were estimated with the package *lme4* of R statistical software (version 2.15.1, R Development Core Team 2012). We considered 11 candidate models (Table 1) for each time period (day or night) and each species to test for density-dependence and functional responses in the selection of corn fields. The covariate that was associated with density of conspecifics was standardized by subtracting its mean and dividing by its standard deviation to improve model convergence and to reduce collinearity between interaction terms (Quinn & Keough 2002). Multicollinearity was low in all candidate models, as the variance inflation factor of each covariate was always < 10 (Dormann et al. 2013). We compared nested models based Akaike's Information Criterion (AIC) and AIC weights (ω). When several nested models received similar support ($\Delta\text{AIC} < 2$), we applied the principle of parsimony by retaining the model with fewer parameters (Burnham & Anderson 2002).

We evaluated model robustness of all species using 5-fold cross-validation, which consisted of developing RSFs with 80% of the locations (training set), and then testing the predictive power of these RSFs with the 20% of locations that were withheld (testing set) (see Boyce et al. 2002 for details). We carried out the procedure 100 times to obtain average Spearman rank correlations (\bar{r}_s) for which a high \bar{r}_s indicates high predictive power. Combined with information criteria, 5-fold cross-validation has also been used to identify the best model.

We also estimated the relative probability of co-occurrence between raccoons and striped skunks by multiplying their respective relative probabilities of occurrence. The relative probabilities of occurrence of each species S (\hat{w}_s) was scaled between 0 and 1 following:

$$\hat{w}_s = \frac{w_s(\mathbf{x}) - w_{s \min}}{w_{s \max} - w_{s \min}} \quad (2)$$

Table 1. Description of the eleven candidate resource selection functions (RSFs) used to test the combined effects of density-dependence and functional responses in habitat selection of raccoons and striped skunks during daytime and night-time in the Montérégie and Estrie regions, Québec, Canada

Model	No.	Model structure
Land cover selection	1	Land cover †
Density-dependence	2	Land cover selection model + Corn × Density ‡
Functional response	3	Land cover selection model + Corn × Corn-forest edge §
	4	Land cover selection model + Corn × Prop. corn ¶
	5	Land cover selection model + Corn × Corn-forest edge + Corn × Prop. corn
Density-dependence + functional response	6	Density-dependence model + Corn × Corn-forest edge
	7	Density-dependence model + Corn × Prop. corn
	8	Density-dependence model + Corn × Corn-forest edge + Corn × Prop. corn
Density-dependence × functional response	9	Density-dependence model + Corn × Corn-forest edge + Corn × Density × Corn-forest edge
	10	Density-dependence model + Corn × Prop. corn + Corn × Density × Prop. corn
	11	Density-dependence model + Corn × Corn-forest edge + Corn × Prop. corn + Corn × Density × Corn-forest edge + Corn × Density × Prop. corn

† Included corn fields, crops, open-uncultivated areas, agricultural corridors, anthropogenic areas, water bodies, wetlands, and others. The covariate “forest” was used as the reference category.

‡ Density (individuals/100 trap nights/km²) of raccoons for RSFs in this first species or density of striped skunks for RSFs in this second species within the 100% MCP of each radio-tracked individual

§ Density (km/km²) of corn-forest edges within the 100% MCP of each radio-tracked individual

¶ Proportion of corn fields within the 100% MCP of each radio-tracked individual

where $w_s(\mathbf{x})$ corresponds to Equation (1), and $w_{s \max}$ and $w_{s \min}$ are, respectively, the smallest and largest RSF values (Johnson et al. 2004) for each species S, which is either raccoon or striped skunk. The relative probability of co-occurrence between raccoons and striped skunks was estimated by $\hat{w}_{\text{raccoon}} \times \hat{w}_{\text{striped skunk}}$ (see Courbin et al. 2009).

3. Results

Habitat selection by raccoons during night-time was best described by the model accounting for the interaction between conspecific density and density of corn-forest edges or the proportion of corn fields (Model 11; Table S2). This model had high predictive power ($\bar{r}_s = 0.97$; Table 2) and received essentially all empirical support ($w_i \geq 0.99$; Table S2). For raccoons during the day, the best model (Model 3; Table S2) was a functional response involving the density of corn-forest edges (model robust to cross-validation: $\bar{r}_s = 0.98$; Table 2). For striped skunks during the day, the best model (Model 6; Table S3) accounted for an additive effect of conspecific density and density of corn-forest edges, whereas at night, the best model (Model 7; Table S3) considered the additive effect of conspecific density and the proportion of corn fields. Both models had good predictive power ($\bar{r}_s = 0.78$ for the Model 6 of day and $\bar{r}_s = 0.86$ for Model 7 of night; Table 3).

3.1. Response of raccoons and striped skunks to agriculturally fragmented landscapes

Relative to forests, raccoons selected anthropogenic areas throughout the day (Table 2). At night, they also selected wetlands and agricultural corridors while avoiding crops and open areas (Table 2). Striped skunks selected agricultural corridors at night and avoided crops and open areas during the day (Table 3).

The selection of corn fields by the two species was subject to functional responses and density-dependence. During the day, the avoidance of corn fields was dependent upon the variation encountered in the density of corn-forest edges. For example, both raccoons and striped skunks had stronger avoidance of corn fields when the density of corn-forest edges was

Table 2. Selection coefficients (β) and 95% confidence intervals (CI) of fixed effects, and variance (σ^2) and standard errors (SE) of random effects of the best resource selection function (RSF) describing habitat selection by raccoons during daytime and night-time. The \bar{r}_s of 5-fold cross-validation is given for each of the two models (day vs. night).

Fixed effect	Night		Day	
	β	95% CI	β	95% CI
Land cover type †				
Corn	1.206	[1.081, 1.331]	-2.672	[-2.960, -2.383]
Crop	-1.219	[-1.289, -1.148]	-2.798	[-2.925, -2.671]
Corridor	0.226	[0.162, 0.291]	-1.064	[-1.164, -0.965]
Open	-0.366	[-0.422, -0.309]	-1.676	[-1.760, -1.593]
Anthropogenic	0.489	[0.372, 0.606]	1.295	[1.130, 1.460]
Water	0.125	[-0.165, 0.415]	-2.337	[-2.971, -1.704]
Wetland	0.483	[0.273, 0.694]	-1.077	[-1.380, -0.775]
Other	-1.039	[-1.320, -0.757]	-0.531	[-0.851, -0.212]
Corn × Density	-0.010	[-0.126, 0.106]
Corn × Corn-forest edge ‡	0.237	[0.119, 0.356]	-0.593	[-0.961, -0.225]
Corn × Prop. corn §	-5.571	[-6.009, -5.132]
Corn × Density × Corn-forest edge	0.187	[0.058, 0.315]
Corn × Density × Prop. corn	-1.147	[-1.612, -0.681]
Random effect	σ^2	SE	σ^2	SE
Year	0.003	0.055	0.057	0.239
Specimen ID × Year	0.020	0.141	0.200	0.447
5-fold: \bar{r}_s (range)	0.97 (0.90-1)		0.98 (0.94-1)	

† Reference category was forest

‡ Density (km/km²) of corn-forest edges within the 100% MCP of each radio-tracked individual

§ Proportion of corn fields within the 100% MCP of each radio-tracked individual

Table 3. Selection coefficients (β) and 95% confidence intervals (CI) of fixed effects, and variance (σ^2) and standard errors (SE) of random effects of the best resource selection function (RSF) describing habitat selection by striped skunks during daytime and night-time. The \bar{r}_s of 5-fold cross-validation is given for each of the two models (day vs. night).

Fixed effect	Night		Day	
	β	95% CI	β	95% CI
Land cover type [†]				
Corn	-1.175	[-1.601, -0.748]	-1.881	[-3.454, -0.308]
Crop	-0.289	[-0.642, 0.064]	-0.942	[-1.502, -0.382]
Corridor	0.946	[0.574, 1.317]	0.321	[-0.255, 0.897]
Open	0.202	[-0.137, 0.541]	-0.725	[-1.294, -0.156]
Anthropogenic	0.263	[-0.207, 0.733]	-1.448	[-2.360, -0.537]
Wetland	0.009	[-1.402, 1.420]
Corn \times Density	0.811	[0.302, 1.320]	-1.663	[-4.176, 0.850]
Corn \times Corn-forest edge [‡]	-1.082	[-2.030, -0.133]
Corn \times Prop. corn [§]	0.688	[0.209, 1.167]
Random effect	σ^2	SE	σ^2	SE
Specimen ID	0	0	0	0
5-fold: \bar{r}_s (range)	0.86 (0.62-1)		0.78 (0.39-0.95)	

[†] Reference category was forest

[‡] Density (km/km²) of corn-forest edges within the 100% MCP of each radio-tracked individual

[§] Proportion of corn fields within the 100% MCP of each radio-tracked individual

relatively high in their 100% MCP (negative Corn \times Corn-forest edge interaction; Tables 2 & 3). At night, striped skunks decreased their avoidance of corn fields when the proportion of corn fields increased within 100% MCPs (positive Corn \times Prop. corn interaction; Table 3). This avoidance further decreased with increasing density of striped skunks within 100% MCPs (positive Corn \times Density interaction; Table 3). In contrast, the selection of corn fields was not density-dependent during daytime.

Unlike striped skunks, raccoon selection of corn fields changed during night-time with conspecific density and either the density of corn-forest edges or the proportion of corn fields. The selection of corn fields increased when both conspecific density and density of corn-forest edges increased within 100% MCPs (positive Corn \times Density \times Corn-forest edge interaction; Table 2). For example, raccoons showed stronger selection for corn fields at a low density of conspecifics when their 100% MCP contained a relatively low density of corn-forest edges (Figure 1A). Conversely, at a high density of conspecifics, the selection for corn fields was stronger in 100% MCPs that encompassed a high rather than low density of corn-forest edges (Figure 1A). This model prediction (Figure 1A) strongly differs from what would have been expected without accounting for density-dependence in functional responses (Figure 1B). The selection of corn fields further decreased with both the density of conspecifics and the proportion of corn fields within 100% MCPs (negative Corn \times Density \times Prop. corn interaction; Table 2). For example, raccoons displayed stronger selection for corn fields when 100% MCPs were composed of a small rather than large proportion of corn fields, and this selection was the highest at a high density of conspecifics (Figure 2A). This prediction (Figure 2A) differs from a poorer model that would not account for density-dependence in functional responses (Figure 2B).

Given the observed patterns of habitat selection by both species, the probability of raccoon-striped skunk co-occurrence was highest in agricultural corridors (Figure 3).

4. Discussion

Our study provides empirical evidence that functional responses can be density-dependent. McLoughlin et al. (2010) emphasize the risk of applying habitat selection models for conservation and management, unless the models account for the influence that spatial

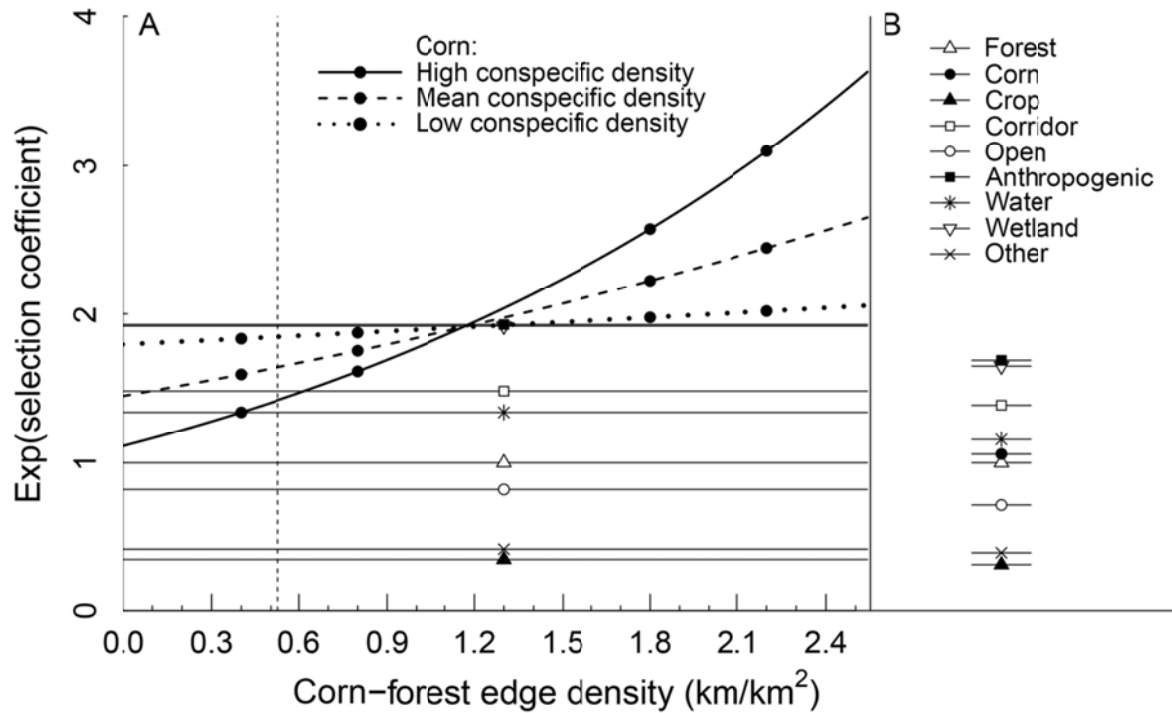


Figure 1. (A) Odd ratios (exp[selection coefficient]) of the resource selection function (RSF) predicting the occurrence of raccoons in corn fields during night-time as a function of the density of corn-forest edges at three levels of conspecific density within the 100% MCP (Model 11, Table 2). High density represents the value at 75th percentile in the distribution of conspecific density, which corresponds to a density of 26.8 individuals per 100 trap nights/km². Low density represents the value at 25th percentile in the distribution of conspecific density, which corresponds to a density of 13.1 individuals per 100 trap nights/km². Mean density represents the mean of conspecific density, which corresponds to a density of 19.2 individuals per 100 trap nights/km². The vertical dashed line corresponds to the mean density of corn-forest edges. (B) Odds ratios of the land cover selection model (Model 1, Table 1) of raccoons during night-time are shown as a comparison point.

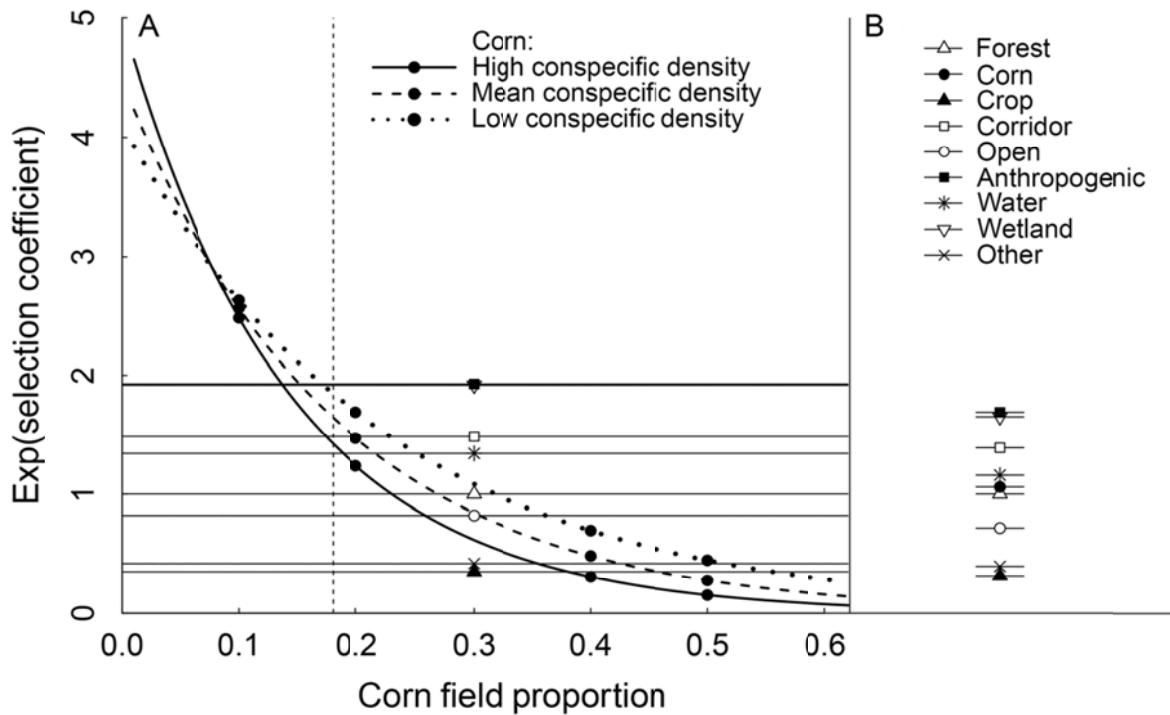


Figure 2. (A) Odd ratios ($\exp[\text{selection coefficient}]$) of the resource selection function (RSFs) predicting the occurrence of raccoons in corn fields during night-time as a function of the proportion of corn fields at three levels of conspecific density (Model 11, Table 2). High density represents the value at 75th percentile in the distribution of conspecific density, which corresponds to a density of 26.8 individuals per 100 trap nights/km². Low density represents the value at 25th percentile in the distribution of conspecific density, which corresponds to a density of 13.1 individuals per 100 trap nights/km². Mean density represents the mean of conspecific density, which corresponds to a density of 19.2 individuals per 100 trap nights/km². The vertical dashed line corresponds to the mean proportion of corn fields. (B) Odds ratios of the land cover selection model (Model 1, Table 1) of raccoons during night-time are shown as a comparison point.

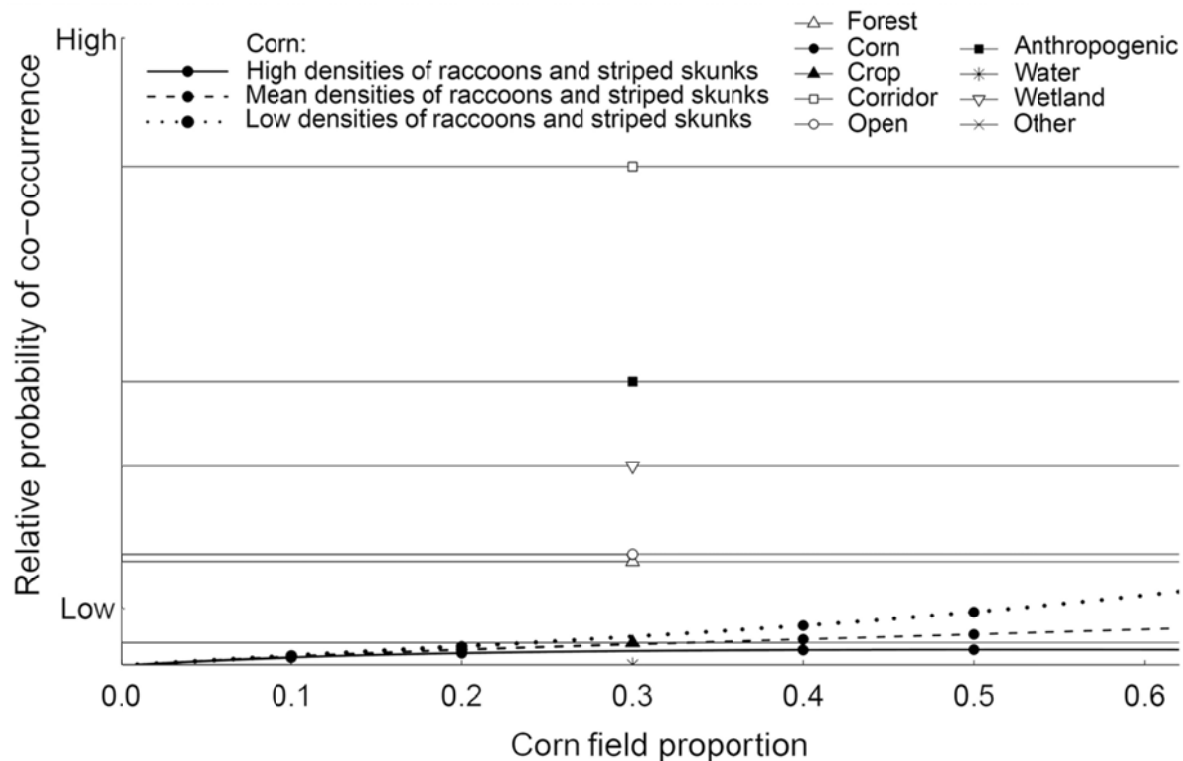


Figure 3. Relative probabilities of raccoon-striped skunk co-occurrence during night-time as a function of the proportion of corn fields at three levels of conspecific density. The relative probabilities of co-occurrence were estimated by multiplying the relative probability of occurrence of each species (Model 11, Table 2 for raccoons and Model 7, Table 3 for striped skunks). High density represents the value at 75th percentile in the distribution of raccoon and striped skunk densities, which corresponds to a density of 26.8 raccoons per 100 trap nights/km² and a density of 3.2 striped skunks per 100 trap nights/km². Low density represents the value at 25th percentile in the distribution of raccoon and striped skunk densities, which corresponds to a density of 13.1 raccoons per 100 trap nights/km² and a density of 1.8 striped skunks per 100 trap nights/km². Mean density represents the mean of raccoon and striped skunk densities, which corresponds to a density of 19.2 raccoons per 100 trap nights/km² and a density of 3 striped skunks per 100 trap nights/km².

variation in animal density and resource availability can have on habitat selection decisions. Our study supports their contention. We show that by integrating density-dependent functional responses of two of the main hosts of the raccoon rabies virus variant into RSFs, the models can more accurately identify landscape areas where hosts are most likely to occur at high densities. Given that areas of host aggregations correspond to areas of high risk of disease transmission, our study stresses the importance of accounting for density-dependent functional responses when planning control activities that are aimed at minimizing disease spread and persistence [*e.g.*, sample analyses from trappers, examination of road-killed animals, increase of public health monitoring (Sternler et al. 2009)].

Many studies have reported functional responses for various species (Myrsterud & Ims 1998, Mauritzen et al. 2003, Hebblewhite & Merrill 2008, Godvik et al. 2009, Herfindal et al. 2009, Gillies & St. Clair 2010, Moreau et al. 2012, Roever et al. 2012). We also detected functional responses in the selection of corn fields by raccoons and striped skunks. For example, when resting during the daylight hours, both species avoided corn fields more strongly in areas that contained high densities of corn-forest edges. In general, resting behavior of raccoons and striped skunks at day should coincide with the increasing use of forests as function of their availability in the landscape because these habitats offer numerous den sites and occasional prey items for both species (Gehrt 2003, Rosatte & Larivière 2003, Hwang et al. 2007, Wilson & Nielsen 2007).

Striped skunks displayed density-dependence in their selection of corn fields. During their nocturnal activities, when they are most active, striped skunks avoided corn fields less strongly in areas with high compared to low conspecific densities. Unlike raccoons, striped skunks are rather solitary animals that do not tend to aggregate in particular areas (Broadfoot et al. 2001, Houle et al. 2011). Nevertheless, this species would be more likely to encounter conspecifics in agricultural corridors than in corn fields, presumably because, unlike corn fields, the corridors that contain rock piles left by farmers, can accommodate numerous terrestrial insects, which constitute their main food source (Rosatte & Larivière 2003).

Functional responses and density-dependence in habitat selection are often studied separately, but our study is the first to our knowledge that integrates animal density into functional responses. The synergistic effects of variation in conspecific density and resource

availability on habitat selection were detected by incorporating an interaction term between the two factors. In areas of low raccoon densities, the relative probability of raccoon occurrence in corn fields was independent of corn-forest edge density. Conversely, at high raccoon densities, the selection of corn fields was the highest in areas with high densities of corn-forest edges and a low proportion of corn fields. This observation suggests that at high conspecific densities, raccoons tend to aggregate in areas where corn fields of small size are largely interspersed with forest patches. Similarly, Retamosa et al. (2008) found that smaller corn fields with a high proportion of their perimeter adjacent to forests tended to have higher rates of corn damage by raccoons than larger corn fields. Moreover, many studies have found that raccoon abundance is positively related to a high proportion of forest edges bordering corn fields in trapping sites (Pedlar et al. 1997, Heske et al. 1999, Beasley & Rhodes 2008, Houle et al. 2011). Our density-dependent functional responses further revealed that the spatial pattern of raccoons in landscapes with abundant corn-forest edges depends on the overall availability of corn fields and on conspecific density.

4.1. Implications for disease transmission

The lack of accurate knowledge regarding the spatio-temporal dynamics of raccoons and striped skunks in landscapes that are fragmented by agriculture is such that oral vaccine baits are often distributed homogeneously (Boyer et al. 2011) over large areas (Slate et al. 2005). To have the greatest effect at the lowest cost, a maximum number of potential hosts should come across vaccine baits. Whereas surveillance activities are partly associated with human population densities and local health expenditures (Childs et al. 2007), the efficiency of disease control programs strongly relies upon an accurate identification of areas with high host densities where epizootic risk is highest (Houle et al. 2011, Rees et al. 2011a). We show that the omission of density-dependence in functional responses may lead to poor predictions of host spatio-temporal distributions, which might result in vaccination campaigns that do not target the best areas. For example, a model without density-dependent functional responses would have predicted that the risk of encounter between raccoons should be highest in anthropogenic areas and wetlands (Figures 1B & 2B). In contrast, our density-dependent functional responses revealed that high raccoon densities are most likely to occur in areas with high densities of corn-forest edges and a low proportion of corn fields (Figures 1A & 2A).

These areas are therefore likely to contribute substantially to rabies outbreaks and to the spread of the virus through more frequent contacts between raccoons.

When infectious diseases infect more than one host species (Woolhouse et al. 2001), the rate of disease transmission depends upon the distributional dynamics of all hosts (Holt et al. 2003). Some host species can have a strong impact on pathogen spread and act as the main reservoir of infection (Haydon et al. 2002, Lembo et al. 2008, Streicker et al. 2013). In the case of the raccoon rabies virus variant, raccoons are the main hosts and can infect striped skunks (Guerra et al. 2003). The density of oral vaccine baits should therefore be distributed not only in proportion to the relative probability of occurrence of each host species, as expected from density-dependent functional responses in habitat selection, but also based on the relative probability of co-occurrence of the two species to reduce the risk of cross-species contamination. Based on this information, together with predictions from the top-ranking raccoon and striped skunk RSFs, we suggest that oral vaccine baits should not be evenly spread; rather, they should be deployed at relatively high densities at the edges of corn fields bordering forests, and along agricultural corridors in areas with high densities of corn-forest edges and a low proportion of corn fields during the corn maturation stage.

In agriculturally fragmented landscapes, the plasticity in selection of corn fields by raccoons and striped skunks is linked to changes in both conspecific density and the spatial structure or availability of corn fields. Consequently, these factors must be taken into consideration when devising control and prevention plans that would increase the efficiency of vaccination operations against rabies. Our study shows that wildlife managers and epidemiologists can benefit from considering density-dependence in functional responses of habitat selection by increasing their ability to predict the spatial distribution of infectious disease hosts.

5. Supplemental material

Table S1. Definition of landscape covariates that were included in resource selection functions (RSFs) and used to test the combined effects of density-dependence and functional responses on habitat selection by raccoons and striped skunks in each period of the day (day vs. night) in the Montérégie and Estrie regions, Québec, Canada

Variable	Description	Range
Forest	Forest patches	1 or 0
Corn	Corn fields	1 or 0
Crop	Crop fields including cereal fields (oat, wheat, soybean, hay, and barley) and vegetable and fruit crops	1 or 0
Corridor	Agricultural corridors (10-m buffer around each agricultural field, i.e., corn and crop fields)	1 or 0
Open	Open-uncultivated areas (grasslands and wastelands)	1 or 0
Anthropogenic	Anthropogenic areas with food for raccoons and striped skunks (commercial and industrial areas, housing areas, garbage dumps, and campgrounds)	1 or 0
Water	Water bodies (lakes, rivers, and streams)	1 or 0
Wetland	Riparian areas (20-m buffer around each water body, i.e., lake, river, and stream) and wetlands	1 or 0
Other	Anthropogenic areas without food for raccoons and striped skunks (quarries and gravel-pits)	1 or 0
Density	Relative abundance (number of unique individuals captured per 100 trap nights) of raccoons in the 100% MCP of each radio-tracked individual or Relative abundance (number of unique individuals captured per 100 trap nights) of striped skunks in the 100% MCP of each radio-tracked individual	6.36-27.45 0.88-6.25

Corn-forest edge	Density (km/km ²) of forest edges bordering corn fields in the 100% MCP of each radio-tracked individual	0-2.5
Prop. corn	Proportion of corn fields in the 100% MCP of each radio-tracked individual	0-0.69

Table S2. List of candidate resource selection functions (RSFs) for raccoons during each period of the day (day vs. night) in the Montérégie and Estrie regions, Québec, Canada. The number of parameters (K), Akaike’s Information Criterion (AIC), AIC differences (Δ AIC), AIC weights (ω), and average Spearman rank correlation (\bar{r}_s) of 5-fold cross-validation are presented. The selected models are identified in bold.

No.	Candidate model	K	AIC	Δ AIC	ω	\bar{r}_s
<i>Night</i>						
11	Density-dependence model + Corn \times Corn-forest edge + Corn \times Prop. corn + Corn \times Density \times Corn-forest edge + Corn \times Density \times Prop. corn	16	62263.0	0.00	0.997	0.97
10	Density-dependence model + Corn \times Prop. corn + Corn \times Density \times Prop. corn	14	62274.6	11.61	0.003	0.97
8	Density-dependence model + Corn \times Corn-forest edge + Corn \times Prop. corn	14	62282.8	19.88	0.000	0.97
7	Density-dependence model + Corn \times Prop. corn	13	62286.6	23.64	0.000	0.97
5	Land cover selection model + Corn \times Corn-forest edge + Corn \times Prop. corn	13	62297.2	34.27	0.000	0.97
4	Land cover selection model + Corn \times Prop. corn	12	62298.3	35.28	0.000	0.97
9	Density-dependence model + Corn \times Corn-forest edge + Corn \times Density \times Corn-forest edge	14	62902.5	639.54	0.000	0.93
6	Density-dependence model + Corn \times Corn-forest edge	13	62915.2	652.22	0.000	0.98
2	Land cover selection model + Corn \times Density	12	62932.8	669.81	0.000	0.85
3	Land cover selection model + Corn \times Corn-forest edge	12	62937.4	674.47	0.000	0.91
1	Land cover selection model	11	62951.0	688.05	0.000	0.95

<i>Day</i>						
11	Density-dependence model + Corn × Corn-forest edge + Corn × Prop. corn + Corn × Density × Corn-forest edge + Corn × Density × Prop. corn	16	30224.9	0.00	0.331	0.98
6	Density-dependence model + Corn × Corn-forest edge	13	30226.3	1.44	0.161	0.98
3	Land cover selection model + Corn × Corn-forest edge	12	30226.3	1.46	0.159	0.98
8	Density-dependence model + Corn × Corn-forest edge + Corn × Prop. corn	14	30227.1	2.23	0.109	0.98
10	Density-dependence model + Corn × Prop. corn + Corn × Density × Prop. corn	14	30227.7	2.89	0.078	0.98
5	Land cover selection model + Corn × Corn-forest edge + Corn × Prop. corn	13	30227.9	3.08	0.071	0.98
9	Density-dependence model + Corn × Corn-forest edge + Corn × Density × Corn-forest edge	14	30228.3	3.43	0.059	0.98
7	Density-dependence model + Corn × Prop. corn	13	30230.5	5.69	0.019	0.98
2	Land cover selection model + Corn × Density	12	30232.5	7.66	0.007	0.97
4	Land cover selection model + Corn × Prop. corn	12	30234.6	9.79	0.002	0.98
1	Land cover selection model	11	30234.7	9.88	0.002	0.98

Table S3. List of candidate resource selection functions (RSFs) for striped skunks during each period of the day (day vs. night) in the Montérégie and Estrie regions, Québec, Canada. The number of parameters (K), Akaike’s Information Criterion (AIC), AIC differences (Δ AIC), AIC weights (ω), and average Spearman rank correlation (\bar{r}_s) of 5-fold cross-validation are presented. The selected models are identified in bold.

No.	Candidate model	K	AIC	Δ AIC	ω	\bar{r}_s
<i>Night</i>						
7	Density-dependence model + Corn \times Prop. corn	10	1933.0	0.00	0.333	0.86
11	Density-dependence model + Corn \times Corn-forest edge + Corn \times Prop. corn + Corn \times Density \times Corn-forest edge + Corn \times Density \times Prop. corn	13	1933.2	0.24	0.295	0.86
8	Density-dependence model + Corn \times Corn-forest edge + Corn \times Prop. corn	11	1934.4	1.46	0.161	0.86
10	Density-dependence model + Corn \times Prop. corn + Corn \times Density \times Prop. corn	11	1934.7	1.71	0.142	0.86
2	Land cover selection model + Corn \times Density	9	1938.9	5.97	0.017	0.89
1	Land cover selection model	8	1939.3	6.30	0.014	0.89
9	Density-dependence model + Corn \times Corn-forest edge + Corn \times Density \times Corn-forest edge	11	1940.0	6.99	0.010	0.89
3	Land cover selection model + Corn \times Corn-forest edge	9	1940.4	7.44	0.008	0.88
4	Land cover selection model + Corn \times Prop. corn	9	1940.7	7.70	0.007	0.87
5	Land cover selection model + Corn \times Corn-forest edge + Corn \times Prop. corn	10	1940.7	7.77	0.007	0.88
6	Density-dependence model + Corn \times Corn-forest edge	10	1940.8	7.85	0.007	0.89

<i>Day</i>						
9	Density-dependence model + Corn × Corn-forest edge + Corn × Density × Corn-forest edge	10	725.6	0.00	0.553	0.79
11	Density-dependence model + Corn × Corn-forest edge + Corn × Prop. corn + Corn × Density × Corn-forest edge + Corn × Density × Prop. corn	12	727.4	1.89	0.215	0.77
6	Density-dependence model + Corn × Corn-forest edge	9	728.6	2.99	0.124	0.78
8	Density-dependence model + Corn × Corn-forest edge + Corn × Prop. corn	10	730.5	4.98	0.046	0.77
3	Land cover selection model + Corn × Corn-forest edge	8	731.7	6.11	0.026	0.78
5	Land cover selection model + Corn × Corn-forest edge + Corn × Prop. corn	9	732.7	7.16	0.015	0.74
10	Density-dependence model + Corn × Prop. corn + Corn × Density × Prop. corn	10	733.0	7.43	0.013	0.75
2	Land cover selection model + Corn × Density	8	736.2	10.64	0.003	0.66
1	Land cover selection model	7	736.3	10.77	0.003	0.62
7	Density-dependence model + Corn × Prop. corn	9	737.8	12.23	0.001	0.65
4	Land cover selection model + Corn × Prop. corn	8	738.2	12.62	0.001	0.63

CHAPITRE 3

Individual-based models reveal a functional link between the risk of disease spread, conspecific density, and landscape connectivity

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Résumé

Dans beaucoup de systèmes hôtes-pathogènes, la transmission de pathogènes requiert des contacts directs entre des individus hôtes infectés et sains. Les taux de contacts *per capita* peuvent fortement dépendre des patrons de déplacement des individus dans le paysage. La connectivité fonctionnelle peut donc influencer les interactions entre des individus. Cependant, peu d'études ont exploré le lien fonctionnel entre les taux de contacts, la densité de congénères et la connectivité du paysage. En construisant un modèle spatialement explicite basé sur l'individu, nous avons examiné comment des règles empiriques de déplacement font émerger des patrons spatiaux de taux de contacts chez des hôtes potentiels de maladies infectieuses dans des paysages hétérogènes. Dans un premier temps, nous avons développé des modèles dynamiques de connectivité fonctionnelle en caractérisant les comportements de déplacement de rats laveurs munis de colliers GPS, qui sont les principaux hôtes d'un variant du virus de la rage. Les rats laveurs porteurs de colliers GPS étaient plus susceptibles de choisir des grandes parcelles d'habitat qui étaient atteintes en traversant des chemins de moindre coût, et avaient des temps de résidence relativement longs dans les zones anthropiques, en particulier durant le jour. Dans un deuxième temps, nous avons utilisé ces règles empiriques de déplacement afin de simuler les déplacements de rats laveurs dans différents paysages virtuels qui différaient dans la densité de congénères, de même que dans la disponibilité des forêts et l'arrangement spatial de corridors agricoles. Les simulations ont révélé trois patrons dans les taux de contacts. Premièrement, une petite portion de rats laveurs simulés était responsable de la plupart des contacts dans les paysages virtuels, un patron qui émergeait malgré que tous les rats laveurs simulés obéissaient aux mêmes règles de déplacement. Deuxièmement, les taux de contacts *per capita* augmentaient linéairement avec la densité de congénères dans la plupart des paysages virtuels, ce qui indique que la transmission de la rage du raton laveur devrait dépendre de la densité d'individus infectés plutôt que de la proportion d'individus infectés. Troisièmement, l'impact de la connectivité fonctionnelle sur les taux de contacts *per capita* variait fortement entre les paysages virtuels. La relation pouvait être positive, négative, ou quadratique selon le type de milieu où les taux de contacts avaient lieu et sa disponibilité dans le paysage. Notre étude montre que des règles empiriques de déplacement peuvent résulter en des patrons spatiaux complexes de taux de contacts. La forte hétérogénéité spatiale observée dans les taux de contacts montre que l'efficacité d'interventions de contrôle

particulière peut fortement varier selon la densité de congénères, la composition du paysage et la connectivité fonctionnelle. Notre étude établit des relations fonctionnelles qui permettent d'ajuster ces interventions aux changements du paysage.

Abstract

In many host-pathogen systems, pathogen transmission requires close contact between infectious and susceptible hosts. The contact rates among individuals depend upon how they move in the landscape. Functional connectivity can thus affect interactions between individuals. Yet few studies have explored the interplay between contact rates, conspecific density, and functional connectivity. Using a spatially explicit individual-based model, we investigated how empirical movement rules translate into spatial patterns of contact rates among disease hosts in complex landscapes. We developed dynamic models of functional connectivity by characterizing movement behaviors of radio-collared raccoons, which are the main hosts of the raccoon rabies virus. On this basis, we simulated space-use dynamics of raccoons in virtual landscapes varying in conspecific density, forest availability, and landscape connectivity. We then characterized spatial patterns in the density of per capita contact rates of simulated raccoons. Radio-collared raccoons were more likely to choose large habitat patches that were reached by traveling along least-cost paths, and had relatively long residence times in anthropogenic areas, especially during daytime. These movement rules that were applied to simulated raccoons in virtual landscapes revealed three key patterns in contact rates. First, few simulated raccoons were responsible for most contacts between individuals, a pattern that emerged even though all simulated raccoons obeyed the same movement rules. Second, per capita contact rates increased linearly with population density under most conditions, which indicates that raccoon rabies transmission should be density-dependent rather than frequency-dependent. Third, functional connectivity created a broad range of patterns in the density of per capita contact rates from decreasing to increasing values, depending upon the availability of land cover types. Overall, the contacts between hosts tended to occur at highest densities in forests, anthropogenic areas, and agricultural corridors. We show that complex patterns of contact rates can emerge from simple empirical movement rules and, therefore, can be key drivers of disease spread dynamics. The strong spatial heterogeneity observed in contact rates implies that the effectiveness of particular control interventions can strongly vary depending upon host density, landscape composition, and functional connectivity. This study provides key functional relationships for tailoring interventions to landscape changes.

1. Introduction

Quantifying contact rates among individual hosts is fundamental for predicting the dynamics of infectious disease spread in wild populations and, thus, for developing cost-effective disease control strategies (Cross et al. 2012, Craft 2015). In particular, the pathogen transmission rate depends upon the rate at which an individual host comes into contact with another individual, and the probability that such contact is infectious (Begon et al. 2002). Simple mathematical formulations of disease transmission dynamics predict that contact rates either increase linearly with population density (density-dependent transmission), or are constant irrespective of population density, leading to frequency-dependent transmission (McCallum et al. 2001). Empirical studies have shown, however, that contact rates could follow a nonlinear relationship in which contact rates increase with population density but become saturated at high density (Ramsey et al. 2002, Ji et al. 2005, Habib et al. 2011), implying that pathogen transmission dynamics in wildlife often lie between extreme assumptions of density-dependent and frequency-dependent transmission (Smith et al. 2009b). Although previous research has shown that this nonlinearity could be driven by changes in host behavior that is associated with social group ranges (Habib et al. 2011) or individual home ranges after density reduction (Ramsey et al. 2002), the role of spatial heterogeneity in shaping such patterns of disease transmission remains unclear.

To optimize control interventions, quantifying variation in contact rates among individual hosts and across space is needed (Paull et al. 2011); some individuals in the landscape can have a disproportionately high number of contacts compared to the mean, which can cause “superspreading” events over large scales (Lloyd-Smith et al. 2005). For example, Woolhouse et al. (1997) proposed the 20/80 rule, wherein $\approx 20\%$ of infected hosts (known as “superspreaders”) are responsible for 80% of infection transmission in host-pathogen systems. Although biological characteristics of individual hosts such as age, sex, body condition, behavior, and genetic diversity have been recognized as being significant sources of variation in contact rates by affecting individual susceptibility and competence (Wilson et al. 2001), few studies have assessed the interplay between host contact rates and landscape physiognomy. Knowledge of the interactions between contact rates and landscape characteristics can directly inform on the likely locations of hotspots for pathogen transmission.

In heterogeneous landscapes, maintaining connectivity between habitat patches is important for biodiversity conservation (Fahrig & Merriam 1985), but could also enhance the spread and transmission of infectious diseases. For example, in the Great Plains of North America (Canada and USA), sylvatic plague (*Yersinia pestis*) was more likely to spread among colonies of black-tailed prairie dogs (*Cynomys ludovicianus*) that were spatially close together and located in close proximity to dispersal corridors (Collinge et al. 2005, Johnson et al. 2011). Landscape connectivity can affect disease transmission and spread because it determines the spatial dynamics of animal movement and the contact risk among potential hosts (Meentemeyer et al. 2012).

In landscapes where high-quality habitat patches can be delimited over space, mobile animals must decide how long to remain within a patch, where to go next, and how to get there. These decisions can strongly depend upon the structural and functional connectivity of the landscape (Dancose et al. 2010, Courbin et al. 2014). Structural connectivity describes the physical links between habitat patches, such as the Euclidean distance between them (Tischendorf & Fahrig 2000, Kindlmann & Burel 2008). Animals, however, do not necessarily navigate between high-quality patches along straight paths. Functional connectivity accounts for the adjustment of animal movements to the characteristics of the surrounding matrix (Taylor et al. 1993, Dancose et al. 2010). Although such fine-scale movements can directly alter the contact rates between individual hosts (Tracey et al. 2014), studies of spatial dynamics of infectious diseases rarely consider functional connectivity. This oversight could affect our understanding of pathogen transmission and spread processes in heterogeneous landscapes. A modeling tool that incorporates functional connectivity could improve the ability to anticipate the spatial dynamics of disease spread and transmission in wildlife populations.

Spatially explicit individual-based models (IBMs) provide a modeling framework to simulate complex dynamic systems where emergent phenomena can be observed (Railsback 2001, Matthews et al. 2007). In spatially explicit IBMs, individuals are represented as mobile entities that interact with their environment and other individuals (Grimm & Railsback 2005). The advantage of IBMs is that they can integrate stochastic and spatially dependent processes at the individual level that are difficult to quantify empirically (DeAngelis & Mooij 2005).

Consequently, IBMs have been largely used for modeling animal movement in heterogeneous landscapes (Kramer-Schadt et al. 2004, Palmer et al. 2011, Tracey et al. 2014).

In this study, we built an IBM to assess how changes in conspecific density, landscape composition, and functional connectivity alter contact rates between individual hosts. To do this, we integrated components of space use in the IBM by estimating from empirical data, residence time within high-quality habitat patches and choice of the next high-quality patch, and by simulating intra- and inter-patch movements in different virtual landscapes that differed in habitat availability and landscape connectivity. The model has been constructed for raccoons (*Procyon lotor* L.), one of the main hosts of the raccoon rabies virus variant in North America (Finnegan et al. 2002).

2. Materials and Methods

2.1. Simulated landscapes and individuals

To assess the influence of changes in landscape composition and functional connectivity, we developed an IBM using Netlogo version 5.0.5 (Wilensky 1999) and simulated the movement of raccoons in 15 virtual landscapes differing in terms of forest proportion and spatial arrangement of agricultural corridors (Figure 1). These two landscape components were defined from agriculturally fragmented landscapes in the Montérégie region of southern Québec (Canada), where 104 rabies cases had been reported between 2006 and 2009 (Côté et al. 2012).

The virtual landscapes consisted of 1000×1000 cells and had an extent of 100 km². We defined cells of 10×10 m, which corresponds to the minimal width of agricultural corridors that were delimited by 10-m buffers around agricultural fields by Tardy et al. (2014). The set of adjacent cells that were composed of the same land cover type defined a habitat polygon. Each cell was also identified by its centroid and was characterized by state variables referring to habitat polygons to which they belonged, *i.e.*, the unique ID number of the polygon, size of the polygon, and movement cost. The virtual landscapes were comprised of eight land cover types that are typical of agriculturally fragmented landscapes: forests, corn (maize) fields, other crops (including vegetable and fruit crops, together with cereal fields such as oat, wheat,

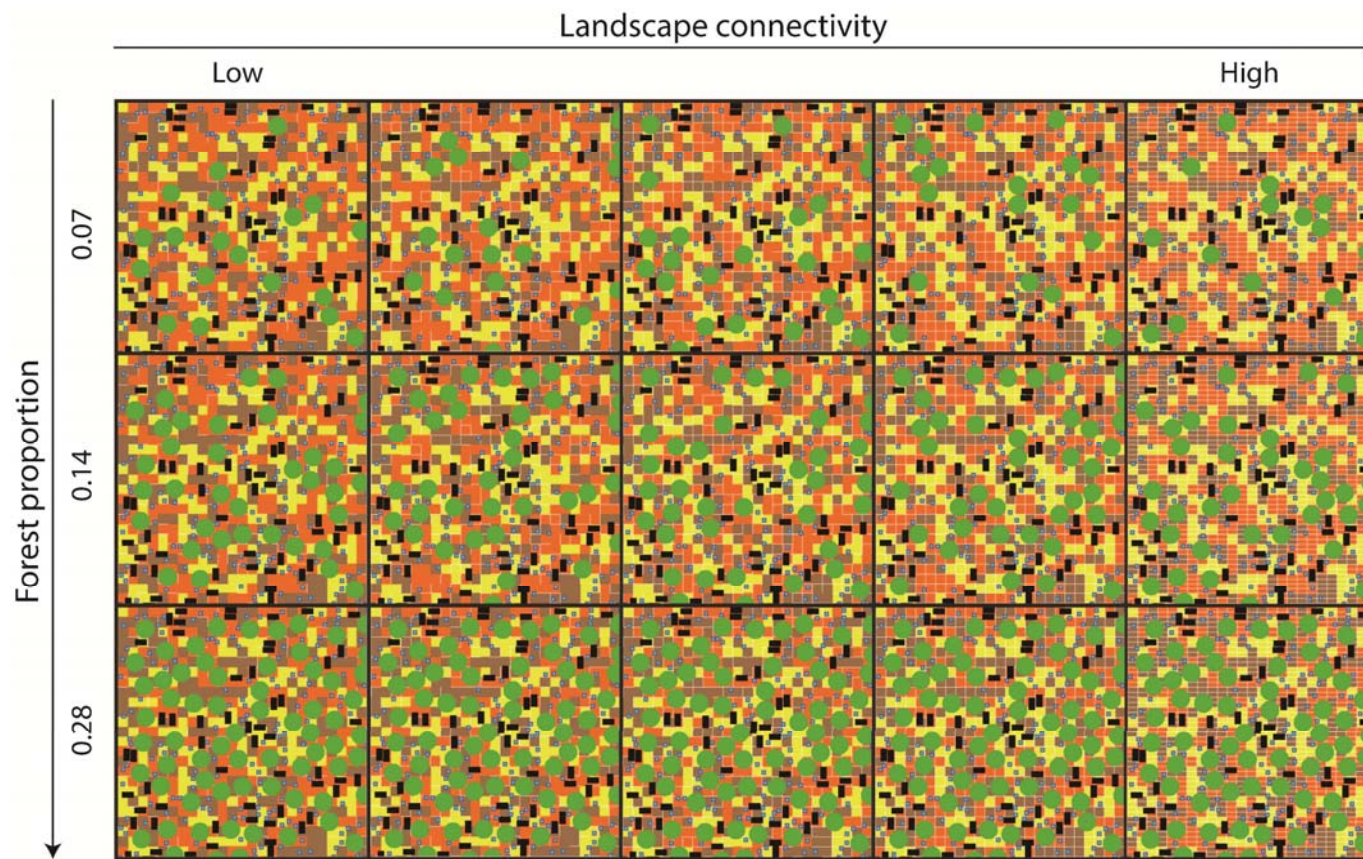


Figure 1. 15 virtual landscapes were simulated that differed in forest proportion and spatial arrangement of agricultural corridors (represented by a white grid). The random configurations of agricultural corridors were built by randomly removing 25 %, 50 %, and 75 % of grid square edges; the two systematic configurations were defined by varying the length/width ratio of grid squares (ratio = 1:1; ratio = 2:1). The virtual landscapes were composed of eight land cover types: forests (represented in green), cornfields (yellow), crops (orange), open-uncultivated areas (brown), water bodies (cyan), wetlands (blue), anthropogenic areas (black), and agricultural corridors (white). Landscape connectivity was defined as the average number of agricultural corridors connecting polygons of a given land cover type in the virtual landscape.

soybean, hay, and barley), open-uncultivated areas, water bodies (lakes), wetlands (including riparian areas around lakes), anthropogenic areas, and agricultural corridors (Figure 1).

Using a grid pattern to represent agricultural corridors, we defined two systematic arrangements of agricultural corridors by varying the length/width ratio of grid squares: ratio = 1:1 (*i.e.*, length/width = 20/20 cells, which result in a grid of 50×50 squares) and ratio = 2:1 (*i.e.*, length/width = 20/10 cells, which result in a grid of 50×100 squares). A grid square was composed of several cells. The 2:1 ratio corresponded to the highest ratio of agricultural fields that is observed in the Montérégie region, and was estimated from satellite images of the Montérégie region that were acquired in 2011 by the Financière Agricole du Québec. By using the 1:1 ratio as the reference grid, we also drew three random arrangements of agricultural corridors by randomly removing 25 %, 50 %, and 75 % of square sides in the grid. Landscape connectivity was defined as the average number of agricultural corridors connecting polygons of a given land cover type in the virtual landscapes (similar to the measure of “node degree” in a network; Rayfield et al. 2010). In agriculturally fragmented landscapes, agricultural corridors are used by raccoons to move between habitat patches (Tardy et al. 2014). In addition, we included three levels of forest proportion: 0.7, 0.14, and 0.28. The proportion of 0.14 corresponded to the mean proportion of forests that is observed in the Montérégie region. The total areas of forests (11.16 ha), anthropogenic areas (3.07 ha), and wetlands (0.28 ha) did not change between the virtual landscapes, and were estimated from 1:15,000 scale aerial photographs of the Montérégie region that had been taken in 1999 by the Ministère des Ressources Naturelles et de la Faune (Québec Ministry of Natural Resources and Wildlife). While the proportion of anthropogenic areas, wetlands, and lakes remained constant in the virtual landscapes, variation in the proportions of cornfields, crops and open-uncultivated areas resulted from gradients in forest proportion and corridor arrangement (Figure S1).

Simulated individuals were raccoons and were characterized by a unique ID number, a unique ID number of habitat polygon, and coordinates of the cell centroid where they were located during a simulation, departure and arrival time in the habitat polygons. The individuals were also defined by state variables that were linked to the components of space use, *i.e.*, residence time within the high-quality habitat polygons, unique ID number of the next high-quality polygon that would be visited, and the list of cells that would be traversed to go to the

next polygon. To assess the influence of changes in conspecific density, we varied four levels of density of simulated raccoons in each virtual landscape: 0.1, 1, 5, and 10 raccoons/km².

2.2. Modeling of space use components

To model mechanisms of functional connectivity, land cover types of virtual landscapes were summarized as high-quality habitat polygons and the habitat matrix (Dancose et al. 2010). We considered polygons of forests, cornfields, anthropogenic areas, and wetlands as high-quality polygons because these land cover types are rich in resources and are strongly selected by raccoons (Tardy et al. 2014). Agricultural corridors and the other land cover types (*i.e.*, crops, open-uncultivated areas, and lakes) represented the matrix, as these land cover types either are used by raccoons to move within the landscape or are avoided (Tardy et al. 2014). We built four submodels to integrate the components of space use in the IBM: 1) residence time in the high-quality polygons, 2) movement within the high-quality polygons, 3) choice of the next high-quality polygon, and 4) movement between the high-quality polygons. The parameters that were included in the submodels were estimated from empirical data. These data were obtained through Global Positioning System (GPS)-based tracking of 54 raccoons from 2009 to 2011 in two areas of southern Québec, Canada. The first area was located in the Montérégie region (45°23'23''N, 73°06'05''W), and the second, in the Estrie region (45°28'54''N, 71°40'05''W). Both areas were spatially near and had habitat characteristics that were similar to the areas where rabid raccoons had been detected. More details are given in Tardy et al. (2014) (section “Monitoring of habitat selection by raccoons”).

2.2.1. Residence time in high-quality polygons

In the IBM, each simulated raccoon moves within a high-quality polygon until a predetermined residence time in the polygon is exceeded. From GPS locations (2-h relocation interval), we assessed habitat characteristics that influence average time (in hours) spent by raccoons in the high-quality polygons. As proposed by Bastille-Rousseau et al. (2011), residence time was defined as the duration from the arrival of individuals to their departure from a polygon, and was estimated by considering the number of successive GPS locations along parts of the movement path entering and leaving a polygon. To correct for missing GPS locations (48 %) often caused by forest cover interference, each location was adjusted by a

weighting factor (Frair et al. 2010) that was defined by 1/elapsed time (in hours) between the location at time t and the location at time $t - 1$ (the weighting factor for the first location of each radio-collared raccoon was equal to 0). The weighting factor was varied between 0 and 1. In this way, the locations that were close in time had a greater influence in the estimation of model parameters. We built a linear mixed-effects model to estimate residence time as a function of habitat characteristics. The model included a random intercept for “individual” nested within “year” to account for the hierarchical structure of the data, to account for the unbalanced number of observations among raccoons, and to accommodate for non-independence of observations of the same raccoon within a given year (Gillies et al. 2006). The linear mixed-effects model had the following general structure:

$$y_{ikt}(\mathbf{x}) = \beta_0 + \beta_{\text{Land cover}} x_{\text{Land cover } ikt} + \beta_{\text{Area}} x_{\text{Area } ikt} + \beta_{\text{Land cover} \times \text{Area}} x_{\text{Land cover } ikt} x_{\text{Area } ikt} + \beta_{\text{Land cover} \times \text{Time}} x_{\text{Land cover } ikt} x_{\text{Time } ikt} + \gamma_{0 kt}$$

where $y_{ikt}(\mathbf{x})$ represents the log-transformed residence time in high-quality polygon i for raccoon k within year t , β_0 is the mean intercept, β are coefficients for covariates x , and $\gamma_{0 kt}$ is the random intercept associated with raccoon k nested within year t . The dependent variable was log-transformed to improve the normality of its distribution. The term $x_{\text{Land cover } ikt}$ corresponds to the land cover type (*i.e.*, forest, cornfield, anthropogenic area, or wetland) of high-quality polygon i for raccoon k within year t (coded as a dichotomous covariate). The term $x_{\text{Area } ikt}$ is the log-transformed area (ha) of high-quality polygon i for raccoon k within year t . This covariate was also standardized by subtracting its means and dividing by its standard deviation to improve model convergence and to reduce collinearity between interaction terms (Quinn & Keough 2002). We dropped the “Wetland \times Area” interaction because it caused multicollinearity (variance inflation factor > 10 ; Dormann et al. 2013). The term $x_{\text{Time } ikt}$ represents either the day (coded as 1) or night (coded as 0) period during which raccoon k within year t is in high-quality polygon i . Like Forester et al. (2009), we included this covariate as an interaction term to capture variation in residence time during the time period (night and day). Further, we added a variance structure to stabilize residual heteroscedasticity by allowing for variance increases or decreases with predicted values

(Pineiro & Bates 2000). Normality of random effects and residuals, together with variance homogeneity, were respected. The model estimates were computed with the package *nlme* of R statistical software (R Development Core Team 2012).

2.2.2. Movement within high-quality polygons

In the IBM, movement of simulated raccoons within high-quality polygons was modeled as a random walk model (Turchin 1998). We randomly selected a random step from the turning angle (*i.e.*, degree of directionality between the current and previous step) distribution (range = 0-360°) of radio-collared raccoons that was specific to each high-quality land cover type and time period (day: mean = 179° for forests, 193° for cornfields, 174° for anthropogenic areas, 177° for wetlands; night: mean = 180° for forests, 179° for cornfields, 171° for anthropogenic areas, 191° for wetlands). In the IBM, each simulated raccoon randomly moved into one of eight adjacent cells from their current cell.

2.2.3. Choice of the next high-quality polygon

Once a simulated raccoon left a high-quality polygon, the individual had to choose which high-quality polygon to visit next. We first calculated the relative probability of use of all available high-quality polygons that were situated within a 2-km buffer around the simulated raccoon, and then the simulated raccoon moved to the polygon with the highest relative probability of use. The probabilities that were considered in the IBM were determined from an empirical model. We used sequences of GPS locations (2-h relocation interval) from radio-collared raccoons to characterize their successive use of high-quality polygons. Following the approach proposed by Dancose et al. (2010), we identified a high-quality polygon that contained at least one GPS location (*i.e.*, the source polygon) and the high-quality polygons that were visited next (*i.e.*, the destination polygon). Each destination polygon was then matched with 10 random high-quality polygons selected within a 2-km radius of the source polygon to estimate availability of landscape attributes. The 2-km buffer encompassed > 99 % of distances between the source and destination polygons. We contrasted habitat characteristics of destination (score = 1) and associated random (score = 0) polygons by using conditional logistic regressions, in which each stratum included one destination polygon and its 10 associated random polygons (Fortin et al. 2005a, Dancose et al. 2010). All strata for a given

radio-collared raccoon nested within a given year were assigned to a unique cluster to obtain robust standard errors (Fortin et al. 2005a). The model had the following general structure:

$$w_{jkt}(\mathbf{x}) = \exp(\beta_{\text{Land cover}} x_{\text{Land cover } jkt} + \beta_{\text{Area}} x_{\text{Area } jkt} + \beta_{\text{Cost}} x_{\text{Cost } ijkt} + \beta_{\text{Land cover} \times \text{Residence}} x_{\text{Land cover } jkt} x_{\text{Residence } ikt})$$

where $w_{jkt}(\mathbf{x})$ represents the relative probability of use of destination or random polygon j for raccoon k within year t , and β are coefficients for covariates x . The term $x_{\text{Land cover } jkt}$ corresponds to the land cover type (*i.e.*, forest, cornfield, anthropogenic area, or wetland) of destination or random polygon j for raccoon k within year t (coded as a dichotomous covariate). The term $x_{\text{Area } jkt}$ is the log-transformed area (ha) of destination or random polygon j for raccoon k within year t . We dropped the “Wetland \times Area” interaction because it caused multicollinearity (variance inflation factor > 10 ; Dormann et al. 2013). The term $x_{\text{Cost } ijkt}$ is the log-transformed cost of the least-cost path (LCP) between source polygon i in which raccoon k within year t is located and destination or random polygon j . By using the cost index during nighttime or daytime for each land cover type (see the section “Movement between high-quality polygons” for details), the LCP cost was calculated by summing the cost value of each landscape cell along the radio-collared raccoon path (O’Brien et al. 2006). The term $x_{\text{Residence } ikt}$ is the log-transformed residence time (in hours) in source polygon i in which raccoon k within year t is located (see the section “Residence time in high-quality polygons” for details). This covariate was not included as a simple effect in the model, but as an interaction term because each destination polygon and its 10 associated random polygons were assigned with the same log-transformed residence time (Fortin et al. 2009). We built models for each land cover type of source polygons by using the package *clogit* of R statistical software (R Development Core Team 2012). We evaluated model robustness by using 5-fold cross-validation that was adapted for case-control designs (see Fortin et al. 2009 for details). We performed the procedure 100 times to obtain average Spearman rank correlations (\bar{r}_s) for which a high \bar{r}_s indicates high predictive power.

2.2.4. Movement between high-quality polygons

The simulated raccoons followed the LCP between the cell in which they were located during the simulation and the next high-quality polygon to move towards this polygon. To build the LCP, we defined a resistance surface, which represents the relative costs of moving that are associated with each land cover type (Remais et al. 2010). Similarly to O'Brien et al. (2006), the resistance surface was generated by taking the inverse of the odds ratio ($1/\exp[\text{selection coefficient}]$) of the land cover selection model in Tardy et al. (2014) for day and night. Each land cover type was thus assigned to a cost value during nighttime or daytime (Table S1). We used the A-star search algorithm to find the “best” LCP between the cell where the simulated raccoon was located during the simulation and all cells situated at the edge of the next high-quality polygon (Hart et al. 1968). This algorithm has the advantage to be faster than Dijkstra's algorithm because it reduces the search space of the LCP by considering only the cells that have a greater chance of appearing in the path (Soltani et al. 2002).

2.3. Simulation experiments and data analysis

The IBM evolved according to discrete 3-minute time steps. We used this temporal scale because preliminary analyses have shown that radio-collared raccoons moved at a rate of about 200 m/h (as also reported by Rosatte et al. 2010). Thus, simulated raccoons should take about three minutes to cross a 10-m cell. In agriculturally fragmented landscapes in southern Québec, corn (*Zea mays* L.) is the main food source of raccoons (Rivest & Bergeron 1981) when it becomes available (about 1 August – 15 October). Instead of scaling the temporal extent over the entire period of corn maturation, we ran our model over four weeks (28 days) from 1 August because home range size of radio-collared raccoons remained stable during this period (Figure S2). At the beginning of each simulation, the time counter and then the cells of the virtual landscape were initialized. The time counter started 1 August at 00:00. Once the landscape cells were initialized, simulated raccoons were randomly placed within cells of virtual landscapes (there was no minimum or maximum number of simulated raccoons per cell). Within a single time step, the state variables of landscape cells were updated, and then simulated raccoons moved on a cell and updated their location. Finally, the time counter was updated once all simulated raccoons had made a move (Figure 2). As stochasticity was only included in the placement of simulated raccoons within cells, 100 simulation replicates for

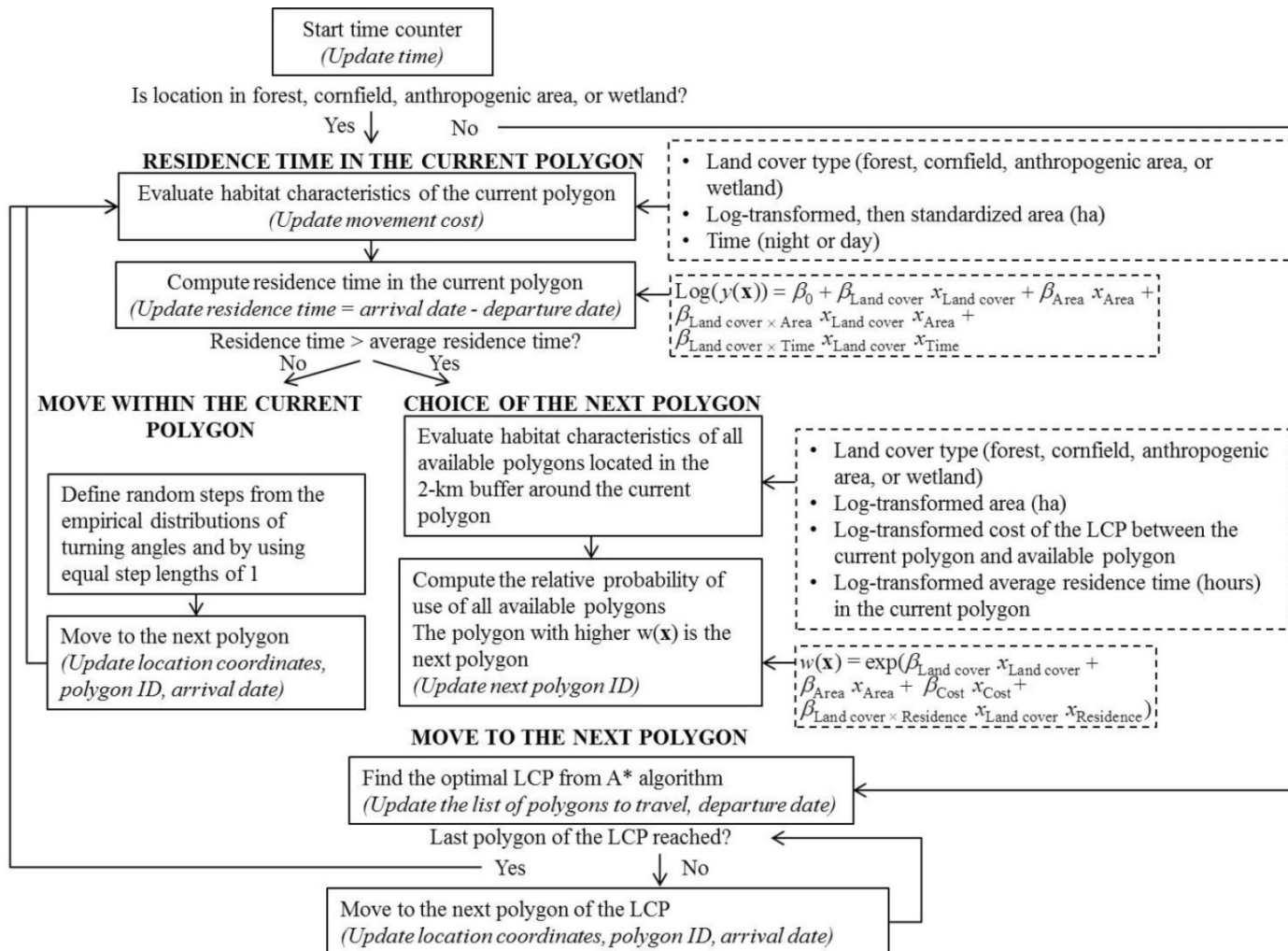


Figure 2. General scheduling of processes of space-use dynamics. Within a single time step, the cells of virtual landscapes were updated, and then simulated raccoons moved to a cell and updated their location. The time counter was updated once all simulated raccoons had made a move.

each virtual landscape including 0.1 raccoon/km² and 15 simulation replicates for each virtual landscape containing 1, 5, and 10 raccoons/km² were sufficient to obtain low standard deviations around mean values of per capita contact rates. The 15 virtual landscapes were static during a simulation and between simulations. For directly transmitted diseases, transmission of infectious pathogens depends upon the number of direct contacts per time unit between individual hosts (McCallum et al. 2001). In the IBM, a direct contact between two simulated raccoons happened when both individuals co-occurred in the same cell. Simulated raccoons moved independently of each other individual in all simulations.

From the IBM, we executed a total of 2175 simulations (*i.e.*, 100 replicates \times 15 virtual landscapes \times 1 level of conspecific density corresponding to 0.1 raccoon/km², and 15 replicates \times 15 virtual landscapes \times 3 levels of conspecific density corresponding to 1, 5, and 10 raccoons/km²) in which each simulated raccoon had 13,441 steps (one step was recorded at each 3-minute time step over 28 days). For each virtual landscape and level of conspecific density, we computed 1) the number of per capita cumulative contacts (*i.e.*, average number of conspecifics that have been in contact with a given simulated raccoon) within any given land cover type and time period, and 2) the number of per capita unique contacts (*i.e.*, average number of different conspecifics that have been in contact at least once with a given simulated raccoon) within any given land cover type and time period. We considered these two metrics because they provide different information about contact events. For example, seven contacts for a given simulated raccoon could be distributed as either four contacts with one conspecific and three contacts with another conspecific or one contact with seven different conspecifics. While the probability of transmitting infectious pathogens tends to increase when individuals repeatedly contact conspecifics (Creech et al. 2012), modeling of unique contacts can be used to characterize superspreading events (Clay et al. 2009). Finally, for each virtual landscape and level of conspecific density, we estimated the density of cumulative and unique contact rates per simulated raccoon within any given land cover type and time period by dividing the number of per capita cumulative or unique contacts by the total area occupied by this land cover type. From per capita contact rates, we performed three types of analyses.

First, we assessed the variation in contact rates among simulated raccoons based upon the frequency distribution of unique contacts (simulation mean values) per individual for each

virtual landscape and each conspecific density (Perkins et al. 2003, Clay et al. 2009). The corrected moment estimate k was used to quantify aggregation in the frequency distributions (Elliott 1971). When k is large (> 20), the distribution is random, whereas when k is near zero, the distribution is highly aggregated and follows a negative binomial distribution (Elliott 1971, Wilson et al. 2001). A frequency distribution of unique contacts per individual that is highly aggregated suggests the presence of heterogeneity in contact patterns with a small portion of hosts supporting the majority of contacts. Using Lorenz curves (Lorenz 1905), we then explored the relationship between the cumulative percentage of unique contacts and the cumulative percentage of simulated raccoons that had the highest number of unique contacts in virtual landscapes with a maximal density of 10 raccoons/km² (also see Poulin 1993 for a detailed application in a host-parasite system). This relationship was used to determine if the contact dynamics of simulated raccoons at high conspecific densities could follow the 20/80 rule of Woolhouse et al. (1997).

Second, we modeled the density of per capita cumulative and unique contact rates as a function of conspecific density for each land cover type of virtual landscapes during day and night by using nonlinear least-squares regressions that had the same structure as the Equation (2) of Smith et al. (2009b). We then estimated the values of q because this parameter controls the concavity of contact rate-density relationships (Smith et al. 2009b). When $q = 0$, per capita contact rates increase linearly with population density (leading to density-dependent transmission), and when $q = 1$, per capita contact rates are independent of population density (leading to frequency-dependent transmission). Other values of parameter q yield nonlinear relationships (see Figure 2A in Smith et al. 2009).

Third, we represented 1) the density of per capita cumulative and unique contact rates within each land cover type as a function of conspecific density for each combination of levels of forest proportion and spatial arrangement of agricultural corridors specific to virtual landscapes, and 2) the density of per capita cumulative and unique contact rates within forests, cornfields, and anthropogenic areas as a function of landscape connectivity for each combination of levels of forest proportion and conspecific density to describe the functional relationship between the contact rates, conspecific density, and landscape connectivity. For the second plots, we considered the density of per capita cumulative and unique contact rates

within forests, cornfields and anthropogenic areas because the first plots showed that these land cover types contained a higher density of cumulative and unique contact rates compared to other land cover types (see section “Results”).

2.4. Validation

To validate our IBM, we verified that emergent behaviors of simulated raccoons were representative of those of radio-collared raccoons. We used raster representations of real landscapes in the Montérégie region, and from these rasters that had the same spatial resolution as virtual landscapes (*i.e.*, size of the study area = 100 km², size of cells = 10 × 10 m), we ran our IBM with simulated raccoons that were placed at the centroid of each radio-collared raccoon’s home range ($N = 12$). We compared the home range size and proportion of returns within forests, cornfields and anthropogenic areas between radio-collared and simulated raccoons. Home ranges were built by using a Brownian bridge movement model that estimates utilization distributions of animals from their movement trajectories (Horne et al. 2007).

3. Results

3.1. Empirical movement rules

Radio-collared raccoons spent from < 1 to 77 h in individual habitat polygons (mean = 1.52 h). Residence time in habitat polygons was higher during the day when raccoons are less active than at night (Table 1). Time spent in anthropogenic areas was four times longer during the day than at night. Residence time further depended upon polygon size in the landscape, with raccoons displaying longer residence times in large than in small cornfields (Table 1).

Radio-collared raccoons were also more likely to choose habitat polygons that were reached by traveling along a path with relatively low movement costs (Table 2). Except for wetlands, raccoons more strongly selected large than small polygons (Table 2). In addition, raccoons leaving a forest polygon were more likely to transit to a cornfield than another forest polygon (Table 2). When raccoons left cornfields, however, they avoided ending up again in cornfields and wetlands relative to forests (Table 2). The probability of transiting from anthropogenic areas to wetlands was lower than the probability of transiting from anthropogenic areas to forests (Table 2). Furthermore, raccoons were less likely to move from

Table 1. Parameter estimates (β) and 95% confidence intervals (CI) of fixed and random effects of a linear mixed-effects model predicting residence time of radio-collared raccoons within high-quality habitat polygons (*i.e.*, forest, cornfield, anthropogenic area, and wetland) located in the Montérégie and Estrie regions, Québec, Canada. The values of marginal and conditional R^2 are also presented.

Fixed effect ^a	β	95% CI
Intercept	-0.791	[-1.117; -0.466]
Corn	-0.224	[-0.285; -0.164]
Anthropogenic	0.371	[0.219; 0.522]
Wetland	-1.441	[-1.595; -1.286]
Log(Area)	-0.007	[-0.084; 0.069]
Forest \times Log(Area)	0.009	[-0.090; 0.107]
Corn \times Log(Area)	0.385	[0.291; 0.480]
Anthropogenic \times Log(Area)	-0.095	[-0.205; 0.016]
Forest \times Day	0.607	[0.534; 0.680]
Corn \times Day	0.558	[0.383; 0.732]
Anthropogenic \times Day	1.383	[1.098; 1.668]
Wetland \times Day	0.757	[0.416; 1.097]
Random effect		
Year	0.263	[0.078; 0.888]
Specimen ID	0.386	[0.306; 0.488]
Marginal R^2	0.46	
Conditional R^2	0.98	

^aThe model included the land cover type (*i.e.*, forest [reference category], cornfield, anthropogenic area, or wetland) of polygon, the log-transformed, then standardized area of polygon, the time period (*i.e.*, night [reference category] or day)

Table 2. Parameter estimates (β) and 95% confidence intervals (CI) of conditional logistic models predicting, from high-quality source polygons (*i.e.*, forest, cornfield, anthropogenic area, and wetland), which high-quality habitat polygon will be visited next among those available within a 2-km radius around radio-collared raccoons in the Montérégie and Estrie regions, Québec, Canada. The \bar{r}_s of 5-fold cross-validation are also given for each of the four models.

Choice of the next polygon	From forest		From cornfield		From anthropogenic area		From wetland	
	β	95% CI	β	95% CI	β	95% CI	β	95% CI
Corn	0.868	[0.383; 1.353]	-1.020	[-1.412; -0.627]	0.141	[-0.383; 0.666]	-0.297	[-1.543; 0.949]
Anthropogenic	0.129	[-0.300; 0.558]	-1.082	[-2.537; 0.373]	-5.697	[-8.530; -2.864]	-1.780	[-3.471; -0.088]
Wetland	-0.519	[-1.287; 0.250]	-0.960	[-1.550; -0.370]	-1.241	[-1.950; -0.532]	-1.248	[-2.631; 0.135]
Log(Area)	0.499	[0.356; 0.641]	0.441	[0.295; 0.586]	0.414	[0.139; 0.690]	0.275	[-0.014; 0.565]
Log(LCP cost + 1)	-1.002	[-1.051; -0.952]	-1.054	[-1.175; -0.933]	-0.707	[-0.815; -0.598]	-0.845	[-0.995; -0.695]
Forest \times Log(Residence time)	-0.167	[-0.545; 0.211]	0.043	[-0.218; 0.304]	-0.006	[-0.293; 0.282]	-0.732	[-1.548; 0.083]
Corn \times Log(Residence time)	-0.066	[-0.426; 0.294]	0.109	[-0.185; 0.402]	0.016	[-0.282; 0.313]	-0.758	[-1.514; -0.002]
Anthropogenic \times Log(Residence time)	-0.127	[-0.467; 0.213]	0.005	[-0.443; 0.452]	-0.547	[-0.854; -0.240]	-0.866	[-1.890; 0.159]
5-fold cross-validation (\bar{r}_s)	0.93		0.97		0.86		0.80	

^aThe model included the land cover type (*i.e.*, forest [reference category], cornfield, anthropogenic area or wetland) of the next or random polygon, the log-transformed area (ha) of the next or random polygon, the log-transformed cost of least-cost path (LCP) linking the source polygon with the next or random polygon, and the log-transformed residence time in the source polygon.

wetlands to anthropogenic areas than from wetlands to forests (Table 2). Residence time influenced the choice of the next polygon when raccoons were within anthropogenic areas and wetlands. The probability that the next visited polygon was an anthropogenic area or cornfield decreased as raccoons spent an increasing amount of time in anthropogenic areas and wetlands, respectively (Table 2). Therefore, the movement rules were context-dependent, which created strong spatio-temporal variation in path trajectories. We used these movement rules in our spatially explicit individual-based model to assess how landscape physiognomy should influence the contact rates among raccoons.

3.2. Variability in contact rates among simulated raccoons

The per capita unique contact rates varied broadly among simulated raccoons, depending upon both conspecific density and landscape characteristics. For each combination of levels of forest proportion, spatial arrangement of agricultural corridors and conspecific density, the frequency distribution of unique contacts per simulated raccoon did not follow a random distribution. The distribution was highly aggregated ($k < 20$; Figure S3), suggesting that a minority of simulated raccoons was responsible for a large number of unique contacts in the virtual landscapes. For example, 15 % of simulated raccoons (min = 8 %; max = 21 %) that had the highest number of unique contacts in the virtual landscapes with a maximal density of 10 raccoons/km² accounted for 90 % of all unique contacts (Figure S4). The percentage of simulated raccoons that were responsible for 90 % of all unique contacts was higher in landscapes that were highly connected by agricultural corridors and contained a low rather than a high proportion of forests (Figure S4).

3.3. Relationship between contact rates, conspecific density, and landscape connectivity

In most conditions, the parameter q in the contact rate-density equation of Smith et al. (2009b) did not differ from 0, indicating that per capita cumulative and unique contact rates were simply density-dependent in virtual landscapes (Table S2). Overall, the density of per capita contact rates was higher in forests, anthropogenic areas and cornfields (ranked from highest to lowest) than in wetlands, crops or open-cultivated areas during both day and night (Figures 3 & 4). Per capita cumulative contact rates were observed at their highest densities in

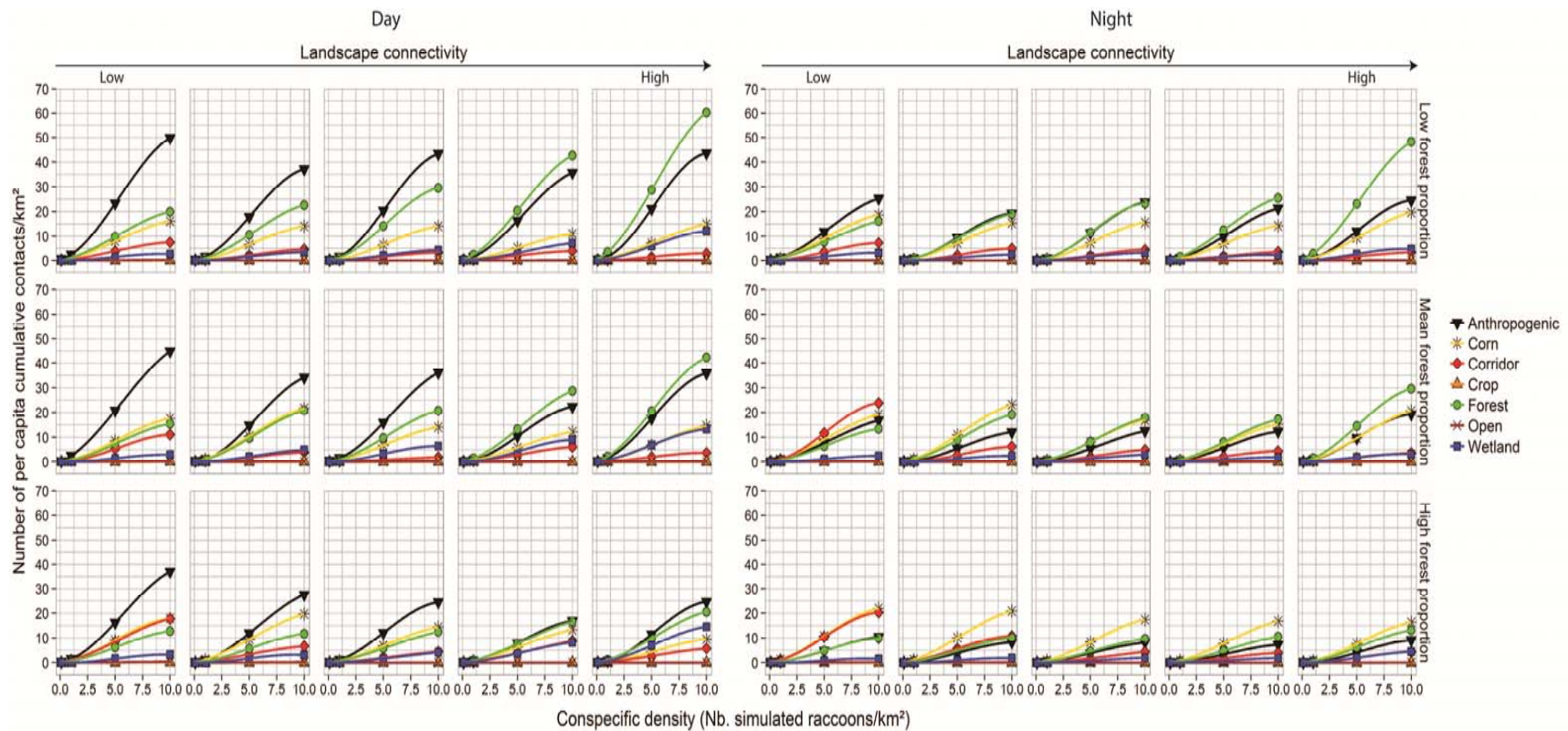


Figure 3. Density of per capita cumulative contact rates within land cover types (*i.e.*, anthropogenic areas, cornfields, agricultural corridors, crops, forests, open-uncultivated areas, and wetlands) of virtual landscapes as a function of conspecific density for each level of forest proportion (right-axis) and spatial arrangement of agricultural corridors (top-axis) during the day and night

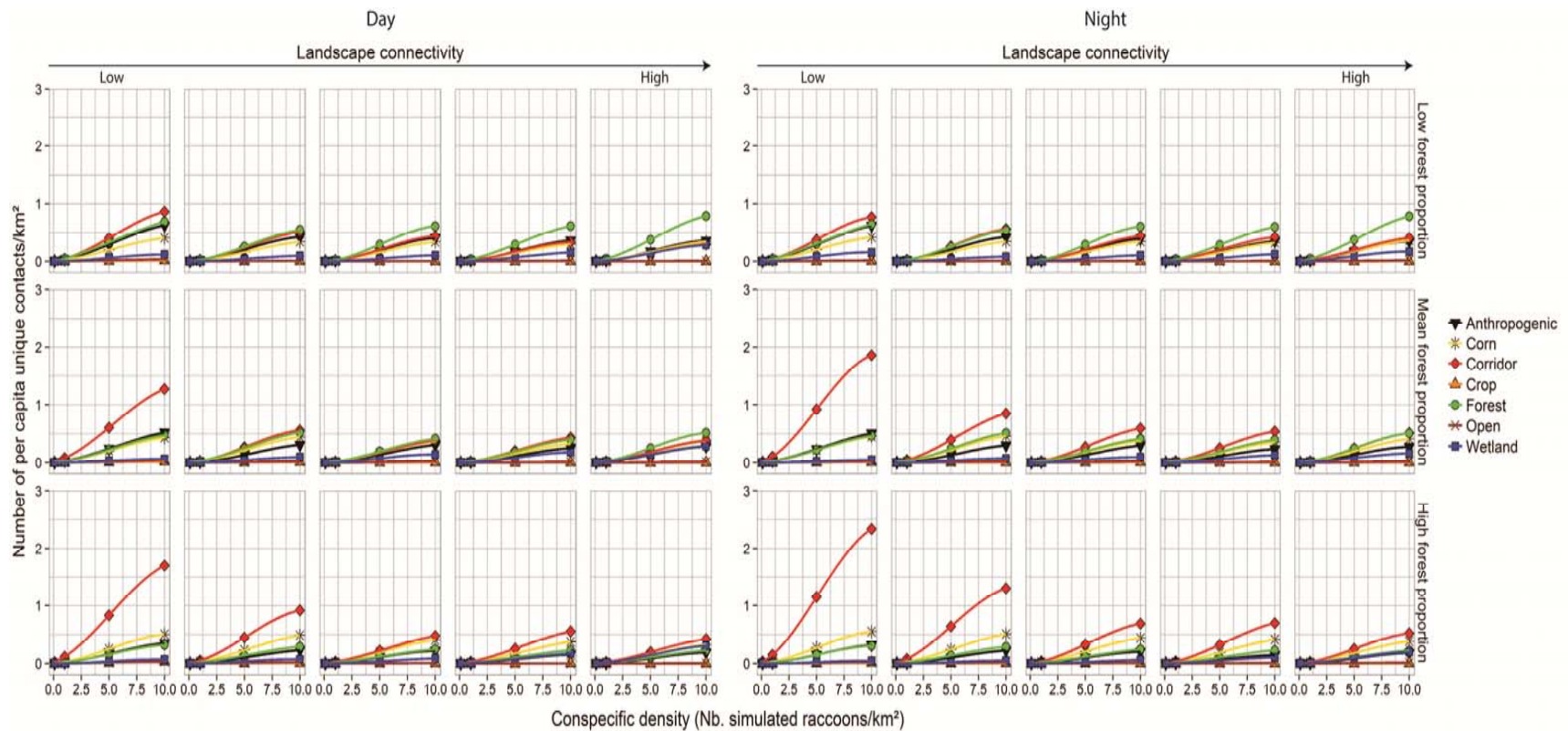


Figure 4. Density of per capita unique contact rates within land cover types (*i.e.*, anthropogenic areas, cornfields, agricultural corridors, crops, forests, open-uncultivated areas, and wetlands) of virtual landscapes as a function of conspecific density for each level of forest proportion (right-axis) and spatial arrangement of agricultural corridors (top-axis) during the day and night

forests and anthropogenic areas during the day, especially in landscapes with a low proportion of forests (7 %) and high or low connectivity by agricultural corridors, respectively (Figure 3). We observed differences between spatial distributions of per capita unique and cumulative contact rates. For example, when landscapes were poorly connected by agricultural corridors or contained a high proportion of forests (28 %), the density of per capita cumulative contact rates was highest in anthropogenic areas during the day (Figure 3). Under the same conditions, however, per capita unique contact rates occurred at highest densities in agricultural corridors (Figure 4). Also, when landscapes were composed of a high forest proportion, the highest densities of per capita cumulative contact rates were observed in cornfields during the night (Figure 3). In contrast, under the same conditions, the density of per capita unique contact rates was highest in agricultural corridors (Figure 4).

We observed effects of functional connectivity on the density of per capita contact rates that depended upon land cover types and the proportion of forests. We provide an example for each of the three trends. First, the density of per capita cumulative contact rates in forests increased with connectivity of forests by agricultural corridors, and this increase was steeper in landscapes with a low rather than a high proportion of forests (Figure 5). Second, the density of per capita contact rates in cornfields decreased with connectivity of cornfields by agricultural corridors (Figures 5 & 6). At low connectivity of cornfields, per capita contact rates occurred at the highest densities in landscapes that were composed of a high rather than a low proportion of forests. Third, connectivity of anthropogenic areas by agricultural corridors had a convex quadratic relationship with the density of per capita contact rates in anthropogenic areas, with highest densities of per capita contact rates being observed in landscapes that were poorly or highly connected by agricultural corridors and comprised of a relatively small proportion of forests (Figures 5 & 6). This trend was also observed for the per capita unique contact rates in forests (Figure 6).

3.4. Validation

Simulated raccoons in the real landscape were able to reproduce some behaviors of radio-collared raccoons. In particular, home range sizes between radio-collared (86.06 ± 12.42 ha; Mean \pm SE) and simulated raccoons (76.56 ± 11.51 ha) were not significantly different (two-sample t -test: $t = 0.56$, $df = 21.87$, $P = 0.58$; Figure S5). Similarly, the proportion of

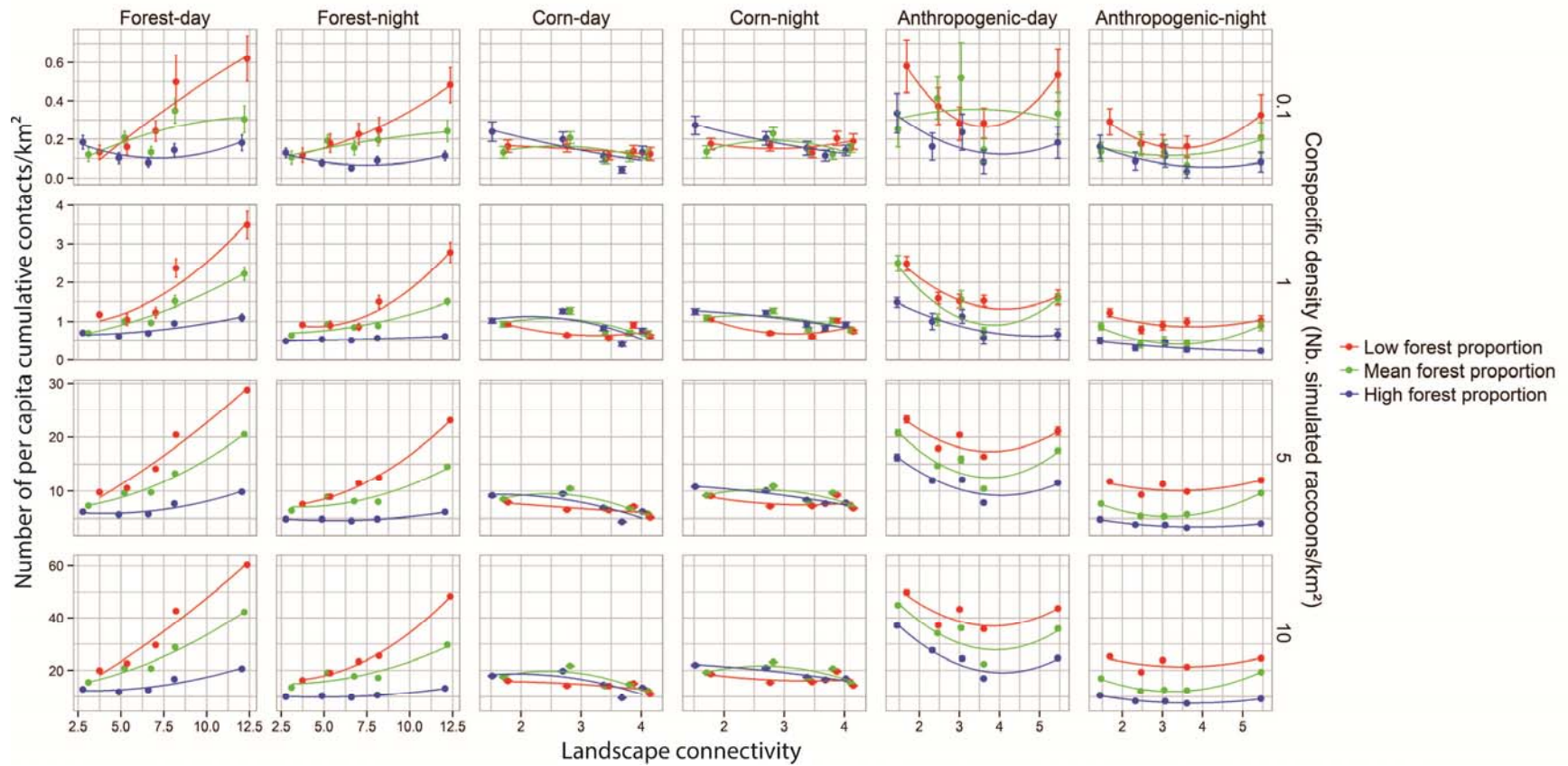


Figure 5. Density of per capita cumulative contact rates within major land cover types (*i.e.*, forests, cornfields, and anthropogenic areas) of virtual landscapes as a function of landscape connectivity for each level of forest proportion and conspecific density (right-axis) during the day and night. The mean values (represented by points) and their corresponding standard errors (represented by vertical lines) are represented. A smooth curve is drawn through the points. Landscape connectivity was defined as the average number of agricultural corridors connecting polygons of a given land cover type in the virtual landscape.

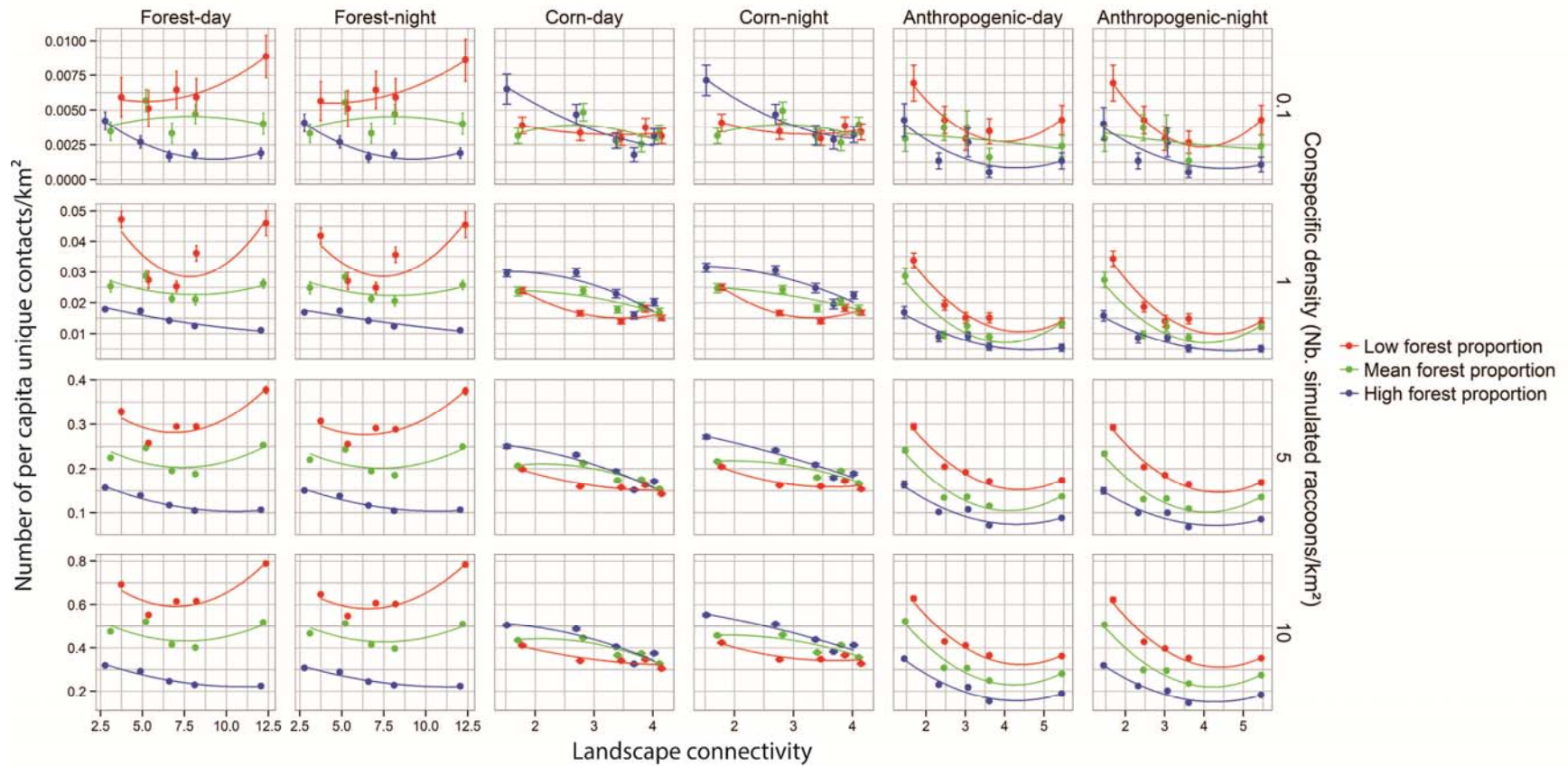


Figure 6. Density of per capita unique contact rates within major land cover types (*i.e.*, forests, cornfields, and anthropogenic areas) of virtual landscapes as a function of landscape connectivity for each level of forest proportion and conspecific density (right-axis) during the day and night. The mean values (represented by points) and their corresponding standard errors (represented by vertical lines) are represented. A smooth curve is drawn through the points. Landscape connectivity was defined as the average number of agricultural corridors connecting polygons of a given land cover type in the virtual landscape.

returns within high-quality habitat polygons did not differ between radio-collared (0.38 ± 0.13) and simulated raccoons (0.37 ± 0.21) (two-sample t -test: $t = 0.01$, $df = 3.35$, $P = 0.99$; Figure S6).

4. Discussion

Our spatially explicit individual-based model illustrates that contact patterns are driven by functional connectivity, which in turn varies with conspecific density and landscape physiognomy. Quantifying variability in contact rates among hosts and across space is fundamental to implementing cost-effective interventions that can successfully limit infectious disease spread (Paull et al. 2011). Our study contributes in that respect by characterizing three general patterns in per capita contact rates that emerge naturally from empirical movement rules derived from radio-collared raccoons. First, we observed strong disparity in contact rates among simulated raccoons, with a minority of individuals being responsible for a majority of the contacts among conspecifics. Second, per capita contact rates increased linearly with population density, indicating that raccoon rabies transmission should be density-dependent instead of frequency-dependent under most conditions. Third, depending upon land cover types and landscape composition, functional connectivity had a broad range of effects on the density of per capita contact rates among hosts, from increasing to decreasing densities of contact rates. All these patterns emerged from simple empirical movement rules derived from the interplay between the movement of radio-collared raccoons and landscape heterogeneity.

4.1. Movement behavior of radio-collared raccoons

Radio-collared raccoons were more likely to choose forests as their next destination when they were not situated in forests. In particular, raccoons should achieve relatively high fitness by selecting areas that are comprised of a high proportion of forests in landscapes containing few conspecifics (Tardy et al. 2015). Forests offer large quantities of resources, such as den sites (*e.g.*, tree cavities) and food items (*e.g.*, small mammals, birds, insects) (Chamberlain et al. 2002, Wilson & Nielsen 2007). When leaving a forest, raccoons selectively moved to a cornfield. Under high conspecific densities in the landscape, raccoons select cornfields in areas with high densities of corn-forest edges and a low proportion of cornfields (Tardy et al. 2014), presumably to benefit from the proximity and abundance of high-quality

food that is available in cornfields and the safety provided by forest cover in agriculturally fragmented landscapes (Beasley & Rhodes 2008, Houle et al. 2011). We further found that radio-collared raccoons were generally more likely to transit to large polygons and to use paths with low movement costs (*i.e.*, selection for least-cost paths) to proceed towards their next destination. These results support previous studies showing that raccoons can maintain low costs of travel (Porter et al. 2015) and short movement distances (Prange et al. 2003, O'Donnell & DeNicola 2006) when resources are readily available, which suggest that this species can occupy relatively small home ranges (Prange et al. 2004, Beasley et al. 2007b). For example, in the study of Beasley et al. (2007b), home ranges of raccoons (female = 58 ± 7 ha and male = 92 ± 6 ha) were smaller than those reported in other agriculturally fragmented landscapes (4-2560 h; Gehrt 2003). Our empirical models also revealed that radio-collared raccoons had longer residence times in anthropogenic areas compared to other land cover types, particularly during the day when they are less active. In urbanized landscapes, raccoons take advantage of residential areas that provide them with both abundant food sources (*e.g.*, human food, garbage) and resting dens (*e.g.*, burrows under buildings) during the day (Hadidian et al. 1991, Prange et al. 2004).

4.2. Contact heterogeneity among simulated raccoons

Our simulations showed that given the empirical movement rules, only a small portion of a raccoon population should be responsible for the majority of unique contacts. For example, we found that in virtual landscapes with a maximal density of 10 raccoons/km², 15 % of all simulated raccoons that had the highest number of unique contacts accounted for 90 % of all unique contacts. At high conspecific densities in the landscape, the contact dynamics of raccoons should thus approach the 20/80 rule, which is based on the common observation that ≈ 20 % of infected hosts (*i.e.*, those generating the highest number of secondary cases) are commonly responsible for at least 80 % of transmission events within host-pathogen systems (Woolhouse et al. 1997). This pattern has been observed for vector-borne diseases, such as tick-borne encephalitis (Perkins et al. 2003) and West Nile virus (Kilpatrick et al. 2006), as well as for diseases transmitted by direct contact, such as Sin Nombre virus (Clay et al. 2009). Pathogen transmission heterogeneity among hosts is often due to variation in their exposure and susceptibility to pathogens and, in turn, these characteristics are affected by age, sex, body

condition, behavior or genetics of hosts (Wilson et al. 2001). In our case, contact heterogeneity emerges in virtual landscapes from simulated raccoons that all obey the same movement rules. While simulated raccoons started at random locations, their subsequent use of the landscape was such that some simulated individuals exhibited high home range overlap with others, thereby leading to high rates of unique contacts. Given that home range size of simulated raccoons was similar to that of radio-collared raccoons, our simulations demonstrate that simple movement rules in heterogeneous landscapes, combined with stochasticity in conspecific distributions, is sufficient to result in strong disparity in the contribution of individual hosts to infectious disease transmission.

4.3. Spatial heterogeneity in contact rates

In host-pathogen systems, the effect of habitat fragmentation on the dynamics of infectious diseases has been studied theoretically from metapopulation models (Hess 1996, Gog et al. 2002, McCallum & Dobson 2002), which has led to different predictions according to the mode of pathogen transmission. For example, if the transmission rate depends upon the proportion (or frequency) of infected hosts, fragmentation should have no direct effect on transmission within habitat polygons, as this mode of transmission assumes that hosts had the same number of contacts regardless of population density within polygons (McCallum & Dobson 2002). Alternatively, if the transmission rate is dependent upon the density of infected hosts, fragmentation should increase transmission within habitat polygons by reducing animal movements between polygons (Hess 1996, McCallum & Dobson 2002). In our simulation study, the mode of transmission was density-dependent rather than frequency-dependent, with per capita contact rates increasing linearly with conspecific density in most virtual landscapes. The simulations were based on a range of 0 to 10 simulated raccoons/km², which overlaps the observed range of 0.5 to 13.9 raccoons/km² (mean = 5 raccoons/km²) that has been reported for the Montérégie and Estrie regions of southern Québec (Massé 2010). Density-dependent transmission is common in host-pathogen systems (Anderson et al. 1981, Berthier et al. 2000, Brown & Brown 2004). Unlike frequency-dependent models (Thrall et al. 1995), density-dependent models predict the existence of a host density threshold below which infectious pathogens cannot invade or persist in a population of susceptible hosts, and above which the pathogens can spread (Anderson et al. 1981, Getz & Pickering 1983). Accordingly, measures

that can result in a decrease in population density (*e.g.*, using culling or sterilization techniques) should be effective at reducing the risk of raccoon rabies spread.

Our simulations revealed that the density of per capita contact rates tended to be lower in landscapes that were largely comprised of forests (28 %). Because the isolation of forest polygons is lower in landscapes with high rather than low forest cover, short distances between forest polygons decreased the use of agricultural corridors in landscapes that were largely comprised of forests. Thus, increasing forest cover in landscapes that are highly connected by agricultural corridors should decrease the positive effect of functional connectivity on the density of per capita contact rates. We also found that the highest densities of per capita cumulative contact rates should occur in highly connected forest polygons and in poorly connected anthropogenic areas during the day, especially in landscapes containing few forests (7 %). Consistently, forests and anthropogenic areas were strongly selected by radio-collared raccoons. While focusing control interventions on these two land cover types might seem a cost-effective approach for reducing the risk of disease spread, the efficiency of these interventions can strongly vary as a function of landscape physiognomy. In particular, our study shows that contact rates greatly depend upon 1) whether we consider unique or cumulative contacts, and 2) landscape composition and functional connectivity.

4.3.1. Spatial distribution of cumulative versus unique contact rates

We found large differences between areas where cumulative and unique contact rates occurred at highest densities. For example, when landscapes were poorly connected by agricultural corridors or contained a high proportion of forests, per capita cumulative contact rates were observed at highest densities during the day in anthropogenic areas (Figure 3). Under the same conditions, however, per capita unique contact rates were the most abundant in agricultural corridors (Figure 4). When landscapes were composed of a high forest proportion, the density of per capita cumulative contact rates also was highest in cornfields during the night. Under the same conditions, the density of per capita unique contact rates was highest in agricultural corridors. When pathogen transmission is density-dependent, as is expected for raccoon rabies according to our simulations (Figures 3 & 4), per capita cumulative contact rates influence the probability of transmitting or contracting infectious pathogens (Ji et al. 2005, Habib et al. 2011), whereas per capita unique contact rates inform on the risk for

superspreading events (Clay et al. 2009). Thus, forests and anthropogenic areas would be potential hotspots for raccoon rabies transmission among individuals, whereas agricultural corridors would increase the risk of superspreading events. However, in landscapes that are highly connected by agricultural corridors but with $\leq 14\%$ of forests, superspreading events are more likely to occur in forests than in agricultural corridors. Despite some variation among virtual landscapes, our IBM indicates that hotspots are unlikely to be found in crops, wetlands and open areas.

4.3.2. Landscape composition and functional connectivity influence contact rates

Our study demonstrates how functional connectivity can influence the density of per capita contact rates within a given land cover type. For example, when conspecific density was at least 1 individual/km², the density of per capita cumulative contact rates increased in forests as they became more strongly connected by agricultural corridors (Figure 5). This increase was even steeper in landscapes with a low proportion of forests. Agricultural corridors largely determined the functional connectivity in virtual landscapes, which reflected our field observations on radio-collared raccoons in agriculturally fragmented landscapes. Corridors can intensify the use of habitat polygons, either by creating dispersal conduits that facilitate animal movement between isolated habitat polygons (Tewksbury et al. 2002, Levey et al. 2005) or by acting as “drift fences” that intercept animals moving through the matrix and reorienting them to connected polygons (Haddad & Baum 1999, Fried et al. 2005). Accordingly, when moving to forest polygons in landscapes containing a small proportion of forests, simulated raccoons used agricultural corridors, because cost values of moving in agricultural corridors were lower compared to other land cover types (*i.e.*, crops, open areas, and water bodies). The presence of numerous corridors increased accessibility to forest polygons, and when there were relatively few of those polygons, individuals ended up experiencing high densities of contacts in forests. As the proportion of forests increased in the landscape, however, individuals became spread among more forest polygons, and their encounter rate decreased. Under these conditions, functional connectivity tended to only have a weak effect on contact rates, especially at low host densities, because home ranges were broadly distributed in the landscape.

Unlike cumulative contacts, the density of per capita unique contact rates in forest polygons varied following a convex quadratic relationship with forest connectivity by

agricultural corridors in landscapes that were comprised of a small proportion of forests (Figure 6). The density of per capita unique contact rates declined as forest connectivity increased from low to intermediate levels (average range: 3-8 corridors; see Figure 6), and then was augmented with further increases in forest connectivity. A similar pattern was detected in anthropogenic areas, with per capita contact rates being lowest in landscapes where these areas were connected by an average of 3.5 agricultural corridors rather than by fewer or more corridors. The reduction of connectivity decreased the movement of simulated raccoons between polygons, which led to small and overlapping home ranges in the landscape. In particular, simulated raccoons returned to previously visited polygons because their movements were more costly in landscapes with a low rather than a high connectivity by agricultural corridors. For some species living in highly isolated habitat polygons, the surrounding matrix can be perceived as hostile, and individuals may become reluctant to move away from polygons (Krebs et al. 1969, Fortin & Arnold 1997). This situation can lead to local higher densities in the polygons of landscapes that are poorly connected by agricultural corridors than in those of highly connected landscapes where higher movement rates would result in a stronger use of the matrix (Adler & Levins 1994, Bayne & Hobson 1998). When few agricultural corridors were present in the landscape, simulated raccoons also used anthropogenic areas to reach their destination polygon because cost values were lower when moving in these areas than in other land cover types, especially during the day. As the number of agricultural corridors increased in the landscape, simulated raccoons started to rely more upon corridors to reach their destination polygon, and the density of per capita contact rates in anthropogenic areas declines until these areas become more connected.

We also observed that the density of per capita contact rates in cornfields decreased with connectivity of cornfields by agricultural corridors. When connectivity of cornfields was low, per capita contact rates occurred at highest densities in landscapes that were largely comprised of forests (Figures 5 & 6). Given that radio-collared raccoons displayed longer residence times in large cornfields, a decrease in the number of agricultural corridors should be associated with an increase in residence time. This should also result in increased per capita contact rates in cornfields, because cornfields tended to be larger in poorly than highly connected landscapes. In addition, a higher proportion of forests resulted in more frequent transitions between forests and cornfields, thereby increasing the encounter rates of individuals

within cornfields. Overall, these few examples show how simple movement rules can interact with landscape properties to create rather complex patterns of spatial heterogeneity in the risk of disease spread. Such heterogeneity can have strong implications for disease management and prevention.

4.4. Implication for management of infectious diseases

In North America, oral vaccine baits that are used to control rabies virus are often distributed over large areas, which can generate substantial costs (Slate et al. 2005). To achieve an optimal immunization rate at the lowest cost, vaccine bait densities should be distributed as a function of densities of per capita cumulative and unique contact rates in the landscape (Boyer et al. 2011). Often, the predictions regarding the effects of habitat fragmentation on infectious disease dynamics are based on virtual landscapes in which cells are simply classified as low-quality or high-quality habitats (Bonnell et al. 2010, Rees et al. 2013, Tracey et al. 2014). Rioux Paquette et al. (2014), however, have emphasized that the identification of habitat-specific dispersal routes of rabies spread can help to optimize vaccination interventions.

We show that the density of cumulative and unique contact rates can strongly differ among land cover types, depending upon their availability and accessibility, and upon the density of conspecifics in the landscape. While contact patterns that are observed at low conspecific density could imply that oral vaccine baits should be uniformly distributed across the landscape, patterns that are observed at high conspecific density indicate that the efficiency of vaccination strategies depends upon landscape composition and functional connectivity. The distribution of oral vaccine baits should focus on anthropogenic areas in landscapes that are poorly connected by agricultural corridors and which contain a high or low proportion of forests. In landscapes that are highly connected by agricultural corridors and composed of a low proportion of forest, a high density of baits should be dropped within forests and anthropogenic areas. However, oral vaccine baits should be more uniformly distributed in the landscapes that are highly connected by agricultural corridors and encompass a high proportion of forests. Furthermore, control interventions should concentrate a large density of oral vaccine baits within agricultural corridors, especially in landscapes with a high forest extent and few agricultural corridors.

Using a spatially explicit individual-based model, our study shows that a broad range of patterns in per capita contact rates can emerge from simulated raccoons that all obey the same and simple empirically derived movement rules. This strong spatial heterogeneity in contact rates was driven by conspecific density, landscape composition, and functional connectivity. Density-dependent models of functional connectivity thus provide a strong basis for building control and prevention programs of infectious diseases.

5. Supplemental material

Table S1. Parameter estimates (β) and 95% confidence intervals (CI) of fixed effects and costs calculated by inverting the odds ratios [OR = $\exp(\beta)$] of resource selection functions (RSFs) predicting the occurrence of radio-collared raccoons during daytime and night-time in the Montérégie and Estrie regions, Québec, Canada (see Tardy et al. 2014 for more details)

Fixed effect	Night			Day		
	β	95% CI	Cost (OR ⁻¹)	β	95% CI	Cost (OR ⁻¹)
Forest	-	-	1	-	-	1
Corn	0.057	[0.004; 0.111]	0.944	-3.095	[-3.237; -2.953]	22.085
Crop	-1.157	[-1.226; -1.087]	3.180	-2.802	[-2.930; -2.675]	16.485
Corridor	0.328	[0.265; 0.391]	0.720	-1.066	[-1.166; -0.966]	2.904
Open	-0.334	[-0.390; -0.279]	1.397	-1.680	[-1.764; -1.596]	5.366
Anthropogenic	0.524	[0.409; 0.639]	0.592	1.291	[1.126; 1.456]	0.275
Water	0.146	[-0.142; 0.434]	0.864	-2.337	[-2.971; -1.702]	10.346
Wetland	0.501	[0.292; 0.709]	0.606	-1.078	[-1.380; -0.775]	2.937
Other	-0.930	[-1.210; -0.650]	2.534	-0.533	[-0.853; -0.213]	1.705

Table S2. Values of the parameter q from the Equation (2) of Smith et al. (2009b) that was used to model the density of per capita cumulative (1) and unique (2) contact rates as a function of conspecific density in the virtual landscapes during the day and night. The parameter q controls the relationship concavity. When $q = 0$, the per capita contact rates increase linearly with population density (density-dependent), and when $q = 1$, the per capita contact rates are constant irrespective of population density (frequency-dependent) (see Figure 2A in Smith et al. 2009). Other values of parameter q that yield nonlinear relationships are represented in bold (see also Figure 2A in Smith et al. 2009).

Virtual landscape ^a								
Corridor configuration	Forest proportion	Forest	Corn	Anthropogenic	Wetland	Corridor	Open	Crop
1. Cumulative contacts								
<i>Day</i>								
-75%	0.7	-0.08	-0.07	-0.14	-0.04	-0.03	-0.18 *	-0.02
-75%	0.14	-0.13	-0.1	-0.14	-0.13	-0.14	-0.21 *	-0.27
-75%	0.28	-0.09	-0.04	-0.22	-0.12	-0.1	-0.04	-0.17
-50%	0.7	-0.15	-0.16	-0.12	-0.18	-0.18	-0.35 *	-0.4 *
-50%	0.14	-0.15	-0.1	-0.26	-0.23	-0.25	-0.13	-0.17
-50%	0.28	-0.1	-0.09	-0.24 *	-0.02	-0.04	-0.14	0
-25%	0.7	-0.13	-0.17	-0.15	-0.14	-0.14	-0.23	0.01
-25%	0.14	-0.14	-0.11	-0.21	-0.09	-0.26 *	-0.3	-0.42
-25%	0.28	-0.15	-0.1	-0.09	-0.36 *	-0.19	-0.12 *	-0.14 *
Ratio 1	0.7	-0.11	-0.12	-0.17	-0.21	-0.03	-0.3 *	-0.19

Ratio 1	0.14	-0.15	-0.11	-0.17	-0.16	-0.14	-0.26 *	-0.46 *
Ratio 1	0.28	-0.15	-0.13	-0.17	-0.17	-0.2 *	-0.1	-0.35 *
Ratio 4	0.7	-0.11	-0.1	-0.12	-0.09	-0.11	-0.19	0
Ratio 4	0.14	-0.1	-0.15	-0.1	-0.03	0	-0.14	0
Ratio 4	0.28	-0.11	-0.16	-0.17	-0.12	-0.12	0.33	0
<i>Night</i>								
-75%	0.7	-0.13	-0.09	-0.15	-0.09	-0.16	-0.16	0.02
-75%	0.14	-0.12	-0.11	-0.16	-0.17	-0.1	-0.06	-0.34
-75%	0.28	-0.09	-0.08	-0.16	0.03	-0.04	0.04	0
-50%	0.7	-0.14	-0.15	-0.11	-0.18	-0.23	0	0
-50%	0.14	-0.14	-0.12	-0.2	-0.11	-0.25	-0.27	-0.26
-50%	0.28	-0.12	-0.1	-0.15	-0.1	0.01	0.03	-0.07
-25%	0.7	-0.1	-0.16	-0.14	-0.07	-0.19	-0.07	0.1
-25%	0.14	-0.17	-0.12	-0.25 *	-0.28 *	-0.25	-0.27	-0.38 *
-25%	0.28	-0.13	-0.11	-0.13	-0.41	-0.32 *	0.03	0.04
Ratio 1	0.7	-0.08	-0.11	-0.15	0.09	-0.1	-0.29	-0.12
Ratio 1	0.14	-0.14	-0.12	-0.16	-0.19	-0.07	-0.18	-0.22
Ratio 1	0.28	-0.15	-0.14	-0.19	-0.23	-0.16	-0.04	-0.19
Ratio 4	0.7	-0.1	-0.13	-0.1	0.02	-0.15	0.01	0.01
Ratio 4	0.14	-0.09	-0.14	-0.08	0.12	-0.12	-0.07	-0.05
Ratio 4	0.28	-0.14	-0.14	-0.22	-0.24	-0.17	0.09	-0.23 *

2. Unique contacts

Day

-75%	0.7	-0.1	-0.09	-0.13	-0.1	-0.13	-0.08	-0.07
-75%	0.14	-0.12	-0.12	-0.15	-0.08	-0.1	-0.22 *	-0.2
-75%	0.28	-0.08	-0.07	-0.14	-0.07	-0.07	0.02	-0.11
-50%	0.7	-0.14	-0.14	-0.13	-0.21	-0.16	-0.15	-0.32 *
-50%	0.14	-0.12	-0.11	-0.24	-0.22	-0.11	-0.06	-0.1
-50%	0.28	-0.1	-0.11	-0.22	-0.03	-0.09	-0.16	0.02
-25%	0.7	-0.13	-0.17	-0.16	-0.22	-0.17	-0.13	0
-25%	0.14	-0.13	-0.13	-0.21	-0.08	-0.15	-0.22	-0.51 *
-25%	0.28	-0.11	-0.11	-0.1	-0.27 *	-0.13	-0.19 *	-0.23 *
Ratio 1	0.7	-0.1	-0.14	-0.15	-0.23 *	-0.07	-0.24 *	-0.06
Ratio 1	0.14	-0.13	-0.13	-0.17	-0.16	-0.13	-0.16 *	-0.51 *
Ratio 1	0.28	-0.16	-0.16	-0.18	-0.18	-0.15	-0.05	-0.35 *
Ratio 4	0.7	-0.1	-0.13	-0.13	-0.09	-0.13	-0.17	0
Ratio 4	0.14	-0.09	-0.14	-0.1	-0.07	-0.1	-0.14	0
Ratio 4	0.28	-0.12	-0.14	-0.17	-0.13	-0.13	0.07	0

Night

-75%	0.7	-0.1	-0.09	-0.12	-0.04	-0.08	-0.14	-0.1
-75%	0.14	-0.13	-0.12	-0.15	-0.15	-0.07	-0.04 *	-0.3
-75%	0.28	-0.09	-0.08	-0.13	-0.1	-0.07	0.03	-0.43

-50%	0.7	-0.14	-0.14	-0.13	-0.17	-0.15	-0.35 *	-0.44 *
-50%	0.14	-0.12	-0.12	-0.24	-0.15	-0.14	-0.17	-0.35 *
-50%	0.28	-0.1	-0.11	-0.22	-0.1	-0.07	-0.2 *	-0.22 *
-25%	0.7	-0.12	-0.17	-0.16	-0.2	-0.18	-0.15	-0.05
-25%	0.14	-0.13	-0.13	-0.2	-0.1	-0.16	-0.24 *	-0.39 *
-25%	0.28	-0.11	-0.11	-0.09	-0.34 *	-0.12	-0.14	0
Ratio 1	0.7	-0.1	-0.13	-0.15	-0.22	-0.1	-0.26	-0.12
Ratio 1	0.14	-0.13	-0.14	-0.17	-0.21	-0.13	-0.28 *	-0.16
Ratio 1	0.28	-0.16	-0.16	-0.18	-0.17	-0.14	-0.06	-0.21
Ratio 4	0.7	-0.1	-0.13	-0.13	-0.04	-0.11	-0.06	-0.03
Ratio 4	0.14	-0.09	-0.13	-0.09	-0.06	-0.11	-0.17	-0.07
Ratio 4	0.28	-0.12	-0.14	-0.18	-0.11	-0.11	0.05	-0.26 *

^a To build the 15 virtual landscapes, we defined two systematic arrangements of agricultural corridors by varying the length/width ratio of grid squares: ratio = 1:1 and ratio = 2:1, and by using the 1:1 ratio as the reference grid, we drew three random arrangements of agricultural corridors by randomly removing 25 %, 50 %, and 75 % of square sides in the grid. In addition, we included three levels of forest proportion: 0.7, 0.14, and 0.28.

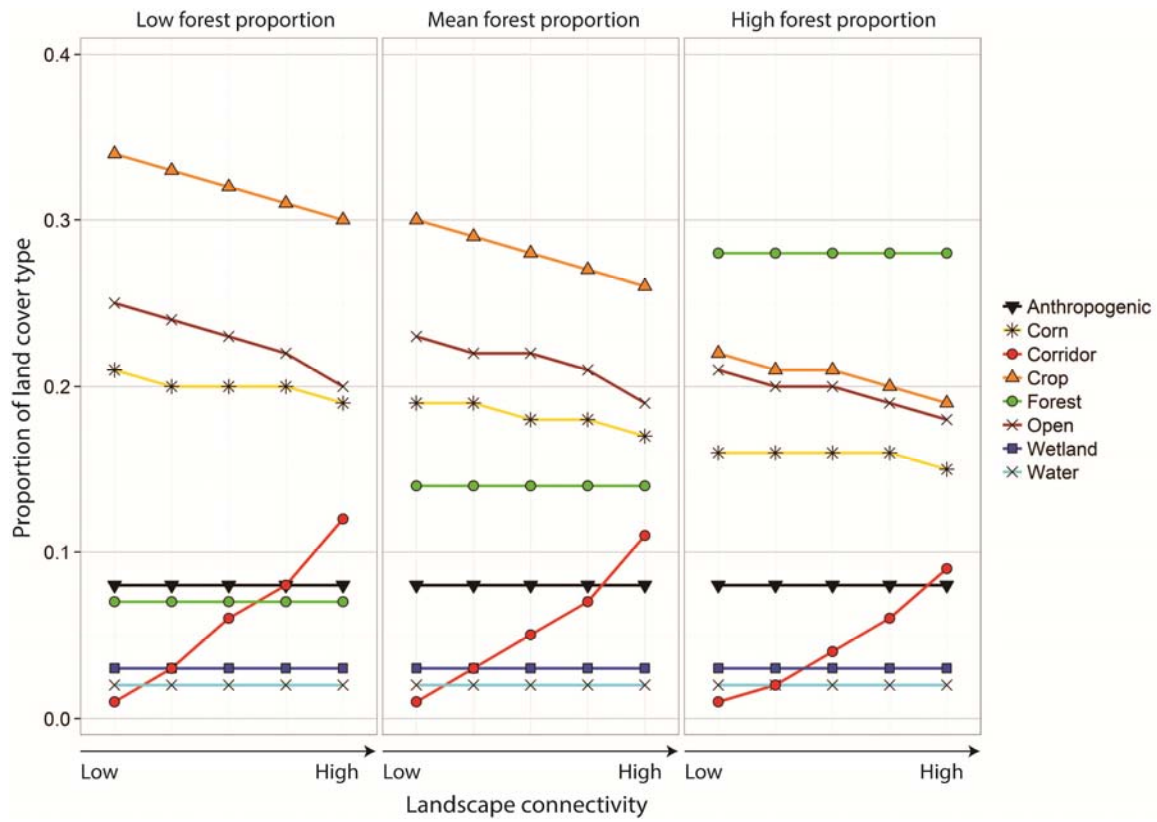


Figure S1. Proportion of each land cover type in the 15 virtual landscapes that varied in forest proportion and spatial arrangement of agricultural corridors

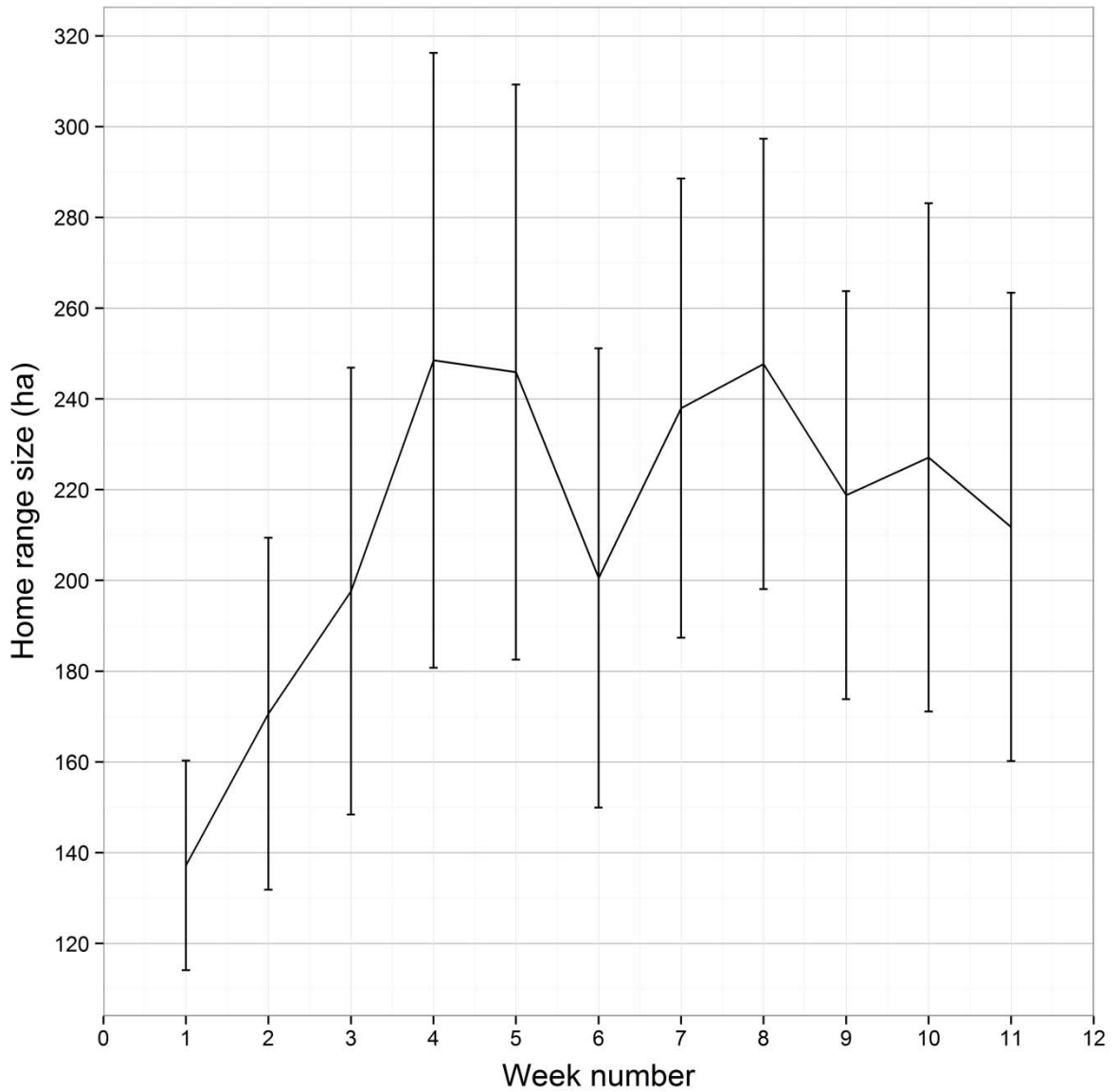


Figure S2. Relationship between mean home range size of radio-collared raccoons that have been monitored from 2009 to 2011 and week number during the GPS-tracking period (1 August – 15 October). Vertical lines represent standard errors of the mean.

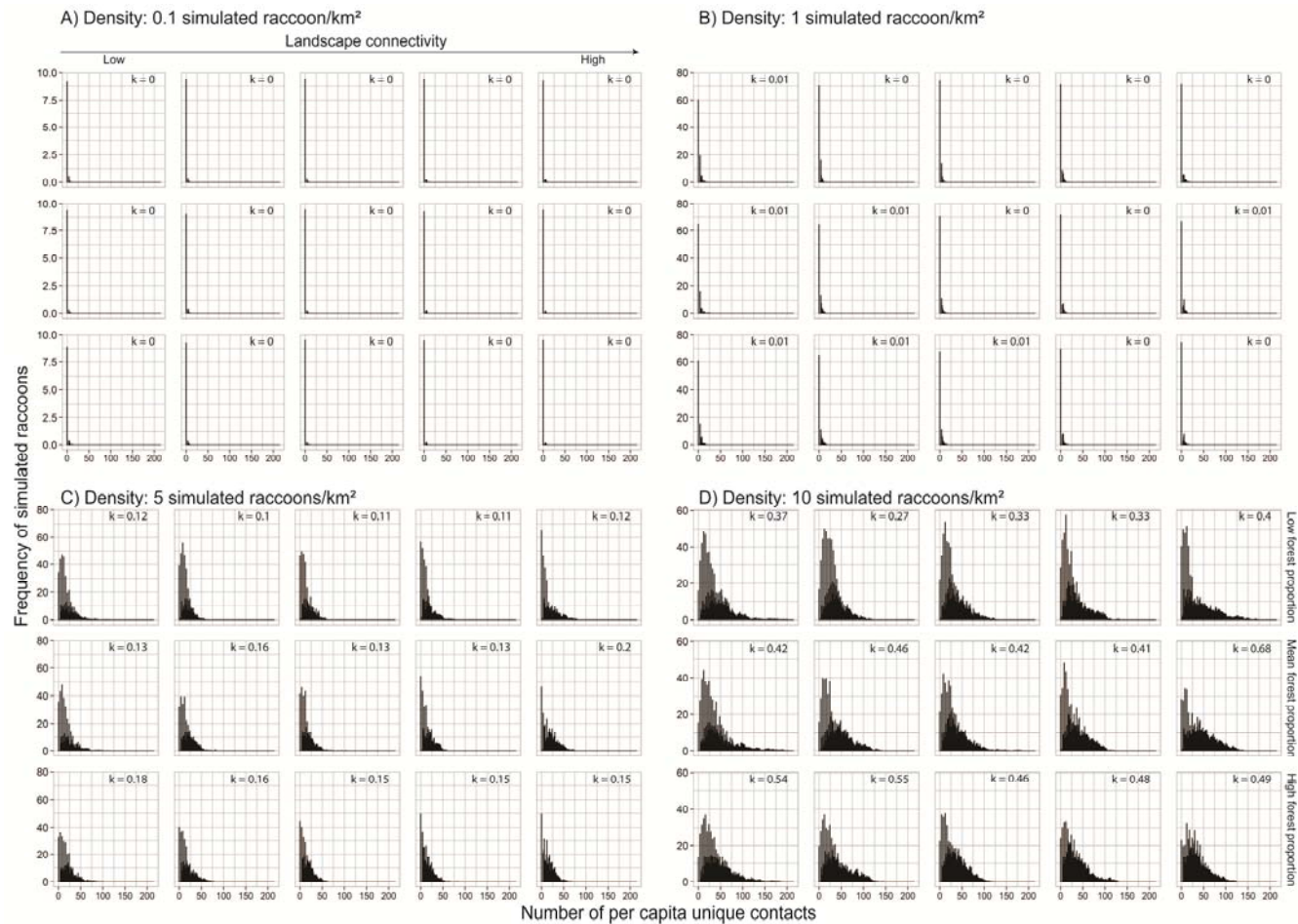


Figure S3. Frequency distributions (simulation mean values) of unique contacts per simulated raccoon for each combination of forest proportion and spatial arrangement of agricultural corridors characterizing the 15 virtual landscapes with densities of 0.1 simulated raccoon/km² (A), 1 simulated raccoon/km² (B), 5 simulated raccoons/km² (C), and 10 simulated raccoons/km² (D). The frequency distributions did not follow a random distribution, but were highly aggregated ($k < 20$).

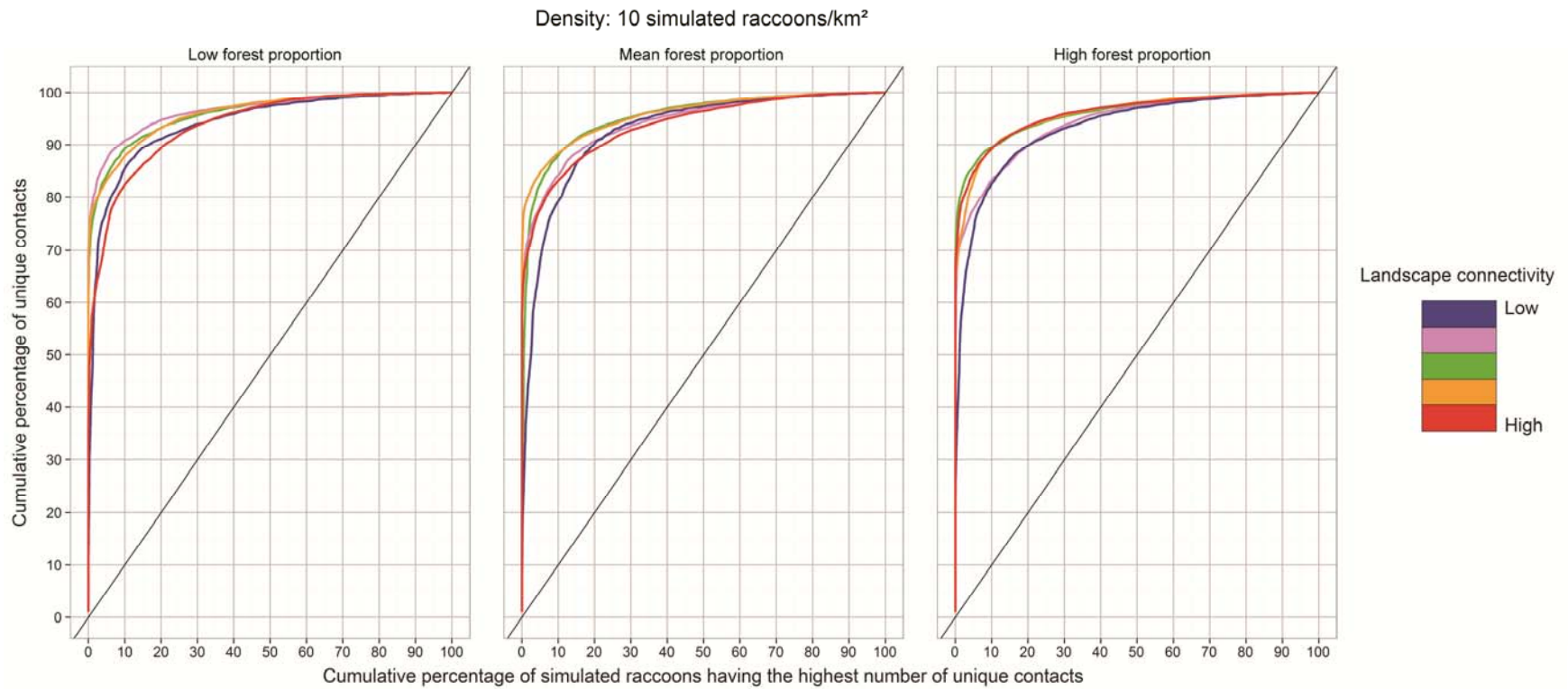


Figure S4. Lorenz curves representing the relationship between the cumulative percentage of unique contacts and cumulative percentage of simulated raccoons (*i.e.*, those with the highest number of unique contacts) for each combination of forest proportion and spatial arrangement of agricultural corridors characterizing the 15 virtual landscapes with a maximal density of 10 simulated raccoons/km². The diagonal line represents the equality line. According to the curves, 15 % of simulated raccoons (min = 8 %; max = 21 %) that had the highest number of unique contacts accounted for 90 % of all unique contacts.

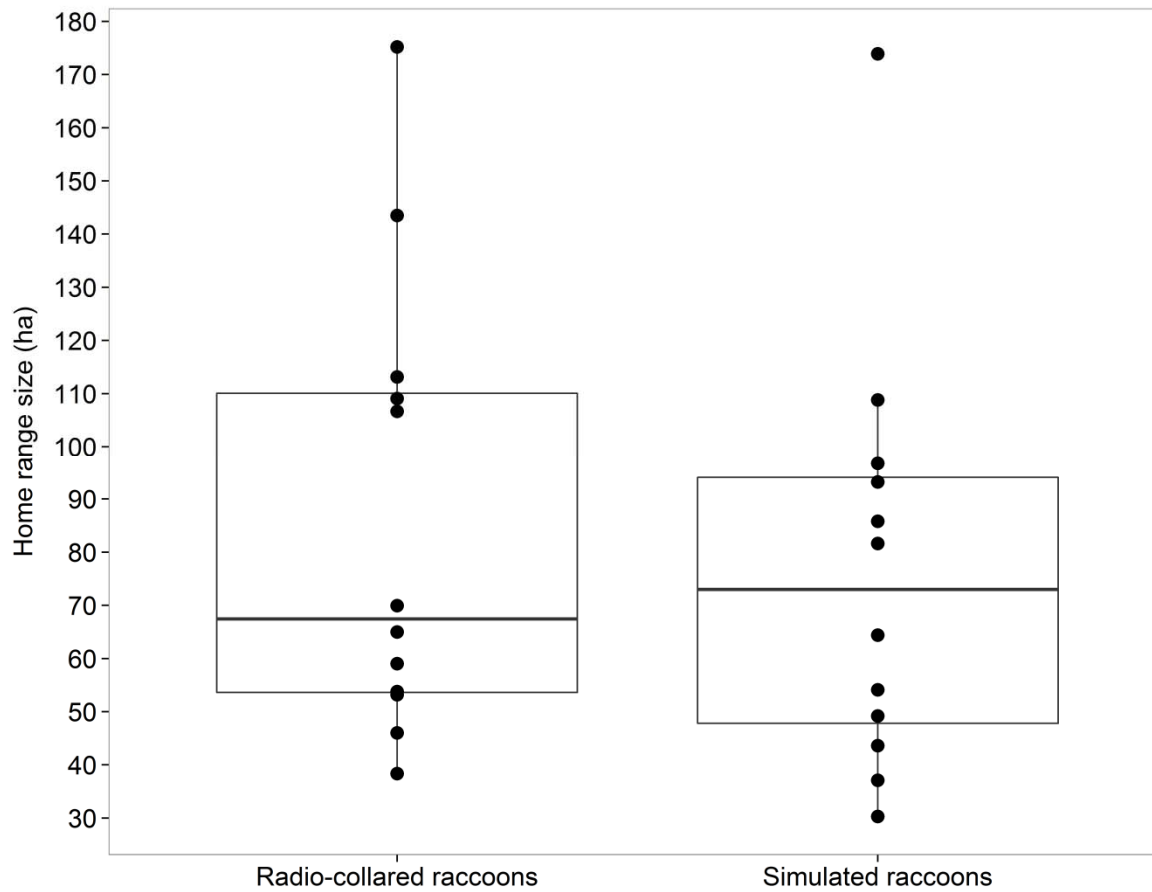


Figure S5. Distributions of home range sizes for radio-collared and simulated raccoons ($N = 12$) in real landscapes. A two-sample t -test revealed that distributions were not significantly different ($t = 0.561$, $df = 21.874$, $P = 0.580$).

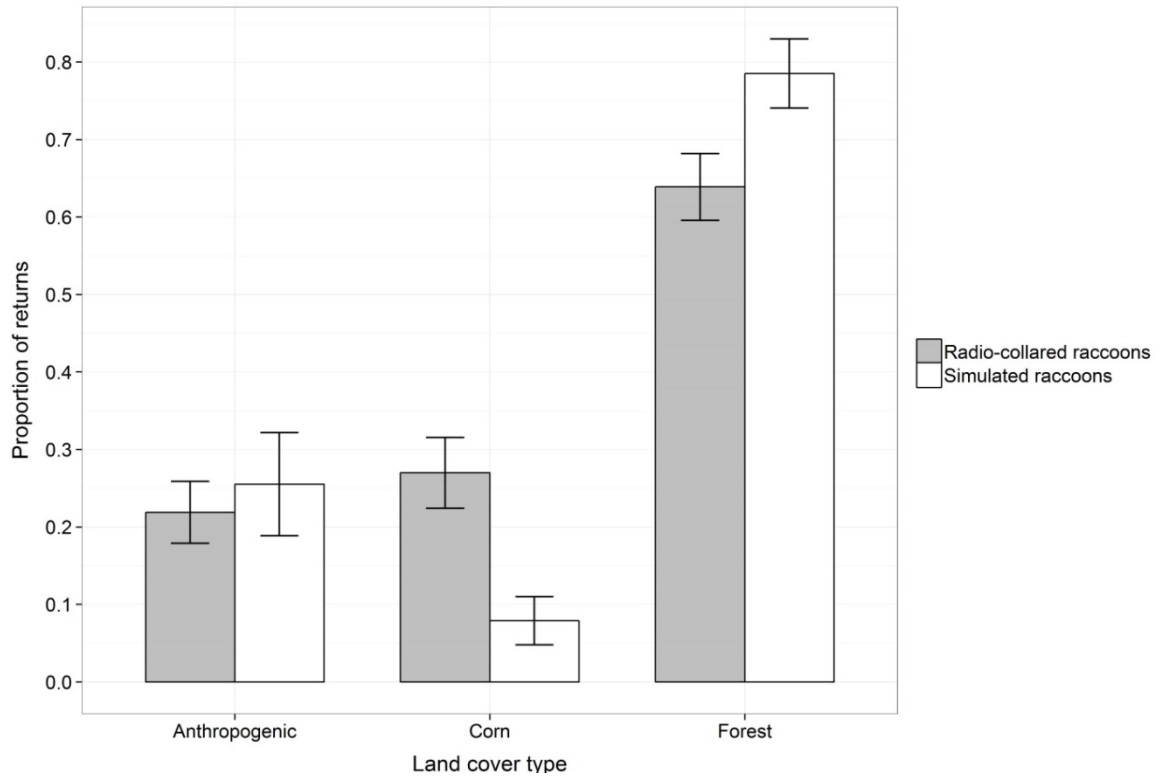


Figure S6. Distributions of mean return proportions within major land cover types (*i.e.*, forests, cornfields, and anthropogenic areas) for radio-collared and simulated raccoons ($N = 12$) in real landscapes. A two-sample t -test showed that distributions were not significantly different ($t = 0.011$, $df = 3.351$, $P = 0.992$). Vertical lines represent standard errors of the mean.

CONCLUSION GÉNÉRALE

Il subsiste très peu d'informations sur les patrons d'utilisation de l'espace des principaux hôtes réservoirs de la rage du raton laveur, en particulier dans les paysages agroforestiers du Nord-Est de l'Amérique du Nord, où le virus reste encore bien présent. Ce manque de connaissances réduit l'efficacité des interventions de contrôle qui tentent de freiner l'expansion de ce virus. Plusieurs études sur la rage du raton laveur se sont intéressées à son épidémiologie (Hubbard 1985, Jenkins & Winkler 1987, Torrence et al. 1992) et au succès des opérations de contrôle de la maladie (Rosatte et al. 1992a, Roscoe et al. 1998, Rosatte et al. 2009) sans tenir compte des contraintes spatiales associées aux changements dans la composition, la structure et la connectivité du paysage. Dans cette optique, cette thèse a permis de mieux comprendre comment les variations dans la densité de congénères et l'hétérogénéité du paysage structurent la répartition spatio-temporelle et les patrons de contacts des individus hôtes. À partir d'une méthode de ré-échantillonnage basée sur des simulations, j'ai illustré dans le chapitre 1 comment la théorie de l'isodar peut être appliquée avec des données de recensement de la faune sauvage pour identifier les stratégies de sélection densité-dépendante de l'habitat à large échelle spatiale sans avoir à prédéfinir des types de milieux. En étudiant, dans le chapitre 2, les processus de sélection de l'habitat à fine échelle spatiale compte-tenu à la fois de la densité de congénères et de la disponibilité des ressources dans le paysage, j'ai fourni un support empirique que les réponses fonctionnelles peuvent être dépendantes de la densité de congénères. Enfin, j'ai évalué dans le chapitre 3 le lien fonctionnel entre les taux de contacts, la densité de congénères et la connectivité fonctionnelle du paysage. Pour cela, j'ai simulé dans un IBM spatialement explicite des dynamiques d'utilisation de l'espace d'individus dans des paysages virtuels qui différaient dans la densité de congénères, la disponibilité des forêts et l'arrangement spatial de corridors agricoles. En utilisant les rats laveurs et les mouffettes rayées comme modèles d'étude, les approches de modélisation développées dans les trois chapitres peuvent aider à mieux orienter les interventions gouvernementales de contrôle et de prévention contre la rage, en identifiant les zones à risque dans la transmission et la propagation de ce virus.

1. Importance de la composition et de la structure du paysage dans la dynamique des maladies infectieuses

Bien que la littérature dans le domaine de l'écologie comportementale abonde d'exemples sur la manière dont l'hétérogénéité du paysage influence la répartition spatio-temporelle des espèces (par exemple, Kie et al. 2002, Revilla et al. 2004, Frair et al. 2005, Pickett & Siriwardena 2011), les effets de la composition et de la structure du paysage sont souvent omis dans l'étude des processus épidémiologiques. Cependant, l'étude de Langlois et al. (2001) est l'une des rares à considérer ces deux composantes du paysage dans un contexte de dynamique de maladies infectieuses. Notamment, les auteurs ont montré que la prévalence des hantavirus chez des populations de souris sylvestres (*Peromyscus maniculatus*) était plus élevée dans les sites qui étaient composés de faibles ou fortes proportions d'habitat de haute qualité pour cette espèce, et augmentait avec le degré de fragmentation des habitats préférés dans les sites du paysage. Néanmoins, les mécanismes comportementaux des individus hôtes en réaction à la composition et la structure du paysage sont généralement méconnus (Ostfeld et al. 2005). Le principal défi en épidémiologie est donc de trouver comment le risque de transmission et de propagation d'agents pathogènes peut être prédit à partir des caractéristiques du paysage. Dans les chapitres 1 et 2, j'ai donc développé deux nouvelles méthodes de travail qui permettent d'anticiper la répartition spatio-temporelle des animaux compte-tenu des variations dans la densité de congénères, ainsi que dans la composition et la structure du paysage.

1.1. Nouvelles approches de modélisation pour évaluer la sélection densité-dépendante de l'habitat des animaux à larges et fines échelles spatiales

Dans le chapitre 1, j'ai développé une méthode de ré-échantillonnage basée sur des simulations qui permet d'appliquer la théorie de l'isodar dans des paysages hétérogènes sans avoir à définir *a priori* des types de milieux. À partir de données de recensement de la faune sauvage, cette méthode contraste des densités animales entre des paires de sous-blocs adjacents qui sont construits selon différentes dispositions et qui sont placés aléatoirement à travers des zones d'étude recensées. Grâce à cette méthode, il est possible d'étudier la sélection densité-dépendante de l'habitat sur de larges étendues géographiques et pour une grande variété

d'espèces, en particulier les méso- et grands mammifères à haute mobilité. Dans la méthode, la répartition et la construction des blocs sont réalisées à l'aide d'un programme informatique dans lequel chaque paramètre spécifique aux blocs, comme leur taille et la distance entre les blocs, est défini directement par l'utilisateur. Le nombre de blocs indépendants qui doivent être répartis dans la zone d'étude est déterminé en examinant la relation entre le nombre maximum de blocs qui peuvent être placés aléatoirement dans la zone d'étude et le nombre minimum d'unités d'échantillonnage qui sont alors contenues dans chaque paire de sous-blocs. Tandis que le nombre de blocs doit être suffisamment élevé pour fournir une taille d'échantillon raisonnable pour les modèles statistiques, le nombre d'unités d'échantillonnage doit aussi être assez large pour estimer de manière adéquate l'abondance animale relative dans les paires de sous-blocs.

Généralement, les études utilisant la théorie de l'isodar évaluent des densités animales dans des unités d'échantillonnage qui sont répliquées dans l'espace et qui sont disposées de manière systématique le long de transects (Morris 1992, Knight & Morris 1996). Les méthodes d'échantillonnage systématique sont souvent employées sur le terrain parce qu'elles sont faciles à utiliser et parce qu'elles fournissent un échantillonnage uniforme à travers la zone d'étude (Krebs 1999). Cependant, ces méthodes ont leur faiblesse. Lorsque les patrons d'abondance montrent une hétérogénéité spatiale (par exemple, une agrégation d'individus) ou une périodicité temporelle, ou si les organismes sont rares, les méthodes d'échantillonnage systématique peuvent donner des estimés de paramètres biaisés en raison de la surestimation de leur variance (Cochran 1977, Morrison et al. 2008). Selon la théorie des probabilités, les méthodes d'échantillonnage aléatoire sont parmi les méthodes les moins biaisées puisque chaque unité d'échantillonnage a une chance égale d'être sélectionnée (Krebs 1999). La méthode de ré-échantillonnage que je propose dans le chapitre 1 est une alternative pour éviter les problèmes statistiques liés aux méthodes d'échantillonnage systématique. Par exemple, en simulant différentes méthodes d'échantillonnage dans une population de grands kangourous rouges (*Megaleia rufa*), Caughley (1977) a montré que les erreurs standards calculées à partir de la méthode d'échantillonnage systématique étaient sous-estimées, fournissant, par conséquent, des intervalles de confiance invalides et des estimés de paramètres moins précis que la méthode d'échantillonnage aléatoire. Grâce aux avantages qu'elle apporte, ma méthode de ré-échantillonnage peut donc être particulièrement utile dans beaucoup de domaines de

l'écologie et en épidémiologie. Tandis que cette première approche de modélisation examine les processus de densité-dépendance dans des zones du paysage composées de plusieurs types de milieux, la deuxième méthode de travail étudie la sélection densité-dépendante pour un type de milieu donné dans des zones du paysage.

Dans le chapitre 2, je propose un cadre analytique qui utilise des fonctions de sélection de ressources [*Resource selection function* (RSF); Manly et al. 2002] pour évaluer les effets simultanés de la densité de congénères et de la disponibilité des ressources sur la sélection de l'habitat. Les RSFs ont été développées en comparant les caractéristiques de l'habitat de localisations observées (codées 1) avec les caractéristiques de l'habitat d'un nombre égal de points (codés 0) qui ont été distribués aléatoirement dans le polygone convexe minimum contenant 100% des localisations [*Minimum convex polygon* (MCP) 100%] de chaque individu porteur d'un collier GPS. Dans un premier temps, les localisations observées et les points aléatoires ont été assignés à un type de milieu, et l'intégration de ces types de milieux dans des régressions logistiques à effets mixtes a permis de caractériser la sélection d'un milieu par les rats laveurs et les mouffettes rayées. Puis, en incluant dans les modèles des interactions doubles entre un type de milieu donné et l'abondance relative de congénères dans le MCP 100%, ou entre un type de milieu et sa disponibilité dans le MCP 100%, j'ai testé, respectivement, la densité-dépendance ou l'existence d'une réponse fonctionnelle dans la sélection de l'habitat. Les réponses fonctionnelles dépendantes de la densité de congénères ont été modélisées à l'aide d'une interaction triple entre un type de milieu, sa disponibilité dans le MCP 100% et l'abondance relative de congénères dans le MCP 100%. Dans ce chapitre 2, j'ai montré que l'omission des réponses fonctionnelles densité-dépendantes dans la sélection de l'habitat pouvait mener à de faibles prédictions sur la répartition spatio-temporelle des animaux. Notamment, j'ai trouvé qu'un modèle qui n'incluait pas l'effet combiné des réponses fonctionnelles et de la densité-dépendance dans la sélection de l'habitat recevait peu de support empirique. Les deux nouvelles approches de modélisation présentées ici ont permis d'acquérir des connaissances sur l'écologie comportementale des rats laveurs et des mouffettes rayées ce qui devrait améliorer l'identification des zones préférentielles chez ces deux espèces.

1.2. Sélection densité-dépendante de l'habitat par les rats laveurs et les mouffettes rayées dans des paysages agroforestiers

Dans le chapitre 1, les modèles isodars ont révélé qu'à faibles abondances de congénères dans le paysage, les rats laveurs et les mouffettes rayées sélectionnaient, respectivement, les zones avec une forte proportion de forêts et les zones composées de nombreuses structures anthropiques, et que cette sélection pour ces zones augmentait avec l'augmentation des différences dans la composition et la structure du paysage entre les paires de sous-blocs adjacents. À plus fine échelle spatiale, le modèle de réponses fonctionnelles densité-dépendantes durant la nuit (Chapitre 2) a montré que lorsque peu de congénères étaient présents dans le paysage, les rats laveurs montraient une plus forte sélection pour les champs de maïs dans les zones avec une faible densité de bordures entre les champs de maïs et les forêts, et une faible proportion de champs de maïs. Dans les paysages contenant peu de congénères, les rats laveurs et les mouffettes rayées devraient donc obtenir une aptitude phénotypique maximale dans les zones avec une forte proportion de forêts et de structures anthropiques (Chapitre 1). La répartition spatio-temporelle des rats laveurs est étroitement liée aux milieux forestiers, particulièrement ceux qui contiennent des structures aquatiques (Chamberlain et al. 2002, Byrne & Chamberlain 2011). Par exemple, Chamberlain et al. (2003) ont trouvé que les rats laveurs sélectionnaient préférentiellement les forêts matures de feuillus et de pins des plaines inondables, probablement parce que ces types de peuplements forestiers fournissent des sites de refuge et de nourriture de haute qualité associés à la présence de structures aquatiques. Les arbres creux et à cavités sont particulièrement importants pour l'élevage des jeunes rats laveurs pendant l'été (Henner et al. 2004), ce qui suggère que les forêts sont des habitats critiques pour la survie et la reproduction de cette espèce. De plus, les forêts abritent des petits mammifères, des oiseaux et des insectes qui sont des sources de nourriture occasionnelles pour les rats laveurs mais aussi pour les mouffettes rayées (Gehrt 2003). Au printemps et à l'été, les mouffettes rayées utilisent les tas de pierre et les terriers souterrains trouvés dans les forêts et dans les zones humides pour la mise bas et l'élevage des jeunes, tandis qu'à l'automne et l'hiver, ce sont les cavités souterraines sous les bâtiments qui sont davantage utilisées par cette espèce (Hwang et al. 2007). Ces cavités servent souvent de sites de repos et de protection contre les prédateurs, mais également contribuent à la thermorégulation (Larivière & Messier 1998, Larivière et al. 1999). Les zones anthropiques

fournissent aux mouffettes rayées mais aussi aux ratons laveurs des sources de nourriture abondantes et facilement accessibles comme de la nourriture humaine ou des déchets (Rosatte & Larivière 2003).

Inversement, dans les paysages avec une forte abondance de congénères, le modèle isodar du chapitre 1 a révélé que les ratons laveurs préféraient les zones avec plutôt de hautes densités de bordures entre les champs de maïs et les forêts, et une forte proportion de champs de maïs, particulièrement lorsque les différences dans la composition et la structure du paysage entre les paires de sous-blocs adjacents étaient élevées. Il est donc attendu une plus faible réduction de l'aptitude phénotypique potentielle chez cette espèce dans ces zones lorsque l'abondance de congénères augmente dans le paysage (Chapitre 1). À partir du modèle de réponses fonctionnelles densité-dépendantes durant la nuit (Chapitre 2), j'ai trouvé qu'à fortes abondances de congénères dans le paysage, la sélection des champs de maïs par les ratons laveurs était la plus élevée dans les zones qui contenaient une forte densité de bordures entre les champs de maïs et les forêts, et une faible proportion de champs de maïs. En accord avec Retamosa et al. (2008), cette observation suggère que les ratons laveurs ont tendance à s'agréger dans les champs de maïs de petite taille qui sont largement entrecoupés par des parcelles de forêt. La structure spatiale des champs de maïs semble avoir un effet important sur la répartition spatio-temporelle de cette espèce à large et fine échelles spatiales. Les ratons laveurs devraient préférer se nourrir à la bordure des champs de maïs et des forêts pour, sans doute, bénéficier d'un compromis entre les forêts qui fournissent des abris de protection, et les champs de maïs qui offrent une source de nourriture abondante et hautement nutritionnelle (Pedlar et al. 1997, Houle et al. 2011). Plusieurs études ont trouvé que l'abondance de ratons laveurs était positivement associée à une haute densité de bordures entre les champs de maïs et les forêts dans les terrains de piégeage (Pedlar et al. 1997, Heske et al. 1999, Beasley & Rhodes 2008, Houle et al. 2011). Notamment, 85% des dommages causés par les ratons laveurs sur les champs de maïs sont produits à l'intérieur des 20 premiers mètres des bordures des forêts (Beasley et al. 2007b, Beasley & Rhodes 2008). Mes résultats suggèrent que la répartition spatio-temporelle des ratons laveurs dans les paysages composés de fortes densités de bordures entre les champs de maïs et les forêts dépend aussi de la disponibilité des champs de maïs et de la densité de congénères.

Contrairement au raton laveur, la moufette rayée est plutôt une espèce solitaire qui vit à des densités relativement faibles (Rosatte et al. 1992b, Gehrt 2004). Par exemple, Rosatte et al. (1992b) ont rapporté des densités moyennes entre 7 et 12 ratons laveurs/km², et entre 2 et 7 moufettes rayées/km² dans des zones urbaines de Toronto (Canada) entre 1987 et 1990. Peu d'études ont identifié des habitats particuliers sujets à une forte densité de moufettes rayées (Broadfoot et al. 2001, Houle et al. 2011). Néanmoins, les résultats des chapitres 1 et 2 ont révélé que les moufettes rayées seraient plus susceptibles de rencontrer des congénères dans les zones avec de hautes densités de bordures entre les champs de maïs et les forêts, et une forte proportion de champs de maïs (Chapitre 1) car ces zones devraient contenir une grande quantité de corridors agricoles qui sont particulièrement prisés par cette espèce durant la nuit (Chapitre 2). Contrairement aux champs de maïs que les moufettes rayées ont d'ailleurs tendance à éviter (Chapitre 2), les corridors agricoles qui contiennent souvent des pierres laissées par les fermiers, abritent de nombreux insectes terrestres qui constituent leur principale source de nourriture (Rosatte & Larivière 2003). Les résultats des chapitres 1 et 2 suggèrent que la sélection densité-dépendante de l'habitat par les ratons laveurs et les moufettes rayées serait à la fois perceptible à fine et large échelles spatiales, confirmant que les stratégies de maximisation de l'aptitude phénotypique peuvent être apparentes à multiples échelles spatiales (van Beest et al. 2014).

2. Importance de la connectivité du paysage dans la dynamique des maladies infectieuses

Les effets de la fragmentation de l'habitat sur la dynamique des maladies infectieuses ont souvent été explorés de manière théorique en utilisant les modèles de métapopulation (Hess 1996, Gog et al. 2002, McCallum & Dobson 2002). Notamment, il a été montré que la fragmentation des parcelles d'habitat qui limite le déplacement des animaux à travers le paysage, favorisait la transmission de pathogènes dans les parcelles en augmentant la densité des individus occupant une parcelle, mais aussi empêchait la propagation de pathogènes parmi les parcelles (Hess 1996, McCallum & Dobson 2002). Cependant, ces études comportent deux principales limites. La première est que les modèles de métapopulation qui ont été utilisés supposent que la matrice de parcelles d'habitat de moins bonne qualité est homogène et que les taux d'immigration entre les parcelles dépendent uniquement de la distance entre les

parcelles. La deuxième est que ces études considèrent dans leurs modèles de métapopulation des équations différentielles déterministes de type « Sains-Infectés-Rétablis » [*Susceptible-Infected-Recovered* (SIR)] qui reposent sur l'hypothèse selon laquelle tous les individus d'une population ont une structure de contacts homogène, c'est-à-dire que chaque individu a la même probabilité de contact avec un autre individu [hypothèse dite de « *homogeneous-mixing* » (Anderson & May 1979, 1991)]. Une étude récente a néanmoins exploré le rôle du comportement de déplacement sur la manière dont la fragmentation de l'habitat influence la transmission et la propagation de maladies infectieuses (Tracey et al. 2014). Cependant, les auteurs de cette étude se sont basés sur des paysages simulés dans lesquels chaque cellule était simplement classifiée en habitat de haute ou faible qualité. Dans le chapitre 3, j'ai évalué comment les changements dans la densité de congénères, la composition du paysage et la connectivité fonctionnelle altèrent les taux de contacts entre des individus hôtes. Pour faire ceci, j'ai construit un IBM spatialement explicite dans lequel j'ai intégré des composantes d'utilisation de l'espace qui étaient basées sur des données empiriques de rats laveurs munis de colliers GPS, et j'ai simulé les déplacements intra- et inter-parcelles de rats laveurs dans 15 paysages virtuels qui différaient dans la densité de congénères, la disponibilité des forêts et l'arrangement spatial de corridors agricoles.

2.1. Règles empiriques de déplacement chez les rats laveurs

Les modèles empiriques utilisés dans l'IBM du chapitre 3 ont révélé que le choix de la prochaine parcelle d'habitat à visiter dépendait du type de milieu de la parcelle, de sa taille et de son accessibilité dans le paysage. En particulier, les rats laveurs munis de colliers GPS choisissaient des parcelles de forêt comme prochaine destination lorsqu'ils n'étaient pas déjà présents dans une forêt. Par contre, lorsqu'ils quittaient une forêt, les rats laveurs sélectionnaient plutôt les champs de maïs. Ces résultats témoignent de l'importance des milieux forestiers et des champs de maïs dans la répartition spatio-temporelle des rats laveurs dans un paysage agroforestier durant la période de maturation du maïs. Les modèles empiriques ont aussi montré que lorsqu'ils quittaient une parcelle d'habitat, les rats laveurs tendaient à transiter vers des parcelles de grande taille et à utiliser des trajets peu coûteux en déplacement pour se rendre vers une parcelle. Ces résultats sont en accord avec de précédentes études qui ont montré que les rats laveurs pouvaient maintenir de faibles coûts de

déplacement (Porter et al. 2015) et se déplacer sur de courtes distances (Prange et al. 2003, O'Donnell & DeNicola 2006) à condition que les ressources soient toujours disponibles, ce qui suggère que cette espèce peut occuper des domaines vitaux relativement petits (Prange et al. 2004, Beasley et al. 2007b). J'ai aussi trouvé que les temps de résidence des rats laveurs dans une parcelle d'habitat étaient quatre fois plus élevés durant le jour que la nuit. En particulier, quand ils sont peu actifs pendant la période du jour, les rats laveurs tendent à dépenser plus de temps dans les milieux anthropiques comparés aux autres types de milieux. Cette espèce répond positivement aux changements anthropiques des paysages étant donné que de fortes abondances de rats laveurs ont été observées dans les milieux urbains (Riley et al. 1998, Prange et al. 2003, 2004). Par exemple, Riley et al. (1998) ont rapporté des densités entre 67 et 333 rats laveurs/km² dans le parc national de Rock Creek à Washington aux États-Unis. Les populations de rats laveurs augmentent dans ces types de milieux car ces derniers fournissent à la fois des sites de refuge durant le jour (par exemple, des cavités souterraines et des terriers) et des sources de nourriture abondantes qui sont facilement accessibles (Hadidian et al. 1991, Bozek et al. 2007).

2.2. Effet de la connectivité fonctionnelle du paysage sur les taux de contacts entre des individus hôtes

Les règles empiriques de déplacement qui ont été appliquées à des rats laveurs simulés ont révélé trois patrons généraux dans les taux de contacts. Premièrement, j'ai trouvé qu'une petite portion de rats laveurs simulés était responsable d'un grand nombre de contacts uniques dans les paysages virtuels. Notamment, 15% des rats laveurs simulés qui avaient un grand nombre de contacts uniques dans les paysages virtuels avec une densité de 10 rats laveurs/km² étaient responsables de 90% des contacts uniques. À hautes densités de congénères dans les paysages agroforestiers, la dynamique de contacts entre des rats laveurs devrait donc s'approcher de la règle du 20/80 de Woolhouse et al. (1997), selon laquelle environ 20% des hôtes infectés (c'est-à-dire, ceux générant un grand nombre de cas secondaires) sont responsables d'au moins 80% du potentiel de transmission dans des systèmes hôtes-pathogènes. D'autres études ont également observé ce patron dans des zoonoses à transmission vectorielle (Perkins et al. 2003, Kilpatrick et al. 2006) ou par contacts directs (Clay et al. 2009). Par exemple, Perkins et al. (2003) ont montré que 20% des souris à cou

jaune (*Apodemus flavicollis*) qui sont des hôtes réservoirs du virus de l'encéphalite à tiques, supportaient 83% des agrégations de co-repas chez les tiques (« *co-feeding* » c'est-à-dire le processus par lequel le virus est transmis aux tiques saines lorsqu'elles se nourrissent à proximité de tiques infectées) et 72% de toutes les larves. Les causes d'une telle hétérogénéité dans la transmission de pathogènes sont souvent associées aux variations dans la susceptibilité (c'est-à-dire, la prédisposition à devenir infecté) et dans les réponses immunitaires chez les individus hôtes (Wilson et al. 2001, Beldomenico & Begon 2010). Dans mon chapitre 3, la forte hétérogénéité dans les taux de contacts émergeait à partir de rats laveurs simulés qui étaient placés aléatoirement dans des paysages virtuels et qui obéissaient aux mêmes règles empiriques de déplacement. En particulier, certains rats laveurs simulés avaient des domaines vitaux qui chevauchaient ceux d'autres congénères, ce qui augmentait, par conséquent, les taux de contacts entre ces individus. Le plus haut pourcentage de rats laveurs simulés responsables d'au moins 90% des contacts uniques était observé dans les paysages qui étaient fortement connectés par les corridors agricoles et qui contenaient une faible proportion de forêts. Dans un contexte de dynamique de la rage, ces individus qui ont un nombre de contacts uniques plus élevé que la moyenne (ou « *superspreaders* ») pourraient causer des événements de propagation à larges échelles spatiales. Cette variabilité dans les patrons de contacts suggère que la vaccination des milieux susceptibles de contenir des « *superspreaders* » pourrait réduire la contamination par le virus de la rage à travers le paysage, et serait une stratégie plus efficace que d'épandre de manière aléatoire des appâts vaccinaux à travers le paysage.

Deuxièmement, mon IBM du chapitre 3 a montré que la dynamique de contacts des rats laveurs simulés dépendait généralement de la densité de congénères (densité-dépendante) plutôt que de la proportion de congénères (fréquence-dépendante), ce qui suggère que la réduction de la densité de population est une mesure justifiée pour limiter la propagation du virus de la rage (Anderson et al. 1981, Barlow 1996). Parfois, les techniques de réduction de la densité de population combinées aux méthodes de vaccination peuvent être recommandées pour éradiquer la rage (Rosatte et al. 2001, Smith & Wilkinson 2003) ou une autre zoonose (Tessaro 1986, Carter et al. 2009). Par exemple, Ramsey & Efford (2010) ont construit un IBM spatialement explicite pour explorer l'efficacité de différentes stratégies de contrôle à contenir un foyer de tuberculose bovine chez les opossums à queue en brosse de Nouvelle-Zélande. Ces

stratégies de contrôle incluait la vaccination orale par le bacille de Calmette et Guérin (BCG), la réduction de population par poison, une combinaison BCG/poison, une combinaison entre BCG et un vaccin de contrôle de la fertilité, et une combinaison BCG/poison/fertilité (Ramsey & Efford 2010). Les auteurs de cette étude ont trouvé que la stratégie de contrôle la plus efficace combinait BCG/poison/fertilité à condition qu'elle soit appliquée tous les trois ans. Comparée aux autres méthodes de contrôle, cette stratégie requiert seulement une zone tampon de 2 à 3 km autour du foyer infectieux.

Troisièmement, mon IBM a révélé que la connectivité fonctionnelle du paysage avait différents effets sur les taux de contacts qui dépendaient fortement du type de milieu et de la composition du paysage. Tout d'abord, la densité de taux de contacts cumulés *per capita* augmentait dans les parcelles de forêt lorsque ces dernières étaient de plus en plus connectées par les corridors agricoles, et cette augmentation était plus élevée dans les paysages qui contenaient une faible proportion de forêts. En particulier, les corridors agricoles dans les paysages avec peu de forêts facilitaient le déplacement des rats laveurs simulés vers les parcelles de forêt isolées, ce qui augmentait les densités d'individus et donc les taux de contacts dans ces parcelles. Notamment, les coûts de déplacement dans les corridors agricoles étaient parmi les plus faibles comparés aux autres types de milieux de la matrice. Par contre, au fur et à mesure que la quantité de parcelles de forêt augmentait dans les paysages avec une forte connectivité grâce aux corridors agricoles, les rats laveurs simulés se dispersaient entre un plus grand nombre de parcelles de forêt, ce qui tendait à diminuer les taux de contacts. Les corridors agricoles contribuent donc fortement à la connectivité fonctionnelle du paysage. Notamment, Haddad & Baum (1999) ont révélé que, dans une matrice de forêts de pins, trois espèces de papillons (*Junonia coenia*, *Euptoieta claudia* et *Phoebis sennae*) atteignaient de plus hautes densités dans des parcelles d'habitat ouvert connectées par des corridors d'habitat ouvert que dans des parcelles non connectées, et que les corridors influençaient sur ces hautes densités selon trois mécanismes potentiels: 1) les papillons se déplaçaient plus fréquemment entre les parcelles connectées, et les taux de déplacement relativement élevés aidaient à maintenir de fortes densités d'individus dans les parcelles, 2) les corridors augmentaient l'effet des bordures sur la densité de papillons et 3) les corridors interceptaient les papillons dans la matrice du paysage et les dirigeaient vers les parcelles connectées, ce qui augmentait les densités d'individus dans les parcelles.

Ensuite, j'ai trouvé que, contrairement aux contacts cumulés, la relation entre la densité de taux de contacts uniques *per capita* dans les forêts et la connectivité des forêts par les corridors agricoles était quadratique de type « convexe », avec des taux de contacts se produisant à plus hautes densités dans les paysages qui étaient faiblement ou fortement connectés par les corridors agricoles et qui étaient composés d'une faible proportion de forêts. Un patron similaire était observé pour les taux de contacts cumulés et uniques dans les zones anthropiques. Notamment, la réduction de la connectivité fonctionnelle du paysage peut sévèrement limiter la distance de déplacement des individus entre les parcelles d'habitat ce qui peut, en retour, diminuer la taille des domaines vitaux et augmenter leur chevauchement spatial (Wauters et al. 1994, Atwood & Weeks 2003, Hinam & St. Clair 2008). Par exemple, Pope et al. (2004) ont montré que des opossums australiens, les grands planeurs (*Petauroides volans*), avaient de plus petits domaines vitaux qui se chevauchaient lorsque les parcelles de forêt d'eucalyptus du Sud-Est de l'Australie étaient fragmentées, menant ainsi à de fortes densités d'individus dans ce type de parcelle. Comme les coûts de déplacement étaient plus élevés dans les paysages contenant peu de corridors agricoles que dans ceux contenant un grand nombre de corridors, les ratons laveurs simulés tendaient à retourner aux parcelles d'habitat précédemment visitées, ce qui augmentait les taux de contacts dans ces parcelles. De plus, les ratons laveurs simulés utilisaient les zones anthropiques pour se déplacer vers leur parcelle de destination étant donné que les déplacements étaient peu coûteux dans ce type de milieu, en particulier durant le jour. L'utilisation fréquente des zones anthropiques dans les paysages qui étaient composés d'une faible quantité de corridors agricoles et de forêts augmentait les taux de contacts dans ce type de milieu. Dans ces paysages, les taux de contacts se produisaient d'ailleurs à plus hautes densités dans les zones anthropiques que dans les forêts ou les champs de maïs.

Enfin, les densités de taux de contacts cumulés et uniques *per capita* dans les champs de maïs diminuaient avec la connectivité des champs de maïs par les corridors agricoles. Les taux de contacts dans les champs de maïs étaient plus susceptibles de se produire à hautes densités dans les paysages qui étaient faiblement connectés par les corridors agricoles et qui englobaient une forte proportion de forêts. Notamment, la diminution des corridors agricoles dans les paysages virtuels augmentait la taille des champs de maïs, ce qui induisait des temps de résidence plus longs et donc des taux de contacts plus élevés dans ce type de milieu, en

comparaison avec des paysages contenant beaucoup de corridors agricoles. En particulier, les rats laveurs porteurs de colliers GPS dépensaient plus de temps dans les grands champs de maïs. De plus, l'augmentation de la proportion de forêts dans les paysages virtuels augmentait les transitions entre les forêts et les champs de maïs, ce qui favorisait les taux de contacts entre les rats laveurs simulés dans les champs de maïs.

3. Implications pour les programmes de contrôle et de prévention des maladies infectieuses

Ma thèse vise à mieux anticiper la répartition spatio-temporelle des populations hôtes compte-tenu des variations dans la densité de congénères et de l'hétérogénéité du paysage afin d'élaborer des stratégies de contrôle et de prévention efficaces visant à réduire la propagation d'agents pathogènes. D'après Haydon et al. (2002), il existe trois tactiques différentes pour contrôler la transmission et la propagation d'agents infectieux: 1) le contrôle de l'infection chez les populations cibles [par exemple, la vaccination humaine contre la rage (Ertl 2009)], 2) le blocage de la transmission des agents pathogènes entre les populations sources et les populations cibles [par exemple, la mise en place de barrières de sécurité pour empêcher l'utilisation des zones de stockage du foin par le wapiti (*Cervus elaphus*) et le cerf sauvage de Virginie (*Odocoileus virginianus*), deux des principaux hôtes réservoirs de la tuberculose bovine au Canada (Nishi et al. 2006)] et 3) le contrôle de l'infection chez les populations sources [par exemple, l'éradication, la vaccination et le contrôle de la fertilité des espèces animales réservoirs (Smith & Cheeseman 2002, Smith & Wilkinson 2003)]. Bien que la première tactique ne requière aucune connaissance sur l'écologie des espèces réservoirs, elle ne permet pas l'éradication des maladies infectieuses à la différence des deux autres tactiques de contrôle. Le succès de ces deux tactiques nécessite l'identification des espèces réservoirs dans les populations sources et, en particulier, des efforts devraient être dirigés dans la compréhension des stratégies comportementales de ces espèces en réaction à leur environnement (Haydon et al. 2002). Ma thèse s'organise autour de cette assertion.

Le manque de connaissances précises sur la répartition spatio-temporelle des populations de rats laveurs et de mouffettes rayées dans des paysages agroforestiers font en sorte que, dans ce type de paysage, les épandages d'appâts vaccinaux qui sont utilisés pour

limiter la propagation du virus de la rage, couvrent souvent de larges zones qui sont peu ou pas fréquentées par les deux espèces (Slate et al. 2005, Boyer et al. 2011). Pour minimiser les coûts financiers et maximiser la prise des appâts vaccinaux par les rats laveurs et les mouffettes rayées, les programmes de vaccination devraient s'appuyer sur l'identification des zones avec une forte concentration d'individus où le risque de contact est élevé (Houle et al. 2011, Rees et al. 2011a). Dans cette perspective, les approches de modélisation qui ont été développées dans les trois chapitres de ma thèse fournissent un cadre analytique utile pour mieux délimiter les zones à risque dans la transmission et la propagation d'agents pathogènes.

Notamment, l'IBM de mon chapitre 3 a montré que les densités de taux de contacts entre des rats laveurs simulés pouvaient fortement différer entre les types de milieux, dépendamment de leur disponibilité et de leur accessibilité dans le paysage, ainsi que de la densité de congénères. Tandis que les patrons de contacts observés à faibles densités de congénères suggèrent que les appâts vaccinaux devraient être répartis de manière uniforme dans les paysages, les patrons de contacts observés à fortes densités révèlent que l'efficacité des stratégies de contrôle dépend grandement de la physionomie du paysage (Chapitre 3). L'étude de Rees et al. (2013) supporte aussi cette dernière affirmation. Notamment, les auteurs ont démontré, à partir d'un IBM spatialement explicite, que l'hétérogénéité spatiale basée sur la taille et la qualité des parcelles d'habitat, ainsi que le niveau d'immunité d'une barrière de vaccination influençaient l'efficacité à contrôler une épizootie de rage dans le paysage. Plus précisément, ils ont trouvé que la probabilité qu'un raton laveur enragé traverse la barrière de vaccination était plus élevée dans des paysages où les parcelles d'habitat étaient de moins bonne qualité et de grande taille, et dans des paysages avec des parcelles homogènes de bonne qualité. Dans leur étude, une épizootie de rage était mieux contrôlée lorsque la barrière de vaccination avait le plus haut niveau d'immunité (> 60%) dans des paysages avec des parcelles d'habitat de bonne qualité et de grande taille. Néanmoins, la plupart des études de dynamique de maladies infectieuses ne tiennent pas compte des paramètres comportementaux de déplacement à fines échelles spatiales compte tenu des caractéristiques du paysage, ce qui peut mener à de faibles prédictions sur les processus de transmission et de propagation de pathogènes dans des paysages hétérogènes [mais voir Tracey et al. (2014)]. En simulant les déplacements intra- et inter-parcelles de rats laveurs dans différents paysages virtuels, mon IBM du chapitre 3 démontre comment la composition du paysage et la connectivité

fonctionnelle peuvent affecter les taux de contacts dans un type de milieu donné. Cette information peut aider à identifier les milieux à risque dans la transmission et la propagation du virus de la rage du raton laveur dans le paysage.

Par exemple, l'IBM a révélé que les plus hautes densités de taux de contacts cumulés *per capita* se produisaient dans les forêts et les zones anthropiques durant le jour, en particulier lorsque les paysages contenaient peu de forêts ($\leq 7\%$) et une forte ou faible quantité de corridors agricoles, respectivement. Alternativement, j'ai trouvé que les densités de taux de contacts uniques *per capita* étaient les plus élevées dans les corridors agricoles, en particulier dans les paysages contenant beaucoup de forêts et peu de corridors agricoles. Globalement, les forêts et les zones anthropiques seraient des milieux à risque dans la transmission du virus de la rage du raton laveur, tandis que les corridors agricoles augmenteraient le risque de propagation de ce virus dans les paysages agroforestiers. Néanmoins, dans les paysages avec une faible proportion de forêts ($\leq 14\%$) et une forte quantité de corridors agricoles, les forêts pourraient être des milieux plus à risque que les corridors agricoles dans la propagation du virus de la rage du raton laveur. Dans cette perspective, les appâts vaccinaux devraient être distribués à hautes densités dans les zones anthropiques lorsque les paysages contiennent peu de corridors agricoles et une forte ou faible proportion de forêts. Dans les paysages contenant une forte quantité de corridors agricoles, les campagnes de vaccination devraient cibler les forêts et les zones anthropiques. Par contre, les appâts vaccinaux devraient plutôt être répartis de manière uniforme dans les paysages qui contiennent beaucoup de corridors agricoles et qui sont composés d'une forte proportion de forêts. Enfin, les campagnes de vaccination devraient aussi concentrer de fortes densités d'appâts vaccinaux dans les corridors agricoles, en particulier dans les paysages avec beaucoup de forêts et peu de corridors agricoles.

Tandis que le chapitre 3 permet de caractériser les paysages qui faciliteraient la transmission et la propagation de pathogènes, les approches de modélisation des chapitres 1 et 2 permettent de délimiter les zones à fortes concentrations d'individus hôtes dans des paysages fragmentés par l'agriculture et contenant une grande quantité de corridors agricoles. D'ailleurs, le chapitre 3 a révélé que ces paysages étaient fortement à risque dans la transmission et la propagation du virus de la rage du raton laveur. Dans le chapitre 2, j'ai montré que l'omission de la densité-dépendance dans les réponses fonctionnelles pouvait mener à de faibles

prédictions sur la répartition spatio-temporelle des animaux, ce qui peut conduire à des campagnes de vaccination qui ne cibleront pas les zones les plus à risque dans la transmission d'agents pathogènes. Par exemple, le modèle qui ne considérait pas les réponses fonctionnelles densité-dépendantes prédisait que la probabilité de rencontre entre des rats laveurs serait plus élevée dans les zones humides. Pourtant, les taux de contacts *per capita* chez cette espèce ont peu de chance de se produire à fortes densités dans ce type de milieu (Chapitre 3). À la place, les réponses fonctionnelles densité-dépendantes (Chapitre 2) suggèrent que les rats laveurs seraient plus susceptibles de s'agréger dans des zones avec une forte densité de bordures entre les champs de maïs et les forêts, et une faible proportion de champs de maïs. Alternativement, les modèles isodars du chapitre 1 prédisent que la transmission entre les rats laveurs et les mouffettes rayées serait plus élevée dans les zones avec une forte densité de bordures entre les champs de maïs et les forêts, et une forte proportion de champs de maïs, puisque ces zones supportaient à la fois une forte concentration de rats laveurs et de mouffettes rayées. De plus, j'ai trouvé dans le chapitre 2 que la probabilité de co-occurrence entre ces deux espèces était la plus élevée dans les corridors agricoles.

Compte tenu des résultats des trois chapitres, je suggère que, dans les paysages agroforestiers de la Montérégie et de l'Estrie, les campagnes de vaccination ciblent les zones avec une forte densité de bordures entre les champs de maïs et les forêts durant la période de maturation du maïs (Chapitres 1 et 2). Dans ces zones, les appâts vaccinaux devraient être répartis à fortes densités le long des bordures entre les champs de maïs et les forêts (Chapitres 1, 2 et 3), le long des bordures des zones anthropiques (Chapitre 3) et le long des corridors agricoles (Chapitres 2 et 3). Globalement, ma thèse démontre, d'une part, que la plasticité dans la sélection de l'habitat par les rats laveurs et les mouffettes rayées est liée aux variations dans à la fois la densité de congénères, la composition et la structure du paysage, et d'autre part, que les fortes hétérogénéités spatiales observées dans les taux de contacts dépendent à la fois de la densité de congénères, de la composition du paysage et de la connectivité fonctionnelle. Conséquemment, ces facteurs devraient être pris en considération lors de l'élaboration des programmes de contrôle et de prévention afin d'augmenter l'efficacité des opérations de vaccination contre la rage du raton laveur.

4. Perspectives de recherche

L'IBM spatialement explicite du chapitre 3 fournit une approche conceptuelle intéressante qui peut être améliorée afin de mieux représenter les systèmes hôtes-pathogènes réels. Dans de tels systèmes, la plupart des pathogènes peuvent infecter plusieurs espèces hôtes (Woolhouse et al. 2001, Dobson 2004, Morgan et al. 2004). Ces pathogènes généralistes sont une menace sérieuse pour la santé humaine et la faune sauvage car une forte prévalence chez les hôtes alternatifs peut augmenter la persistance des agents pathogènes dans l'environnement, et peut conduire à l'extinction des espèces animales (Fenton & Pedersen 2005, Pedersen et al. 2007, Smith et al. 2009a). La transmission de pathogènes entre plusieurs espèces dépend à la fois de la susceptibilité de l'hôte à une infection, des taux de contacts avec d'autres hôtes et de la compétence de l'hôte, c'est-à-dire de l'efficacité avec laquelle un hôte transmet l'infection (Cronin et al. 2010, Paull et al. 2011). Par exemple, si l'hôte principal est un réservoir qui est peu compétent, l'ajout d'autres espèces hôtes qui sont hautement compétentes dans le système peut augmenter la prévalence chez l'hôte principal car ces nouvelles espèces hôtes deviendront de meilleures espèces réservoirs [effet de « *spillover* » (Daszak et al. 2000, Power & Mitchell 2004)]. Alternativement, si l'hôte principal est un réservoir hautement compétent, l'ajout d'autres espèces hôtes qui sont moins compétentes peut diminuer la prévalence chez l'hôte principal car, dans ce cas, ces nouvelles espèces hôtes diminueront la probabilité de rencontre entre le pathogène et l'hôte principal [effet de dilution (Keesing et al. 2006)]. Étant donné que chaque espèce hôte peut afficher des stratégies comportementales distinctes en réaction à leur environnement, le contrôle des maladies infectieuses dans des systèmes multi-hôtes reste donc un des défis les plus importants pour les épidémiologistes. Des études futures devraient donc explorer l'effet des changements environnementaux sur les processus de transmission et de propagation de pathogènes infectieux dans des systèmes multi-hôtes. L'IBM développé dans le chapitre 3 pourrait être utilisé pour étudier les systèmes multi-hôtes.

Le virus de la rage est un exemple classique de pathogènes multi-hôtes dont les espèces réservoirs restent souvent difficiles à identifier (George et al. 2011). Par exemple, dans l'écosystème de Serengeti en Afrique, les chiens domestiques (*Canis familiaris*) sont les principaux hôtes réservoirs de la rage étant donné qu'ils maintiennent en permanence le virus et transmettent l'infection aux populations cibles telles que les animaux domestiques et les

humains (Lembo et al. 2008). Cependant, d'autres espèces sauvages carnivores telles que le chacal à flancs rayés (*Canis adustus*), le chacal à chabraque (*Canis mesomelas*), le ratel (*Mellivora capensis*) ou la hyène tachetée (*Crocuta crocuta*) peuvent aussi transmettre l'infection aux populations cibles bien que ces espèces ne maintiennent pas le virus dans l'écosystème (Lembo et al. 2008). Dans les écosystèmes agroforestiers des régions de la Montérégie et de l'Estrie, les ratons laveurs sont les hôtes réservoirs du virus de la rage du raton laveur et peuvent infecter des hôtes alternatifs tels que les moufettes rayées (Guerra et al. 2003). Dans ce contexte, il serait donc intéressant d'augmenter la complexité de mon IBM en intégrant les mécanismes de connectivité fonctionnelle chez les moufettes rayées. En particulier, le modèle empirique du « choix de la prochaine parcelle d'habitat » du chapitre 3 pourrait inclure la densité-dépendance et des réponses fonctionnelles étant donné que les chapitres 1 et 2 ont révélé que la plasticité dans la sélection de l'habitat chez les ratons laveurs et les moufettes rayées était liée aux changements dans la densité de congénères et la disponibilité des ressources. De plus, il y a un manque d'information sur la manière dont la répartition spatiale de compétiteurs hétérospécifiques influence le déplacement d'un individu. Néanmoins, les études de déplacement des animaux ont bénéficié de l'émergence de modèles de marches aléatoires corrélées et biaisées qui considèrent simultanément des biais internes de déplacement à travers la persistance directionnelle (tendance à se déplacer dans la même direction que le déplacement précédent) et des biais externes de déplacement qui dépendent de la distance vers un individu de l'autre espèce (tendance à se déplacer dans une direction particulière) (Fortin et al. 2005b, Barton et al. 2009). En retour, ces informations permettront d'identifier les secteurs où les taux de contacts interspécifiques sont élevés.

De plus, l'objectif d'une prochaine étude serait d'inclure un modèle épidémiologique de type « Susceptible-Exposé-Infecté-Immunié » [*Susceptible-Exposed-Infected-Recovered* (SEIR)] dans mon IBM afin de modéliser les processus de transmission et de propagation du virus de la rage. Dans ce contexte, l'acquisition de connaissances sur la structure démographique, la survie et le succès de reproduction des populations hôtes est indispensable pour mieux anticiper le risque de propagation de maladies infectieuses (Anderson & May 1991, Diekmann & Heesterbeek 2000). En effet, les paramètres démographiques qui sont à la base des modèles épidémiologiques permettent d'estimer la proportion de nouveaux individus sains qui s'ajoute à la population à chaque pas de temps (Anderson & May 1981). Bien qu'il

existe des études qui ont documenté la survie et la reproduction des rats laveurs et des mouffettes rayées (Fuller & Kuehn 1985, Greenwood et al. 1997, Riley et al. 1998, Mosillo et al. 1999), la majorité de ces études ont été réalisées aux États-Unis où les contraintes environnementales peuvent être différentes de celles au Canada [mais voir Rosatte et al. (2010) qui ont estimé la survie des rats laveurs en Ontario]. Dans cette perspective, il serait donc utile qu'une étude sur le suivi à long terme d'un grand nombre de rats laveurs et de mouffettes rayées marqués soit mise en place pour prédire le potentiel de propagation de la rage du raton laveur au Québec et ailleurs en Amérique du Nord. Des études de terrain devraient également être réalisées pour quantifier les taux de contacts intraspécifiques (entre rats laveurs ou mouffettes rayées) et interspécifiques (entre rats laveurs et mouffettes rayées) compte-tenu des caractéristiques du paysage. Ces études serviront à valider d'une part, les patrons de contacts observés dans le chapitre 3 et, d'autre part, les patrons de contacts qui émergeront d'un prochain IBM spatialement explicite de type SEIR. La plupart des études qui ont documenté les taux de contacts chez des rats laveurs et des mouffettes rayées (Totton et al. 2002, Weissinger et al. 2009, Prange et al. 2011, Robert et al. 2012b) n'ont pas considéré l'effet de l'hétérogénéité du paysage. Surtout, elles ne peuvent pas être utilisées pour valider l'IBM du chapitre 3 car ces études ont estimé un nombre de contacts « par paire d'individus » au lieu de « par individu ».

Au final, l'intégration d'un modèle épidémiologique dans l'IBM spatialement explicite permettra notamment: 1) de déterminer les conditions sous lesquelles la rage devient épidémique et de définir la proportion de la population à vacciner pour éradiquer cette maladie (Anderson et al. 1981, Heesterbeek & Dietz 1996) et 2) d'identifier les individus « *superspreaders* » c'est-à-dire ceux générant un plus grand nombre de cas secondaires dans une population, et de caractériser spatialement les zones à risque où ces individus ont plus de chance de transmettre l'infection (Lloyd-Smith et al. 2005, Paull et al. 2011). Ainsi, les gestionnaires de la faune responsables du contrôle de la rage seront mieux informés sur les zones d'intervention à circonscrire pour, d'une part, diminuer les frais associés à la prévention et au contrôle de la rage et, d'autre part, pour réduire le risque d'exposition à cette maladie mortelle chez les animaux domestiques et les humains.

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